Social and Ecological Aspects of Brain Size Evolution
-
A Comparative Approach

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to my parents,
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Zusammenfassung

Die Evolution der Gehirngröße und der Zusammenhang zur kognitiven Evolution ist seit langem ein heißes Thema in der vergleichenden Biologie. Letztlich ist es das Ziel, das außergewöhnlich große Gehirn und das unvergleichbare Level an Intelligenz in unserer eigenen Spezies zu erklären. Zahlreiche Theorien wurden vorgeschlagen, um die anhaltende Zunahme der relativen Gehirngröße und ihre Variation innerhalb der Wirbeltiere zu erklären. Die Theorien konzentrieren sich entweder auf soziale oder ökologische Faktoren und argumentieren mit einer erhöhten Fitness durch verbesserte kognitive Fähigkeiten oder energetische Einschränkungen, die maßgeblich die Evolution der Gehirngröße gestaltet. Um die zugrundeliegenden evolutionären Muster zu verstehen, ist es entscheidend diese verschiedenen Theorien und Perspektiven zu integrieren, da sie sich nicht gegenseitig ausschließen. Daher wurden mit dieser Doktorarbeit verschiedene Hypothesen der sozialen und ökologischen Wechselbeziehung zur Entwicklung von Gehirngröße getestet und diese zu einem umfangreichen Gefüge zusammengefasst. Die ersten beiden Teile dieser Arbeit untersuchten die Beziehungen zwischen relativer Gehirngröße (relativ zur Körpergrösse) und (i) Gelegenheiten für soziales Lernen, (ii) der Komplexität der Futternische und (iii) Saisonalität und stabilisierter Energieversorgung. Im letzten Teil habe ich die Beziehungen innerhalb eines konzeptionellen Gefüges, welches zwischen evolutionären Möglichkeiten und direkten kognitiven Konsequenzen von vergrößerten Gehirnen unterscheidet, getestet. Dies geschah unter der Berücksichtigung einer Vielzahl von sozialen und ökologischen Faktoren.

Der erste Teil zielte darauf ab zu untersuchen, wie Gelegenheiten für (soziales) Lernen die Evolution von sowohl Futternischenkomplexität als auch der Gehirngröße in verschiedenen Wirbeltierlinien formen. Bei den Vögeln benutzten wir die Anzahl der toleranten Vorbilder und die Zeit in Verbindung mit ihnen als Mass für Gelegenheiten für soziales Lernen. Wir konnten zeigen, dass dort, wo diese Gelegenheiten reichlicher sind, die Arten relativ größere Gehirne entwickelt haben. In Primaten und Karnivoren zeigten wir, dass eine langsame Entwicklung und eine spätere Ernährungsunabhängigkeit mit komplexeren Futternischen zusammenhängen und dass diese wiederum mit relativer Gehirngröße korrelieren (in Primaten die kumulative Summe von Futternischenelementen und in Karnivoren spezifische Elemente davon). Diese Erkenntnisse unterstützen die 'cultural intelligence' Hypothese, die die Koevolution zwischen den Gelegenheiten für sozialen Lernens, der Größe und Komplexität des Verhaltensrepertoires und der Evolution von Kognition nahelegt.

Der zweite Teil konzentrierte sich darauf, wie die Saisonalität und die damit verbundene jährliche Variation der Energieversorgung die Evolution der relativen Gehirngröße bei nicht-primaten Säugetieren beeinflussen. Wir haben die Nutzen- und Kostenperspektive kombiniert indem wir die folgenden beiden nicht-exklusiven Hypothesen testeten: Die 'cognitive buffer' und die 'expensive brain' Hypothese. Nach der Methodik bisheriger Forschungsarbeiten in Primaten unterscheideten wir zwischen der Saisonalität der Umwelt und der tatsächlich erlebten Saisonalität, gemessen durch die Variationen in der Nahrungszusammensetzung. Zuerst haben wir herausgefunden, dass die evolutionäre Zunahme

der Gehirngröße nicht notwendigerweise mit einem höheren Mass an Pufferung der umweltbedingten Saisonalität verbunden ist. Daher haben wir vorgeschlagen, dass die kognitive Pufferung möglicherweise nur in anthropoiden Primaten mit relativ grossen Gehirnen vorkommt. Zweitens zeigten wir, dass der Grad der Schwankungen in energiereicher Nahrung negativ mit relativer Gehirngröße korreliert. Dieses Resultat bestärkt die 'expensive brain' Hypothese, die besagt dass eine stabilisierte und ununterbrochene Energieversorgung entscheidend ist für eine evolutionäre Vergrösserung des Gehirns und für die Evolution der Kognition.

Der letzte Teil dieser Arbeit integrierte die beiden Arten von Hypothesen einschließlich sozialer und ökologischer Faktoren für Primaten. Wir haben zwischen evolutionären Möglichkeiten und kognitive Konsequenzen unterschieden. Als evolutionäre Möglichkeiten definierten wir potentielle Selektionsdrücke, die zu einer Zunahme der Gehirngröße führen können, falls die Kosten für ein vergrössertes Gehirn überwunden werden können. Unter kognitiven Konsequenzen verstehen wir die unmittelbar verbesserten sozialen und ökologischen Fähigkeiten als Folge eines grösseren Gehirns. Wir verwendeten multivariate Statistik und eine phylogenetische Pfadanalyse um die evolutionären Beziehungen innerhalb des vorgeschlagenen konzeptionellen Gefüges zu testen. Die Ergebnisse zeigten, dass ökologische mehr als soziale evolutionäre Möglichkeiten die Evolution von Gehirngröße antreiben. Das bedeutet, dass nur dort, wo ökologische Voraussetzungen eine erhöhte und stabilisierte Energieversorgung begünstigen, eine evolutionäre Zunahme der Gehirngröße möglich ist. Weiterhin zeigten die Analysen, dass die Gehirngröße stark mit den sozialen und ökologischen Konsequenzen korreliert ist und dass diese auch miteinander in hohem Maße korrelieren. Dies deudet darauf hin, dass allgemeine Verhaltensflexibilität stark mit relativer Gehirngröße zusammenhängt, unabhängig von den ursprünglichen Selektionsdrücken. Zusammenfassend schlugen wir vor, dass komplexe soziale Verhaltensweisen nur dort hervortreten können, wo die energetischen Kosten von großen Gehirnen durch ökologische Bedingungen unterstützt werden.

Zusammengefasst zeigt die vorliegende Doktorarbeit, dass nur dort, wo die Ökologie die energetischen Voraussetzungen von vergrösserten Gehirnen begünstigt, sich höhere Kognition entwickeln kann. Darüber hinaus deuten die Ergebnisse darauf hin, dass Gelegenheiten für soziales Lernen den koevolutionären Prozess zwischen ökologischen Voraussetzungen und Hirngröße weiter vorantreiben; dies ist vollkommen mit der Evolutionsgeschichte der Hominin-Linie stimmig. Dabei liefert diese Doktorarbeit wichtige Einblicke in die Entwicklung der Gehirngröße innerhalb der Wirbeltiere und hilft letztlich die Evolutionsgeschichte unserer eigenen Spezies weiter zu verstehen.

Summary

The evolution of brain size and its link to cognitive evolution is since long a hot topic in comparative biology. Ultimately, the aim is to explain the exceptionally large brain and the unmatched level of intelligence in our own lineage. Numerous theories have been suggested trying to explain the continuing expansion of relative brain size and its variation across vertebrate clades. The theories focus either on social or ecological factors, arguing in favor of increased fitness through enhanced cognitive abilities or of energetic constraints shaping the evolution of brain size. To understand the underlying evolutionary patterns, it is crucial to integrate the different theories and perspectives, since they are not mutually exclusive. Therefore, this thesis tested different hypotheses on social and ecological correlates of brain size evolution and also integrated them into a comprehensive framework. The first two parts of this thesis examined the relationship between relative brain size (relative to body mass) and (i) opportunities for social learning, (ii) the complexity of the foraging niche, and (iii) seasonality and stabilized energetic intake. In the last part, I tested the relationships within a conceptual framework differentiating between evolutionary opportunities and direct cognitive consequences of enlarged brains, including a broad variety of social and ecological factors.

The first part's aim was to investigate how opportunities for (social) learning shape the evolution of both foraging niche complexity and brain size in different vertebrate lineages. In birds, we used the number of tolerant role models and the time in association with them as a proxy for opportunities for social learning, and showed that where these opportunities are more abundant, species evolved relatively larger brain sizes. In primates and carnivorans we showed that a slow pace of development and later nutritional independence, respectively, are linked to more complex foraging niches, and that those in turn are linked to relative brain size (in primates the cumulative sum of foraging niche elements, and in carnivorans specific elements thereof). These findings support the cultural intelligence hypothesis, which suggests the coevolution between opportunities for social learning, the size and complexity of the skill repertoire and the evolution of cognition.

The second part focused on how seasonality and the concomitant annual variation in the energetic input has affected the evolution of relative brain size in non-primate mammals. We combined the benefit and cost perspectives by testing the two non-exclusive hypotheses: the cognitive buffer and the expensive brain hypothesis. Following the methodology of previous work in primates, we distinguished between seasonality in the environment and actually experienced seasonality in terms of fluctuations in the diet composition. First, we found that the evolutionary increase in brain size is not necessarily linked to higher degrees of buffering environmental seasonality. Therefore, we suggested that cognitive buffering might be unique to large-brained anthropoid primates. Second, our results showed that the extent to which highly nutritive foods fluctuate with time is negatively associated with relative brain size. This result confirms the expensive brain hypothesis, which argues that a stabilized energetic input is crucial for an increase in brain size and the evolution of cognition.

The final part of this thesis integrated the two classes of hypotheses and also included social and ecological factors in primates. We discriminated between evolutionary opportunities, factors which may facilitate an evolutionary increase in brain size in case the costs and constraints can be overcome, and cognitive consequences, which represent immediately enhanced social and ecological abilities due to increase in brain size. We used multivariate statistics and a phylogenetic path analysis to test for the evolutionary relationships within the proposed conceptual framework. The results showed that ecological more than social opportunities drive the evolution of enlarged brain. This implies that only where ecological preconditions favor an increased and stabilized energetic supply, an evolutionary increase in brain size is possible. Further, the analyses showed that brain size is strongly correlated with both the social and ecological consequences, as well as that they are highly interrelated. This suggests that in primates, regardless of the selective agents, general behavioral flexibility is a close associate of relative brain size. In conclusion, we suggested that only where the energetic expenses of enlarged brains are supported by ecological conditions, complex social processes can become prominent.

In sum, this thesis shows that only where ecology favors the energetic requirements of increased brain sizes, higher levels of cognition can evolve. In addition, the results suggest that opportunities for social learning further facilitate the coevolutionary process between ecological preconditions and brain size, which is fully consistent with the evolutionary history of the hominin lineage. Thereby, this thesis yields important insights in the evolution of brain size across vertebrates and ultimately helps to further understand the evolutionary history of our own species.

Chapter 1

General Introduction

The brain is a fascinating and multifaceted organ. Together with the spinal cord it forms the central nervous system and is responsible for the control and functioning of body physiology, communication, behavioural actions, and most importantly, it is linked to all cognitive processes.
Humans are known for their large brain size and high levels of cognition. Within the last five million years our brains more than tripled in size (from roughly 350cm^3, to about 1350cm^3 volume), and particularly during the last 1.5 millions of years major changes in volume and folding happened within the hominin lineage (reviewed in Geary 2005). On an evolutionary time scale, this is very fast.
Across major vertebrate lineages, there is large variation in (relative) brain size. Mammals and birds having larger brains for their given body mass compared to amphibians, reptiles and fish, also reflecting the evolutionary long-term trend of a general increase in relative brain size (Marsh's rule: Jerison 1973) (Fig. 1.1A). But also within lineages, especially within mammals, relative brain size varies considerably, with primates including humans showing the largest relative brain size across the whole animal kingdom. Those patterns also remain using the number of neurons as a proxy for brain capacity (Herculano-Houzel 2017). The variation in relative brain size across mammalian lineages is represented in Fig. 1.1B.

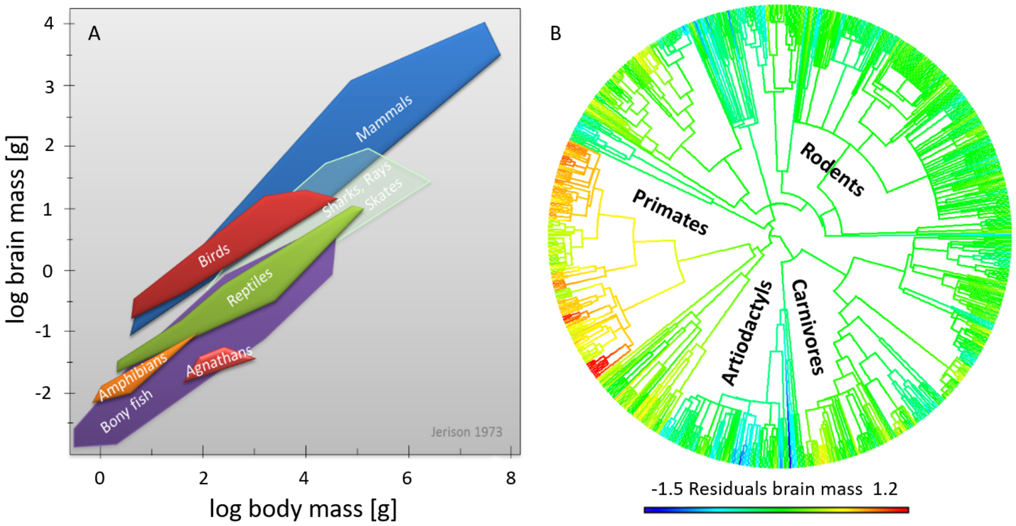

Figure 1.1: A) Brain size variation across the main vertebrate groups given by the relationship between log brain mass and log body mass (modified from Jerison 1973). B) Mammalian phylogenetic tree including four orders: primates, carnivorans, rodents and artiodactyls. The coloring of the branches represent residuals of brain size based on a log-log regression of brain mass and body mass.

The continuing expansion and the massive variation in brain size has elicited attention mainly because the evolution of brain size is closely linked to the evolution of cognition. Various interspecific studies show that brain size is associated with performance in a broad range of different cognitive paradigms, together comprising of what is defined as intelligence in humans (Gottfredson 1997). A comparative study across different vertebrate lineages including mainly primates and birds shows evidence for a close link between the evolution of self-control and brain size (MacLean et al. 2014). Across mammalian carnivorans, Benson-Amram et al. 2016 show that those species better at opening puzzle boxes, and thus better at solving novel problems, are larger-brained. In birds as well as mammals and even reptiles and amphibians, several studies suggest that species with larger brains are more innovative and more successful when introduced into novel environments (Timmermanns et al. 2000, Sol and Lefebvre 2000, Lefebvre et al. 2004, Sol et al. 2005, 2007, 2008; Overington et al. 2009; Amiel et al. 2011; Holekamp et al. 2015). And finally, several comprehensive studies including measurements from multiple domains show that brain size is a good predictor of global cognition in primates (Reader and Laland 2002, Deaner et al. 2007, Reader et al. 2011). Together, these lines of evidence imply that brain size is a good indicator for general cognitive performance (i.e. intelligence), including the abilities to behave flexibly and solve ecological and social problems.
Therefore, to date the main focus of evolutionary research on interspecific brain size evolution is to explain what factors led to certain species having larger brains and thus being more intelligent than others, and ultimately, what led to the unusual brain size and intelligence in our own lineage.

The aim of this thesis is to integrate different aspects of the evolution of brain size and explain brain size variation within and across vertebrate lineages in relation to social as well as ecological factors. This introduction first gives an overview of previously proposed hypotheses trying to explain brain size variation, and how they were tested. Then I introduce the conceptual approach integrating evolutionary drivers and consequences of enlarged brain size. Finally, I present considerations on the methodological approach and a more detailed synopsis of the following chapters.

Explaining Brain Size Variation - Benefits and Costs

Over the last decades, numerous theories have been suggested to explain the interspecific variation in brain size, with the ultimate aim to identify factors which led to the extremely large brains in our own lineage. The hypotheses essentially follow one of two different approaches: some focus on selective benefits in terms of enhanced cognition, which allows for solving complex social and ecological problems, whereas others focus on the energetic costs and constraints of enlarged brains.

Energetic Costs of Enlarged Brains

Brains are unique organs in that they require long periods of development (Janson and van Schaik 1993) and both a large and steady supply of energy, especially during the differentiation phase (Mink et al. 1981; Rolfe and Brown 1997, Bauernfeind et al. 2014). In humans, the brain takes up to 20% of the total resting metabolic rate (Holliday 1986). These high costs likely impose an energetic constraint on evolutionary increases in brain size. Several studies in the 1980s already began to focus on the energetic perspective of brain size evolution, suggesting that the basal energetic throughput determines the maximum potential brain size of a species (Mink et a. 1981, Armstrong 1983, Hofman 1983). Building up on them and on other related work (e.g. Bennett and Harvey 1985), the Expensive Brain Framework (Isler and van Schaik 2009a), also known as the Expensive Brain Hypothesis, combines different non-exclusive pathways illustrating the energetic allocation of brain growth/maintenance in relation to other functions (Fig. 1.2). It suggests that there are two basic ways of how enlarged brains are paid for - either by reducing the energetic allocation to other functions or through an increase in the total energetic turnover (or some combination).

In the first path, an increase in brain size is in trade-off with the energy required for other functions such locomotion or production (including reproduction and growth). This is supported by various studies. Considering the locomotion trade-off, Navarrete et al. (2011) and Heldstab et al. (2016) found evidence that larger brained mammals have smaller adipose depots. They suggest that lower adipose depots, entailing a reduction in the costs of activity and locomotion and thus total energy expenditure, ultimately enable an increase in the energetic allocation to the brain. Furthermore, studies show that species with larger brains show reduced annual fertility (Isler and van Schaik 2009a) and lifetime rates of reproduction (Isler and van Schaik 2009b), supporting the production trade-off.

In the second path, brain enlargement is achieved by a stable net increase in the energetic input. One proxy of the net energy input is the basal metabolic rate (BMR). Not only in primates (Isler et al. 2008) but also across mammals in general (Isler and van Schaik 2006) it is found that an increase in the basal metabolic turnover is correlated with an enlarged brain. On a more ultimate level, a stable net increase in the energetic input allowing for a brain enlargement can be achieved through either improved diet quality (Fish and Lockwood 2003, DeCasien et al. 2017), energy subsidies during breeding (Isler and van Schaik 2009b) or through a stabilized energetic intake (i.e. avoiding periods of starvation in seasonal habitats) (van Woerden et al. 2010, 2012, 2014), two hypotheses for which support is found mainly in primates.

To sum up, larger brains are only possible where either more total energy is available or a reduction in allocation to locomotion or production is possible.

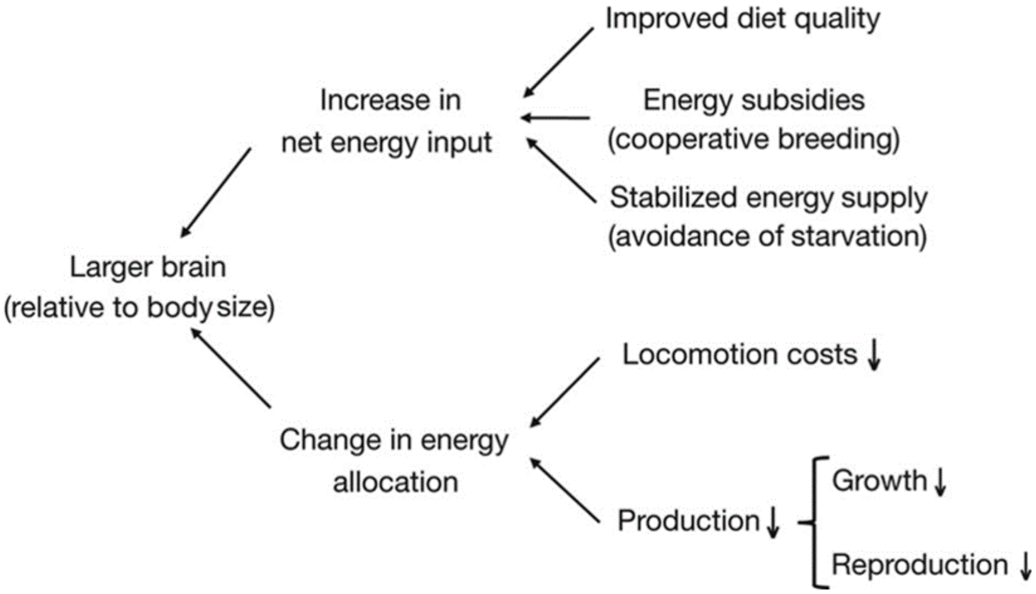

Figure 1.2: Expensive brain framework according to Navarrete et al. 2011. Evolutionary brain enlargement is energetically affordable through two basic, non-exclusive, ways: through an increase in the net energetic input and through a change in the energetic allocation to other functions.

Social Benefits of Enlarged Brains

The Social Brain Hypothesis

Considering the selective benefits, the most prominent hypothesis identifies social complexity as the main driver of brain size evolution, known as the social brain hypothesis (initially known as the Machiavellian Intelligence hypothesis, Byrne and Whiten 1988, Dunbar 1998). It states that large or complex brains are needed to deal with complex social problems. Thus, the size, density and hierarchical structure of the social group in which a species lives and the social challenges this implies are predicted to be directly correlated with cognitive abilities. A modified version of this theory argues that the coordination and negotiation of long-term pair bonds requires enhanced cognition, thus affecting the evolution of brain size (Shultz and Dunbar 2007, 2010). In primates, indeed, various dimensions of social group living including group size, clique size and other social structure characteristics are shown to partly explain variation in size of regions or the overall brain (Sawagachi and Kudo 1990, Dunbar 1992, Pérez-Barbería et al. 2007, Lehmann and Dunbar 2009, Shultz and Dunbar 2007). Further, in birds and mammals, studies found correlative support that the evolution of brain size and thus cognition is related to long-term pair bonding (Emery et al. 2007, Shultz and Dunbar 2007, 2010).
Other studies, however, are not conclusive regarding the social brain hypothesis. MacLean et al. (2009), for instance, found no evidence for a relationship between brain size and both, social group size and pair-bonding in lemurs. Also in carnivorans, the social brain hypothesis lacks persuasive empirical evidence (Finarelli and Flynn 2009, Pérez-Barberia et al. 2007, Holekamp et al. 2015). And very recent study across a broad sample of primate species further calls into question the social brain hypothesis and shows that diet rather than sociality predicts primate brain size evolution (DeCasien et al. 2017).

These controversial findings are based on three main objections against the social brain hypothesis as an exclusive explanation for the evolution of enlarged brains.
First, it does not explain major grade-shifts across taxa (Holekamp 2007, van Schaik et al. 2012,

Holekamp et al. 2015). Lemurs and monkeys show a remarkable difference in relative brain size, but live in comparable social systems and thus require similar socio-cognitive abilities. Along the same lines, many carnivoran species (e.g. hyenas or wild dogs) live in social groups of comparable comlexity to those in primates, but still are relatively smaller-brained than primates.

Second, the social brain hypothesis is inconsistent with the mounting evidence for domain general cognitive abilities, i.e. general intelligence (Burkart et al. 2016). More and more studies in non-human animals suggest that intelligence (as a strong correlate of brain size) is a domain-general construct which allows for behavioral flexibility in different contexts (Deaner et al. 2006, Reader et al. 2011, Navarrete et al. 2016, Burkart et al. 2017). This suggests parallel emergence of cognitive abilities in different domains; thus enhanced cognition allows for complex behavior in not only social but also ecological contexts (see also *Integrating Social and Ecological Aspects of Brain Size Evolution: The Concept of Opportunities and Consequences*, p. 9).

Finally, it ignores that brains are metabolically very expensive in that they need a high and stable energetic input, during development as well as for maintenance. Brains are known to appropriate large portions of the metabolism, especially during the growth phase (Holliday 1986, Bauernfeind et al. 2014), and are at same time highly sensitive to energetic deficits (Levitsky and Strupp 1995, Nowicki et al. 1998). The juvenile risk hypothesis (Janson and van Schaik 1993) suggests that larger brains require slow growth in order to avoid harmful energetic deficits. Further, larger brains are proposed to require a longer period of build-up through learning and practicing of skills before they are fully functioning (needing-to-learn hypothesis: Ross and Jones 1999). Thus, for selection to favor enlarging brains the organism must be able to provide it with an increasing and stable amount of energy, improved survival to compensate for the slower development, or both. Unless this requirement can be met by reducing energy allocated to other functions (Isler and van Schaik 2009a, see *Energetic Costs of Enlarged Brains*, p. 3), selection in favor of improved ecological cognition, with positive consequences for the mean and variance in stable energy intake and for increased survival, may be most likely. Improved cognitive performance as a response to social and ecological environment, therefore, may only lead to increased brain size if it also overcomes these additional costs (Isler and van Schaik 2009a).

The Cultural Intelligence Hypothesis

The cultural intelligence hypothesis (Whiten and van Schaik 2007, van Schaik and Burkart 2011, van Schaik et al. 2012) broadens the perspective of the social brain hypothesis and suggests that the cultural transmission of complex skills is the missing link for understanding the evolution of brain size and cognition.

A large set of foraging skills, also implying higher degrees of behavioral flexibility, is advantageous when it comes to novel or changing environments and ultimately may increase survival (Wright et al. 2010). A complex foraging niche, comprising a large and complex set of skills, which allows for access to highly nutritive and annually stable food sources (Leonard and Robertson 1997), is also expected deliver direct energy for paying the maintenance and growth of a large brain (Gibson 1986).

Since foraging skills are often not simply innate, but are acquired gradually during ontogeny (*primates*: Watts 1985, Johnson and Bock 2004, Schiel et al. 2010; *non-primate mammals*: Rolseth et al. 1994, Sargeant et al. 2005, Thornton and McAuliffe 2006, Sand et al. 2006, Holekamp et al. 1997, Seidensticker and McDougal 1993; *birds*: Norton-Griffiths 1967, Breitwisch et al. 1987, Guo et al. 2010, Carl 1987, Morrison et al. 1978, Burger and Gochfeld 1983), more complex foraging skills are thus likely to require extended periods of acquisition and learning.

The acquisition of skills relies on the continuum between two basic mechanisms - individual exploration and/or socially mediated learning. While through individual exploration, new skills need to be invented over and over again, social transmission represents a more efficient way of skill transmission (van Schaik and Burkart 2011). In order to learn from others, individuals must have the opportunities to spend time in association with tolerant role models. The extent to which individuals can do this has been suggested to affect an individual‘s skill repertoire and innovation propensity (Richerson and Boyd 2000, van Schaik and Burkart 2011). In primates, for example, a cross-species study by Reader and Laland (2002) showed that higher frequencies of social learning are linked to more complex sets of skills such as tool use. Moreover, the percentage of time in association, representative of opportunities for social learning, is positively correlated with the number of complex cultural variations in chimpanzees and orangutans (van Schaik 2003, Whiten and van Schaik 2007).

Furthermore, there are several lines of evidence linking the complexity of skill repertoire and its social transmission to individual learning ability and brain size (i.e. intelligence). First, various studies in birds and primates have shown that social and asocial learning abilities are correlated (Lefebvre and Giraldeau 1996, Lefebvre et al. 1996, Lefebvre 2000, Reader and Laland 2002). And second, the ability to learn complex skills are strongly linked to brain size. There is a considerable amount of comparative evidence, mainly in birds, suggesting that high innovation frequencies, representative for individual learning, and complex skills show correlated evolution with brain size (e.g. Lefebvre et al. 1997, Timmermans et al. 2000).

Taken together, if additionally acquired skills can be translated into fitness benefits and assuming social learning to be more efficient than individual learning, these findings suggest a positive feedback scenario of correlated evolution between social transmission, complexity of skill repertoire (or niche complexity) and intelligence (i.e. brain size, Deaner et al. 2007). Based on this, the cultural intelligence hypothesis (Whiten and van Schaik 2007, van Schaik and Burkart 2011, van Schaik et al. 2012) suggests that cultural transmission of complex skills drive the evolution of intelligence, particularly in species where close proximity with tolerant role models and thus opportunities for social learning are common.

Therefore, longer periods of development and nutritional dependence which go hand in hand with more time in close proximity to tolerant role models and thus more time to acquire skills, are expected to be correlated with larger and more complex sets of skills (i.e. more complex foraging niches) and eventually are expected to be linked to enlarged brains. So far, these links have not been investigated in a cross-species context. The second chapter of this thesis investigates these pathways in a comparative sample of primates and carnivorans. We test whether elongated periods of development and provisioning, offering more opportunities for socially mediated learning, allow for the evolution into more complex foraging niches and, whether the complexity of these foraging niches are related to brain size.

In birds, several studies have found support for the evolutionary links between social learning and behavioral flexibility (Sasvari 1985), as well as behavioral flexibility and brain size (e.g. Overington et al. 2009). Whether highly intelligent avian species also show higher degrees of culture/social learning, however, has not been systematically tested so far. The third chapter of this thesis aims to enlighten the evolutionary framework of the cultural intelligence hypothesis in birds by testing the correlation between opportunities for social learning and brain size. Because direct measurements for the extent of culture are virtually impossible to obtain, especially in the wild, we estimated opportunities for social learning as a function of number of tolerant role models and time in close proximity with them.

Ecological Benefits of Enlarged Brains

Another set of hypotheses proposes that the challenges posed by the interaction with the ecological and physical environment promote the evolution of brain size. The patchy spatio-temporal distribution of food sources (Milton 1988, Gibson 1986) and greater need for orientation in larger home ranges (Clutton-Brock and Harvey 1980) may require higher levels of cognition and ultimately drive the evolution of enlarged brains. Further, the technical intelligence hypothesis (Parker and Gibson 1977, Gibson 1990, Byrne 1997) suggests that extracting protected foods, which often requires complex and coordinated processing techniques, demands higher levels of cognition and ultimately drives the evolution of enlarged brains, which is also supported by a recent comparative study in primates (DeCasien et al. 2017). And finally, from an inclusive ecological perspective, the cognitive buffer hypothesis predicts that more encephalized (brain size relative to body mass) species show a greater general behavioral flexibility and thus are better at responding to seasonal fluctuations and unpredictable changes in the environment ultimately increasing survival rates and longevity (Allman et al. 1993, Sol et al. 2009).

Whether an increase in brain size is eventually favored by natural selection depends on the degree by which the socio- and eco-cognitive benefits outweigh the energetic costs. A species benefits from a larger brain only if enhanced cognition actually translates into improved survival and reproduction. In an ecological environment which entails unavoidable starvation or predation and thus a fast life history, enhanced cognition does not pay off and therefore selection is unlikely to favor an increase in brain size (i.e. life-history filter, cf. van Schaik et al. 2012). In sum, in order to understand the massive cross-species variation in brain size and its underlying evolutionary processes, it is crucial to take both perspectives (costs and benefits) into account.

Combining Costs and Benefits of Enlarged Brains

Seasonality and the Evolution of Brain Size

Seasonality is defined as recurrent fluctuations in climate and environmental productivity. It represents an ideal phenomenon to study the concomitant effects of the cost and benefit perspectives, as it may be both, energetically constraining as well as cognitively challenging.

On the one hand, seasonally recurrent fluctuations in climate and the concomitant variation in food availability strongly affect the energy budget of animals. The low food availability during lean periods in highly seasonal environments poses an energetic challenge for its inhabitant species. Since, as argued above, brains are metabolically very expensive with maintenance and growth requiring a high amount and a continuous supply of energy, the expensive brain framework (Isler and van Schaik 2009a) predicts that higher degrees of seasonality (implying severe periods of food scarcity and thus energy shortages) constrain the evolution of brain size. Therefore, species experiencing higher degrees of seasonality, irrespective of the degree of environmental seasonality, are expected to evolve smaller relative brain sizes (Fig. 1.3A).

On the other hand, as suggested by the cognitive buffer hypothesis, species with an increased brain size, i.e. increased cognitive capacity, are expected to respond more flexibly to seasonal fluctuations in the environment (van Woerden et al. 2010, 2012, 2014). Exploiting alternative food resources in periods where the preferred ones are scarce reduces the variability in energetic input (i.e. experienced seasonality) relative to variability in the environment (i.e. environmental seasonality) (van Woerden et al. 2010, 2012, 2014; Melin et al. 2014) (Fig. 1.3B). Thus, larger-brained species are expected to deal better with seasonally lean periods, and ultimately, to show an increased survival compared to their smaller-brained relatives living in the same habitats (Allman et al. 1993, Sol 2009). The two complementary hypotheses are explained in Fig. 1.3 based on the distinction between environmental and experienced seasonality.

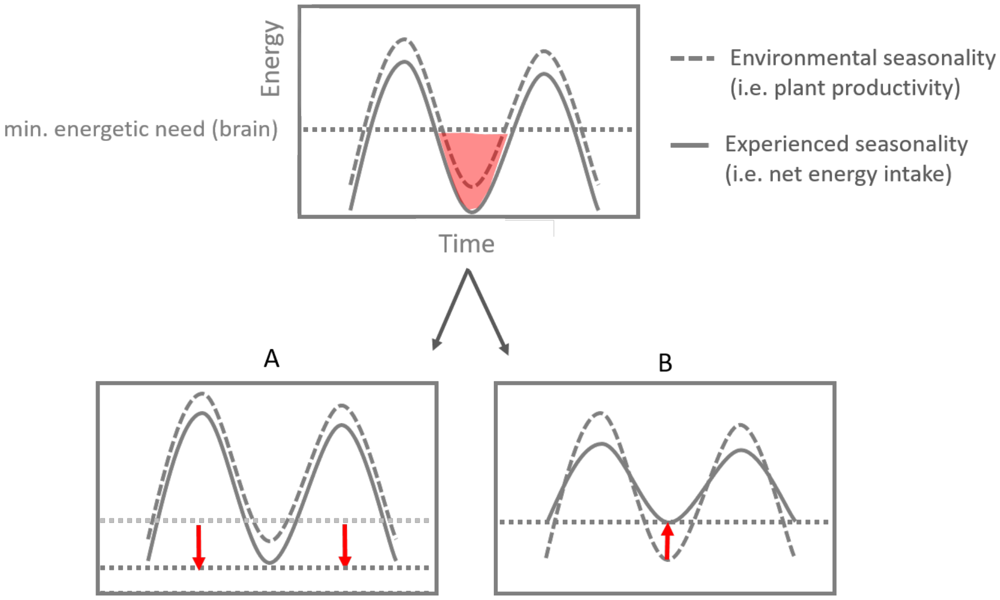

Figure 1.3: Distinction between environmental and experienced seasonality and its relation to brain size according to van Woerden et al. (2010, 2012, 2014). The dashed and solid lines represent the environmental and experienced seasonality, respectively. The dotted line represents the minimum energetic need to maintain a certain brain size. If the energetic requirements during the lean season fall below the minimum energetic need to maintain a certain brain size (red shaded area) as presented in the top panel, either brain size can be reduced to the level of the energetic input during the low season representing the expensive brain hypothesis (A) or the brain and its cognitive capacity is used to find alternative food resources during the lean season which allows to keep the energetic input (i.e. experienced seasonality) relatively constant throughout the year, as predicted by the cognitive buffer hypothesis (B).

Recent work on primates found support for both, the cognitive buffer as well as the expensive brain hypothesis (van Woerden et al. 2010, 2012, 2014). The cognitive buffer hypothesis is shown to apply primarily in anthropoids, and only to a limited extent in lemurs, whereas the expensive brain pattern seems to be more ubiquitous, applying across all primate lineages. Outside the primate clade, currently no study has tested the effect of seasonality on brain size evolution in mammals by systematically distinguishing between experienced and environmental seasonality. Finding out whether the pattern in anthropoids is unique or instead lemurs are the exception is crucial to eventually understand the unmatched degree of cognition in our own lineage. Therefore, the patterns in primates need to be compared in a broad cross-species context including also non-primate mammals.
The aim of the fourth chapter of this thesis is to extend the predictions of the cognitive buffer and expensive brain hypotheses in relation to seasonality to non-primate mammals. Following the methodological approach by van Woerden et al. (2010, 2012, 2014), we also systematically distinguish between experienced and environmental seasonality, and aim to compare the findings in non-primate mammals to the recent findings in primates.

Integrating Social and Ecological Aspects of Brain Size Evolution

The Concept of Opportunities and Consequences

Whether brain size variation is best explained by ecological or social benefits is a long-standing topic of debate. Despite the crucial objections precluding social complexity as the sole, or even main driver of an increase in brain size (see section *The Social Brain Hypothesis*, p. 4), the social brain hypothesis remains to date the most prominent explanation particularly in primates, and thus also humans. For example, Dunbar (2016, p. 59) states that „There is a general consensus that the prime mover in primate brain evolution (and perhaps even that of all mammals and birds) is the evolution of more complex forms of sociality.“ Most previous studies in primates have focused mainly on social factors only or else included only a few simple ad-hoc measures of the ecological domain, such as degree of folivory or terrestriality (e.g. Shultz and Dunbar 2007). A limited set of variables as a proxy for the degree ecological complexity is unlikely to reveal a strong evolutionary pattern. However, most importantly, the increasing evidence that primates show general cognitive flexibility (Deaner et al. 2007, Reader et al. 2011, Burkart et al. 2016), similar to general intelligence in humans, implies that we cannot identify the selective benefits that favored the evolution of larger brains by examining its cognitive consequences because cognitive abilities in the ecological and social domains may be equally improved. In other words, once a large brain has evolved, the enhanced cognition may enable complex behavior in social as well as ecological contexts. To date, the correlates of increased brain size were invariably interpreted as drivers, with encephalization being the direct evolutionary response (e.g. Navarrete et al. 2016). Tests therefore need to carefully distinguish between preconditions that enabled for the evolution of larger brains (potential selective pressures) from their cognitive consequences.
Furthermore, regarding potential selective pressures (irrespective of the general cognitive consequences of enlarged brains), social and ecological factors are also not mutually exclusive and it is reasonable to assume that not the social or physical environment per se but rather a combination, including a wide range of factors from both domains, shape the evolution of interspecific brain size variation. A recent study in primates has integrated various measures including sociality as well as diet and provide evidence that primate brain size evolution is more predicted by diet than sociality (DeCasien et al. 2017). Even though this study provides a systematic empirical approach with convincing results, they included only a limited number of variables and more importantly, did not distinguish between potential drivers and cognitive consequences.

The aim of the fifth chapter of this thesis is to resolve these issues of previous studies by (1) including a comprehensive set of both ecological and social variables and by (2) systematically distinguishing between potential selective pressures (i.e. opportunities) and evolutionary consequences. With this new conceptual approach we try to disentangle what factors allowed for the evolution of enlarged brain in the first place (opportunities), and what factors might simply reflect enhanced cognition of increased brain size (consequences). Across a broad sample of primate species we systematically test the evolutionary associations and directions between brain size, opportunities, consequences. The distinction between opportunities and consequences has not been made before.

As social and ecological *opportunities* we define conditions in which selective pressures toward an enlarged brain may exist. These selection pressures, however, can only act in cases where the fitness benefits of enhanced cognition outweigh the energetic and developmental costs associated with increased brain size. Based thereon, we expect that an increasing number of potential selective pressures can lead to an increase in brain size in some lineages but not in others where energetic costs cannot be offset due to life history constraints, resulting in a moderate statistical correlation (Fig. 1.4A). On the other hand, given the assumption of a form of general intelligence as opposed to a completely modular mind (Geary 2005, Deaner et al. 2006), once a large brain has evolved, it can be used to deal with problems in a broad variety of contexts. This likely includes highly complex social and ecological challenges, such as tool use or coalition formation, which we define as *consequences*. These consequential factors of enlarged brains require extended periods of learning, as shown in chapter 3 of this thesis, and we suggest a large brain to be a necessary precondition for evolving these traits. Mounting evidence from non-human animals indeed suggests that intelligence (as a strong correlate of brain size) is a domain-general construct which allows for behavioral flexibility in different contexts (Deaner et al. 2006, Reader et al. 2011, Navarrete et al. 2016, Burkart et al. 2016). Thus, cognitive adaptations evolved in one context are applicable to other situations; in other words, if a species performs well in one domain it should also perform well in the other domain. Therefore a strong association between brain size and both social and ecological consequential factors is expected (Fig. 1.4B) as well as a strong link within the consequential factors representative for general behavioral flexibility (Fig. 1.4C).

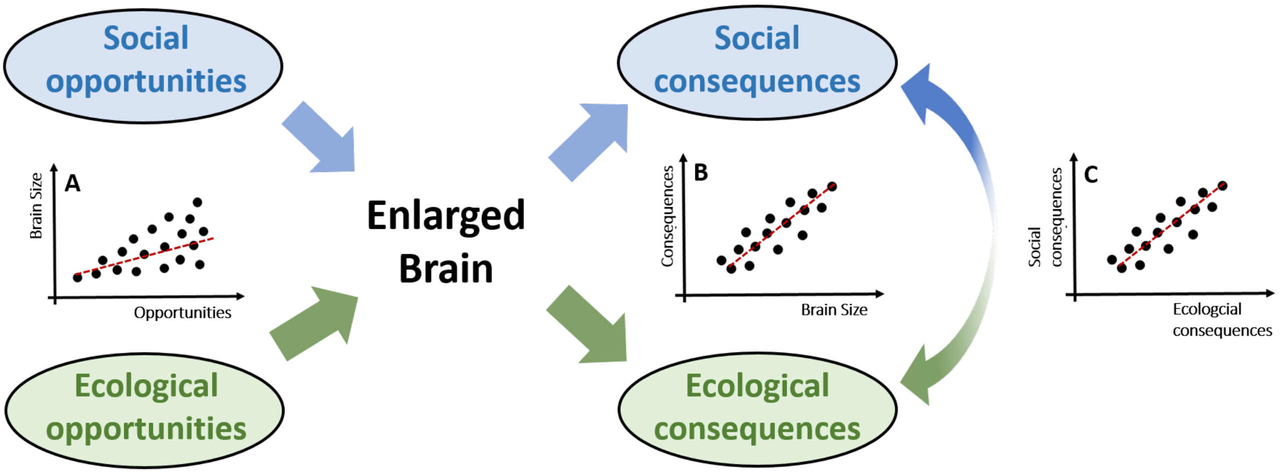

Figure 1.4: Systematic distinction between potential social and ecological selective pressures (i.e. opportunities) and consequences of enlarged brains. Whereas we expect a strong relationship between brain size and consequences as well as within (B, C), the effect of opportunities on brain size is expected to be less strong, because opportunities for selection may not be taken (A).

Phylogenetic Comparative Approach and Methodological Considerations

Phylogenetic Comparative Approach

To understand the potential selection pressures and the consequential adaptations of brain size evolution, a comparative approach is indispensable. Selection experiments are difficult to conduct, not only because of long generation times or ethical concerns, but also because the various influencing factors affecting the evolution of brain size are hard to control (e.g. ecological conditions including seasonality, niche complexity or social aspects such social organization or mating system). There are a few studies in guppies (*Poecilia reticulata*) which tested artificial selection on relative brain size in relation to different traits such as reproduction, gut size, predator behavior and survival (Kotrschal et al. 2013, 2015a,b; van der Bijl et al. 2015). However, due to fundamental physiological differences (endotherm vs. ectotherm), we do not necessarily expect the same adaptations in mammals.

Most importantly, however, patterns within species are not necessarily consistent with patterns across species. For example, from the negative association between brain size and yearly variation in body mass and thus body fat (representing a trade-off between physiological and cognitive buffering: Heldstab et al. 2016), one cannot conclude that individuals of a given species who have smaller brains generally gain more fat. Therefore, large-scale comparative studies are crucial to detect general patterns across species and to understand ultimate evolutionary explanations shaping the evolution brain size. These patterns are basically represented and tested by the correlated evolution between biological traits and brain size.

Phylogenetic Comparative Methods

Part of the variation in relative brain size clusters along more closely related species is illustrated in the phylogeny in Fig. 1.1B. These interspecific similarities can to a lesser or greater extent be attributed to the common evolutionary history of related species, leading to what is known as phylogenetic dependence or phylogenetic inertia (Nunn 2011). This means that data points on a cross-species scale are not necessarily independent from one another. Therefore, statistical models testing interspecific relationships need to take phylogenetic non-independence in account by using phylogenetic comparative methods (Felsenstein 1985). In this thesis, all models testing the effects on and consequences of brain size increase across species in terms of its patterns of correlated evolution are based on phylogenetic least squares regression (PGLS), which accounts for the phylogenetic dependence in the error structure, i.e. residuals (Grafen 1989).

Regression Analysis to Study Correlated Evolution

The study of patterns of correlated evolution using regression analyses requires some special considerations. A regression analysis in general, whether controlled for phylogeny or not, estimates the effect of potentially multiple independent x-variables on a dependent y-variable. Since the regression estimates of x on y, and y on x are not symmetrical, in contrast to a correlation analysis, which trait is set as the independent and which as the dependent variable is crucial. This is evident by algebraically converting the formula of the least squares regression model from y to x (e.g. $y = 1 + 3x$ vs. $x = -1 + \frac{1}{3}y$) and is graphically illustrated in Fig. 1.5. From a biological perspective the symmetry of a relationship between two traits is also not necessarily given. Let us assume, for example, all species which are large-brained show strong cognitive buffering during seasonally lean periods. However, not all species living in seasonal habitats necessarily show and need a large brain, since there are alternative buffering strategies such as hibernation. In other words, the variation in trait y may be explained by the variation in trait x, but not necessarily vice versa. Therefore, in all regression analyses the variables are deliberately and consistently used as independent and dependent variables. In that respect, if explaining variation in brain size is of interest, brain size is set as the dependent variable (*chapter 3*: brain size vs. opportunities for social learning, *chapter 4*: brain size vs. experienced seasonality, *chapter 5*: brain size vs. social and ecological opportunities). However, in case the socio-cognitive or eco-cognitive consequences are to be explained by variation in brain size, brain size is set as the independent variable (*chapter 2*: niche complexity vs. brain size, *chapter 4*: degree of buffering vs. brain size, *chapter 5*: socio- and eco-cognitive consequences vs. brain size).

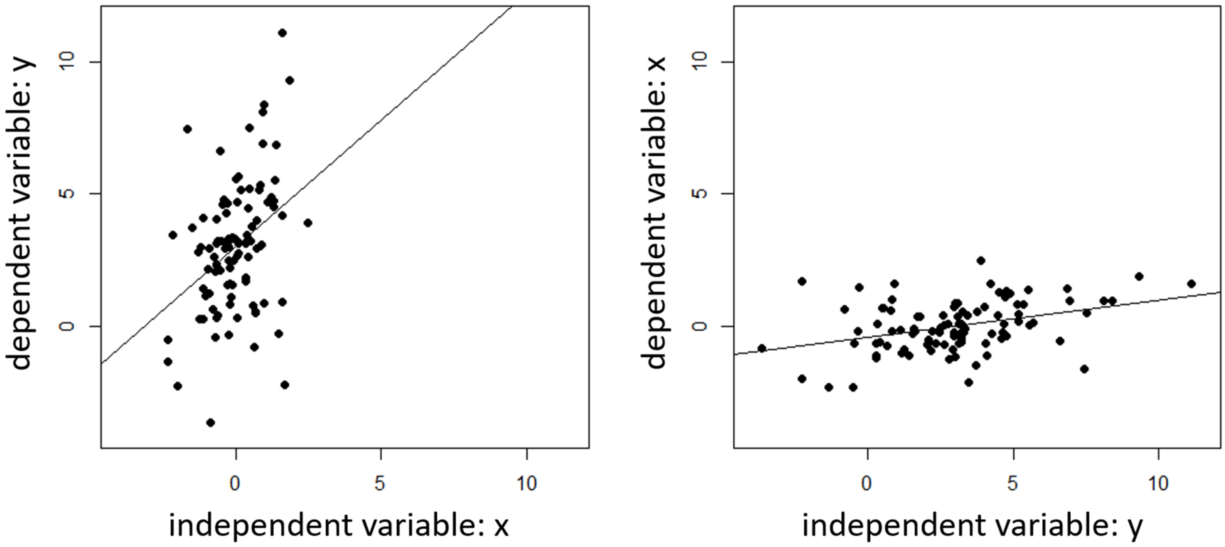

Figure 1.5: Regression analysis x on y and y on x are not symmetric. Using the same data, the slope $\beta = 0.9$ in the left panel is much steeper than $\beta = 0.1$ in the right panel, and the relationships in the two panels are described by two different regression models.

Synopsis of This Thesis

My dissertation aims to investigate different aspects of interspecific brain size evolution in relation to both social and ecological factors, taking the cost as well as benefit perspective into consideration. A comparative phylogenetic approach is used throughout the thesis, and detailed hypotheses as well as an integrative socio-ecological framework are tested by looking at patterns of correlated evolution across vertebrate species.

The thesis is divided in three major parts. The first part, consisting of chapters 2 and 3, focuses mainly on social factors and investigates the framework of the cultural intelligence hypothesis which predicts that the opportunities for socially mediated learning (time in close proximity to tolerant role models) are linked to the complexity of foraging skills (foraging niche complexity) and ultimately to the evolution of brain size. In **chapter 2**, we test whether in primate and carnivoran species more time to learn in terms of delayed reproduction and nutritional independence enabled the evolution into more complex foraging niches, and in turn, whether the complexity of a foraging niche and its ecological skills are related to brain size. In **chapter 3** we test the cultural intelligence hypothesis across a large sample of birds using the length of post-fledging parent offspring association and the number of tolerant role models as measures for the degree of opportunities for social learning and look at patterns of correlated evolution with relative brain size.

The second part, comprising **chapter 4**, focuses on ecological aspects and combines the cost and benefit perspective by investigating how brain size evolution is affected by seasonality in non-primate mammals, and how these patterns compare to the ones in primates (van Woerden et al. 2010, 2012, 2014). Following the methodological approach by previous work in primates (van Woerden 2011, van Woerden et al. 2010, 2012, 2014), we distinguish between environmental seasonality, represented by the annual variation in plant productivity, and the actually experienced seasonality, represented by fluctuations in diet composition compiled from the literature. We look at the cost perspective by testing correlated evolution between experienced seasonality and brain size (expensive brain hypothesis), and at the benefit perspective, by testing the effect of brain size on the degree to which the experienced seasonality is buffered relative to the environmental seasonality (cognitive buffer hypothesis).

In the last part of this thesis, **chapter 5**, we combine a broad range of variables encompassing both the social and ecological domain (including all factors used to test detailed hypotheses in the previous chapters) and introduce a new conceptual approach, which systematically distinguishes between potential selective pressures and direct consequences of enlarged brains. The aim is to integrate the various hypothesized aspects explaining brain size variation and clarify the ongoing debate about the main driving forces in the evolution of brain size across primates. Using multivariate statistics and phylogenetic path analyses we systematically test for the most likely evolutionary directions within the suggested framework of opportunities and consequences and its relationships with relative brain size.

And finally, the general discussion (**chapter 6**) summarizes the findings and their implications of the previous chapters and brings them into context by discussing them in view of the new conceptual approach of evolutionary opportunities and consequences. Further, conclusions are drawn concerning differences between vertebrate lineages and how the findings of this thesis explain the unmatched brain size in our own lineage.

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Chapter 2

Life history, cognition and the evolution of complex foraging niches

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Abstract

Animal species that live in complex foraging niches have, in general, improved access to energy-rich and seasonally stable food sources. Because human food procurement is uniquely complex, we ask here which conditions may have allowed species to evolve into such complex foraging niches, and also how niche complexity is related to relative brain size. To do so, we divided niche complexity into a knowledge-learning and a motor-learning dimension. Using a sample of 78 primate and 65 carnivoran species, we found that two life-history features are consistently correlated with complex niches: slow, conservative development or provisioning of offspring over extended periods of time. Both act to buffer low energy yields during periods of learning, and may thus act as limiting factors for the evolution of complex niches. Our results further showed that the knowledge and motor dimensions of niche complexity were correlated with pace of development in primates only, and with the length of provisioning in only carnivorans. Accordingly, in primates, but not carnivorans, living in a complex foraging niche requires enhanced cognitive abilities, i.e., a large brain. The patterns in these two groups of mammals show that selection favors evolution into complex niches (in either the knowledge or motor dimension) in species that either develop more slowly or provision their young for an extended period of time. These findings help to explain how humans constructed by far the most complex niche: our ancestors managed to combine slow development (as in other primates) with systematic provisioning of immatures and even adults (as in carnivorans). This study also provides strong support for the importance of ecological factors in brain size evolution.

Introduction

There is extensive variation in the foraging niches different mammal species occupy. Whereas some foraging niches seem to be simple because they involve no pre-ingestive processing (e.g., those occupied by grazing ungulates), others appear to be more complex, because obtaining access to food requires multiple processing steps, executed in the correct order and timed properly (as occupied by many primates [e.g., Gibson, 1986; Byrne et al., 1993; Gunst et al., 2010]). Living in a complex foraging niche may bring palpable fitness benefits (Gibson, 1986). First, foods that require a high level of processing, such as underground storage organs, insects or other animal prey consistently show a high nutritive content. Second, because extracted foods are often available year-round, species able to exploit them can live in seasonal environments in which they would otherwise experience a lean season. Understanding the evolution of complex niches is important for human evolution because, unique among primates, human hunter-gatherers (as models for ancestral humans), and indeed humans in general, rely on highly complex forms of extractive foraging and hunting, and so manage to maintain a relatively stable energy intake in a great variety of different environments (Leonard and Robertson, 1997; Kaplan et al., 2000; Berbesque et al., 2014).
So far, no study has systematically examined the factors that allow species to evolve into such complex foraging niches. Occupying a complex foraging niche will generally require lengthy periods of learning, during which failure is common and net yields are low. Since these learning periods are costly we expect them to be connected to life history features that counterbalance these costs. Indeed, we recently found that species with a late age at skill competence (the age at which adult-level skill levels are attained) are those that show one of two enabling factors: post-weaning provisioning or slow, conservative development (Schuppli et al.,2012). Both factors work as an energetic buffer against failures during periods of learning and therefore allow the learning period to be extended (Fig. 2.1). We also found evidence that species with complex foraging niche(with complexity defined as the level of processing required) reach adult-level feeding skills later in development than those that live in simpler niches (Schuppli et al., 2012).

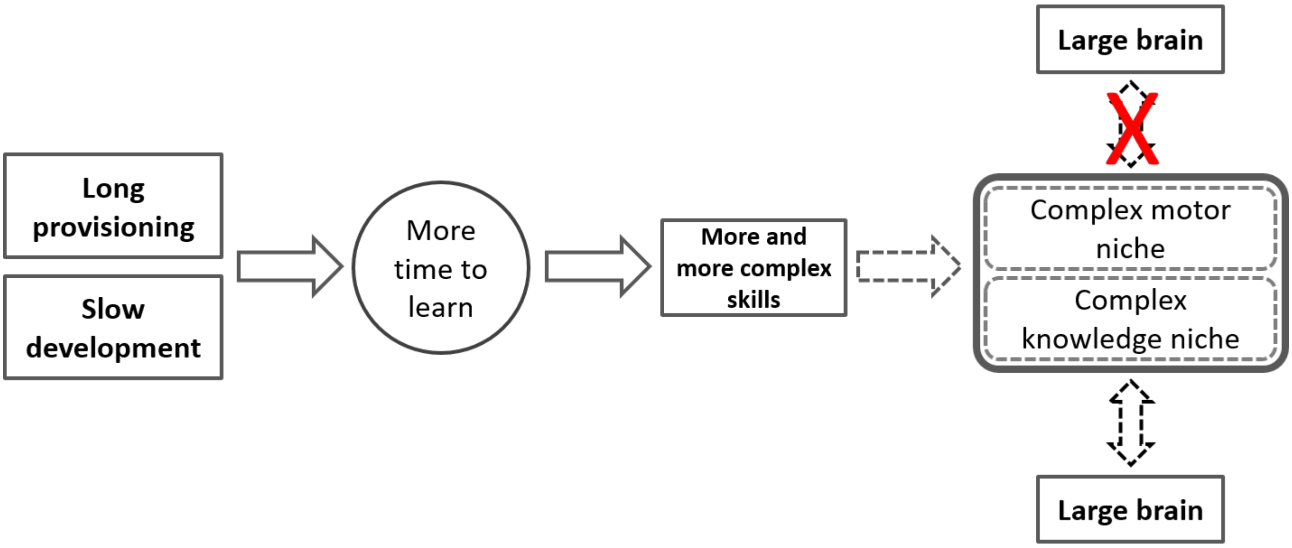


Figure 2.1: Slow development and extended provisioning have been shown to allow for extended periods of learning (later relative age at skill competence [Schuppli at al., 2012]). Here we ask in Part I whether the same two factors ultimately allow species to evolve into more complex niches. In Part II we are interested in how niche complexity relates to relative brain size and expect only the knowledge niche, but not necessarily the motor niche, component to be associated with large relative brain size.

In this paper, we ask whether foraging-niche complexity coevolved with long periods of learning or provisioning and with brain size. Such a three-way relationship has often been suggested by anthropologists, who proposed that slowly developing species do so because they need time to learn skills essential to sustain reproduction (Janson and van Schaik, 1993). A recent study in which this was quantified, however, showed that the time needed to learn these skills limited the duration of development only in a subset of species, including humans (Schuppli et al., 2012), and that the most widespread limiting factor is a tradeoff between energy allocation to needs of a growing body and a growing and differentiating brain. As a result, larger-brained species develop more slowly (Isler and van Schaik, 2009; Barton and Capellini, 2011) and thus reach maturity at a later age, which is compensated for by their improved adult survival (Isler and van Schaik, 2009; Gonzalez-Lagos et al., 2010). In humans, this tradeoff is responsible for our highly delayed maturation and the adolescent growth spurt (Kuzawa et al., 2014), although in humans adult-level skills are reached even later (Kaplan et al., 2000).

Nonetheless, there are good reasons to assume there is a link between niche complexity and brain size. First, larger brains are found in species with higher overall diet quality (Fish and Lockwood, 2003) or those that engage in extensive extractive foraging or tool use (Byrne, 1997; Reader and Laland, 2002; Barton, 2012). Second, larger brains are found in species that can maintain a high and stable energy intake all year round (van Woerden et al., 2010, 2012, 2014), often as a result of extractive foraging techniques (Gibson, 1986) or perhaps because of the ability to locate ephemeral food sources (Milton, 1988). This same argument has also been applied to human evolution. It has repeatedly been suggested that the need to invent complex foraging techniques in an increasingly seasonal habitatwas a driving force in the evolution of human intelligence (e.g., Parker and Gibson, 1977; Byrne, 1997; Anton et al., 2014). However, so far only very few studies have looked at the relation between brain size and niche complexity, and the ones that have focused on a few taxa only and produced inconsistent results (Parker and Gibson, 1977; Milton,1981; Gibson, 1986; Walker et al., 2006).

Here, we first examine whether the two factors that allow for extended periods of learning during development (slow development and post-weaning provisioning) are also a prerequisite for evolving into a more complex foraging niche (Fig. 2.1). Focusing on the direct link between niche complexity and provisioning and pace of development allows us to include a much broader sample of species than in the previous study (Schuppli et al., 2012) where limited data on age of skill competence led to small sample size. Second, in order to attain a better understanding of the cognitive aspect of niche complexity, we examine how different aspects of niche complexity relate to brain size. If we find a relationship between foraging-niche complexity and relative brain size across different species, this may help to explain why species with complex foraging niches are relatively rare and why humans occupy by far the most complex niche.

A key decision in a study of foraging-niche complexity is how to define complexity. Previous studies have ranked the skill requirements of different food types and consistently classified leaves and grasses as less skill intensive than items, such as fruit, that require some kind of manipulation with hands or coordinated movements involving both hands and parts of the mouth (teeth, lips). The ingestion of embedded food items, such as nuts, which require more processing steps is generally considered to require more complex skills (Dittus, 1977; Kaplan et al., 2000; Johnson and Bock, 2004). All these studies thus used the amount of processing with hands or hands and mouth required as a measure of complexity, such that items that need few or no processing steps are rated as less skill-intensive than items that require a feeding technique composed of several steps of processing. Other studies have classified specific elements of the diet or certain processing techniques, such as tool use, extractive foraging or cooperative hunting, as complex since they are based on knowledge and their efficiency improves with causal understanding (Holekamp et al., 1997; Gurven et al., 2006; Lonsdorf, 2006; Gunst et al., 2010).

The patterns found in these studies suggest that ecological niche complexity can be divided into two broad dimensions: knowledge and motor complexity. Knowledge-niche complexity comprises knowing what to eat, where to look for it (which is not always obvious with embedded foods), which processing techniques to use, and how to integrate these techniques into an ordered sequence (cf. Barton, 2012). Since acquiring the requisite knowledge and understanding requires a learning period, we expect to find that species inhabiting complex knowledge niches show a long period of provisioning and/or a slow development. Motor-niche complexity, in contrast, encompasses the motor patterns involved in food acquisition and is consequently determined by the motor skills needed in each single step of food processing. We expect motor-niche complexity to be based more on practice than cognitive understanding. Unfortunately, it will be difficult to clearly distinguish between the two complexity dimensions in all cases since there may be substantial overlap between them.

In this study, we systematically test on a large comparative data set how foraging-niche complexity is related to the two life-history pathways, pace of development and the length of provisioning (Part I) and then, to relative brain size (Part II). We do this in two mammalian lineages: primates and carnivorans. For the life-history pathways, we expect that the pace of development or the length of provisioning underwent correlated evolution with niche complexity, such that species living in more complex foraging niches are characterized by slower development or extended provisioning. We are also interested in how strongly each of the two different dimensions of niche complexity (knowledge and motor) is correlated with development or provisioning. For the link between foraging niche complexity and cognition, we expect that knowledge-niche complexity (comprising knowledge and understanding of a foraging niche) is positively correlated with relative brain size. However, the prediction for the relation between brain size and motor niche is less straightforward. On the one hand, we assume the motor dimension to require extensive practice, but not necessarily understanding and knowledge, and therefore not to rely on enhanced cognition. On the other hand, practice itself as well as sensory-motor processes involved in motor skills are expected to have neural correlates, which would suggest a positive correlation between brain size and motor-niche complexity. In other words, we hypothesize a large brain to be an inevitable prerequisite for species living in a complex knowledge niche but not necessarily for those living in a complex motor niche.

Material and Methods

Data sets

We compiled data sets on the different elements of niche complexity, life history parameters, brain- and body size for 78 nonhuman primate and 65 carnivoran species. Life history, provisioning, brain and body size data were retrieved from established databases (K. Isler, S. M. Graber and S. A. Heldstab, unpublished data; Isler and van Schaik, 2009, 2012; van Woerden et al., 2014). Data on the different elements of niche complexity were taken from the published literature (see Supplementary Online Material [SOM]). We use measurements on overall brain size as this has been shown to be a very good predictor of cognitive abilities (Lefebvre et al., 2004; Deaner et al., 2007) and is a very broadly available measurement in mammals.

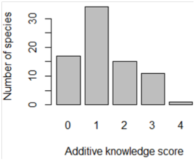
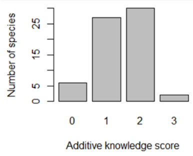
For motor-niche complexity, we divided all species into three complexity categories according to the level of processing involved in food acquisition (Table 2.1). For grazing and folivory, food acquisition generally comprises only one step (bite), whereas for frugivory and insectivory, two basic steps are almost always required (e.g., pick and bite, or peel and bite, or bite and spit), and for extractive foraging and catching mobile prey, three or more basic steps are required (e.g., extract and bite and spit, or catch and kill and bite). As expected, this complexity ranking roughly has a cumulative (Guttman) scaling property, such that species in category 2 or 3 mostly also exhibit elements of category 1, or 1 and 2, respectively.

For knowledge-niche complexity we determined four different cognitively challenging elements found in primates and carnivorans: cooperative hunting, high diet breadth, extractive foraging and tool use. These elements were coded as binary variables, except for diet breadth, where we counted how many different classes of food types a species eats. We also compiled a knowledge-niche complexity score by summing the number of cognitively challenging elements for a certain species, assuming that the more knowledge elements there are, the more complex the overall knowledge niche should be. For the knowledge score we dichotomized diet breadth into a binary variable by assigning one-two different classes of food types to 0 (low), and three and more different food types to 1 (high). In primates, the observed additive knowledge-niche complexity scores ranged from 0 to 4, whereas in carnivorans they ranged from 0 to 3 (Table 2.2).

Table 2.1: Motor-niche complexity categories.

Motor-niche complexity	Niche	Level of processing
1	folivory and grazing	no processing
2	frugivory and insectivory	low-level processing
3	extractive foraging and mobile prey catching	high-level processing

Table 2.2: Distribution of the different knowledge-niche complexity elements and distribution of the additive knowledge-niche complexity score in primates and carnivorans.

	Cognitive elements	**Primates**	**Carnivorans**
Number of species	Cooperative hunting	1	6
	Diet breadth	low: 22; high: 56	low: 7; high: 58
	Extractive foraging	32	26
	Tool use	12	2
Observed knowledge score range			

Variables

To approximate the pace of development we used female age at first reproduction (AFR), controlled for female body mass through multiple regression analysis (see below). The relative length of provisioning was approximated by the total number of days offspring are provisioned, again corrected for body mass. Since there is no post-weaning provisioning in most primate species, we took weaning age as a measure for the length of provisioning for all species except the cooperatively breeding marmosets (*Callithrix jacchus*).

Analysis

All analyses and plots were done using the R programming language (R development Core Team, 2012). More closely related species, in general, show greater similarities in traits because of their shared evolutionary history (Nunn, 2011). To correct for phylogenetic non-independence of the data we used phylogenetic least-squares (PGLS) in the case of multistate ordinal response variables (as justified by the results of Matthews et al., 2010), as implemented in the package caper (Orme, 2011), and phylogenetic logistic regressions (PLR) in the case of binary response variables, as implemented in the package phylolm (Ho and Ane, 2014). The analyses testing the effects on the two foraging niche dimensions were all controlled for body mass (by including it as a factor in the regression models) to ensure that the effects were independent of body mass. In other words, throughout this study we consider life-history traits and brain size relative to bodymass. Residuals of the models, as shown in the graphs, were used for illustrative purposes only. We also controlled for additional potentially confounding variables and provided these analyses in the SOM (Tables S2-S4).

In PGLS, the phylogenetic scaling parameter lambda (λ) (Pagel, 1999), a measure of phylogenetic signal in the model residuals, was estimated based on maximum likelihood as implemented in caper, whereas the other two branch-length transformation factors, delta and kappa, were fixed at 1.

The PLR in phylolm automatically estimates alpha (α), the phylogenetic signal for a binary trait. In contrast to λ, α is based on a Markov process and larger values correspond to a weaker phylogenetic signal (Ives and Garland, 2010). In order to reach evenly distributed residuals around zero, all continuous variables were log-transformed. To assess statistical significance, a 5% level was used. The phylogenetic trees used for the analyses were retrieved and compiled from the published literature (Bininda-Emonds et al., 2007; Perelman et al., 2011). A nexus file was manually extracted from the information provided in Perelman et al. (2011) and is provided in the SOM.

Data classification

We used the published literature to assign species to the various niche categories. However, this was not always straightforward since different sources used different classifications. We therefore repeated our analyses using various classifications, but this did not change our results, which we therefore consider robust. The classification presented here is conservative and in most cases not in favor of our predictions (e.g., *Gorilla gorilla* was not classified as an extractive forager whereas *Callithrix jacchus* was). To further test the robustness of our results, we also dichotomized all our ordinal dependent variables since in most cases this led to more balanced data distributions. This too, did not change the results. Our complete data sets with all classifications and their sources, are provided in the SOM (Table S1).

Results

Part I - Life history pathways and foraging-niche complexity

Motor-niche complexity in primates we found a significant positive effect of the pace of development on motor-niche complexity but no significant effect of the length of provisioning (approximately weaning age; Table 2.3a; Fig. 2.2). For carnivorans, in contrast, we found a significant positive effect of the length of provisioning on motor-niche complexity but no significant effect of the pace of development (Table 2.3b; Fig. 2.2).

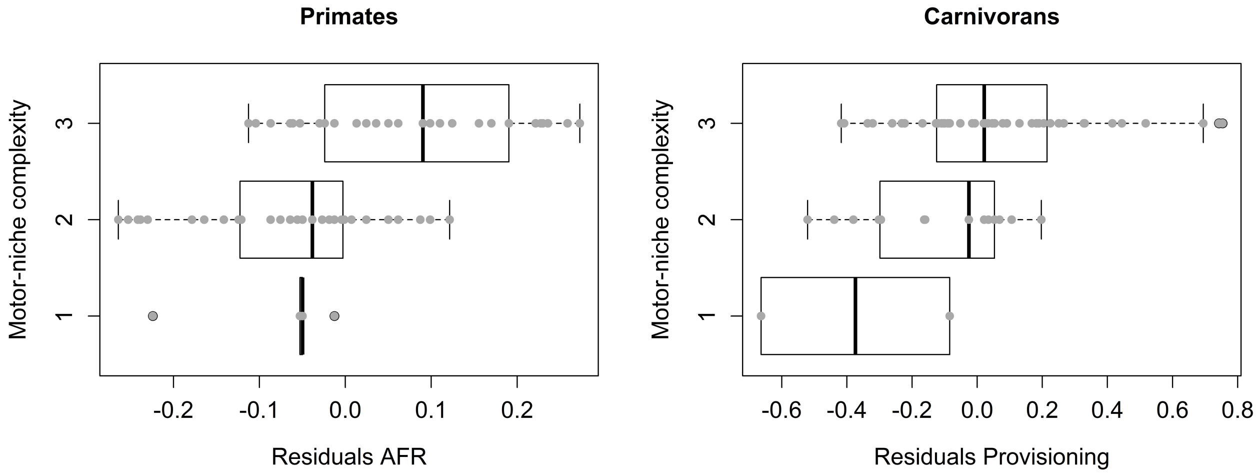


Figure 2.2: Relationships between pace of development (age at first reproduction corrected for body mass) and motor-niche complexity for primates and between length of provisioning (corrected for body mass) and motor-niche complexity for carnivorans.

Table 2.3: Phylogenetic least-square multiple regression models with motor-niche complexity as the response variable and body mass, AFR and length of provisioning as the predictor variables, analyzed separately for the a) 78 primate and b) 65 carnivoran species. Statistical significance (p<0.05) is indicated by bold font.

a) **Primates N=78**						
dependent variable	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
motor-niche complexity	0.22	$\lambda = 0.87$	log body	-0.334	0.104	**0.002**
			log AFR	0.988	0.236	**<0.001**
			log provisioning	-0.012	0.139	0.930

b) **Carnivorans N=65**						
dependent variable	R^2	phylogenetic signal	predictor variables	**estimate**	std. error	p-value
motor-niche complexity	0.16	$\lambda = 0.78$	log body	-0.123	0.088	0.168
			log AFR	-0.228	0.203	0.264
			log provisioning	0.553	0.173	**0.002**

Knowledge-niche complexity. For the overall knowledgeniche complexity score (summed number of cognitively challenging elements) we found the same pattern as for motor niche complexity: in primates, the knowledge-niche complexity score showed a significantly positive correlation with the pace of development, whereas in carnivorans it showed a significantly positive correlation with the length of provisioning (Table 2.4a,b; Fig. 2.3).

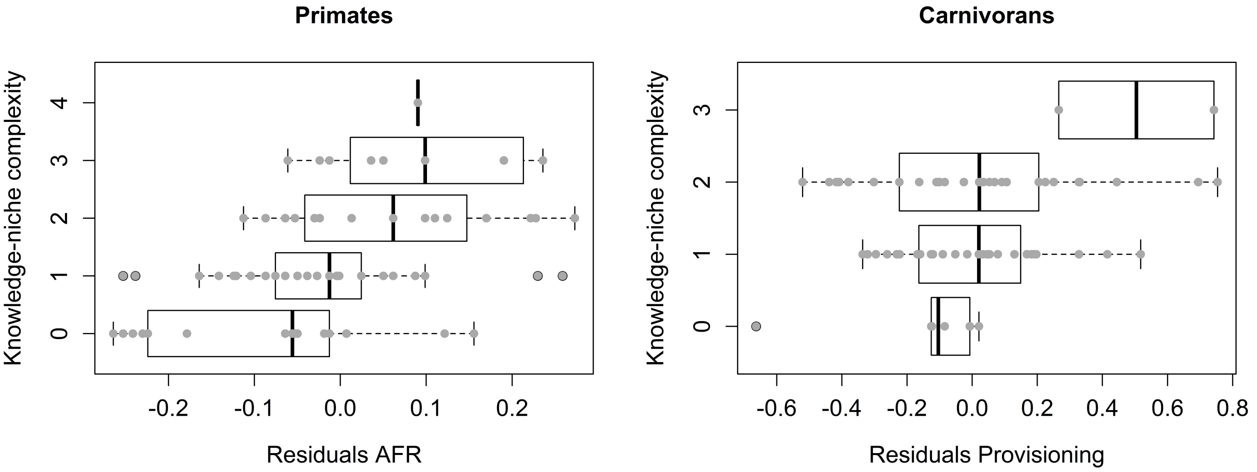


Figure 2.3: Relationships between pace of development (age at first reproduction corrected for body mass) or provisioning(corrected for body mass) and the additive knowledge niche complexity score in primates and carnivorans.

Table 2.4: Phylogenetic least-square multiple regression models with the additive knowledge-niche complexity score as response variable and body mass, AFR and length of provisioning as predictor variables analyzed separately for the a) 78 primate and b) 65 carnivoran species. Statistical significance ($p<0.05$) is indicated by bold font.

a) **Primates N=78**						
dependent variable	R^2	phylogenetic signal	predictor variables	estimate	**std. error**	**p-value**
knowledge-niche complexity	0.41	$\lambda = 0.00$	log body	-0.767	0.308	**0.015**
			log AFR	3.701	0.764	**<0.001**
			log provisioning	0.122	0.478	0.800

b) **Carnivorans N=65**						
dependent variable	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
knowledge-niche complexity	0.15	$\lambda = 0.25$	log body	-0.080	0.125	0.526
			log AFR	-0.452	0.284	0.118
			log provisioning	0.790	0.284	**0.007**

Examining the different elements of knowledge-niche complexity separately, we found that in primates the pace of development had a significantly positive effect on diet breadth, extractive foraging and tool use. Since chimpanzees are the only cooperatively hunting primate species in our data set, we could not evaluate the effect of cooperative hunting statistically, but following our expectations, chimpanzees have a relatively slow pace of development (SOM Table S2a; Fig. S1).

In carnivorans, the length of provisioning had a significant positive effect on diet breadth. For cooperative hunting, therewas a weak trend in the predicted direction whereas for extractive foraging no effect was apparent. For tool use, the small sample size did not allow for statistical testing in carnivorans (SOM Table S2b; Fig. S2).

In primates we found that motor-niche complexity and the additive knowledge-niche complexity score were highly correlated (PGLS: $p < 0.001$, $\lambda = 0.50$). However, no such correlationwas found in carnivorans (PGLS: $p = 0.35$, $\lambda = 0.16$). In order to exclude a spurious effect of pace of development or provisioning on the knowledge-niche complexity score in primates, we included motor-niche complexity as a factor into our analysis of the predictors of the knowledge-niche complexity. We found that the effect of the pace of development on the knowledge-niche complexity score still held when we controlled for motor-niche complexity (primates: p (log AFR) = 0.038, p (motor complexity) < 0.001, $\lambda = 0$; see SOM Table S2a). Detailed statistics on the regression models and further analyses are also shown in the SOM (Table S2 a,b).

Part II - Brain size and foraging-niche complexity

Motor-niche complexity. In carnivorans, there is no significant correlation between motor-niche complexity and brain size (Table 2.5b, Fig. 2.4). Adding the length of provisioning as an additional factor did not change the result (SOM Table S3b). In primates, in contrast, this correlation is significant (Table 2.5a; Fig. 2.4). However, the correlation between brain size and motor niche complexity disappears if we control for AFR (SOM Table S3a).

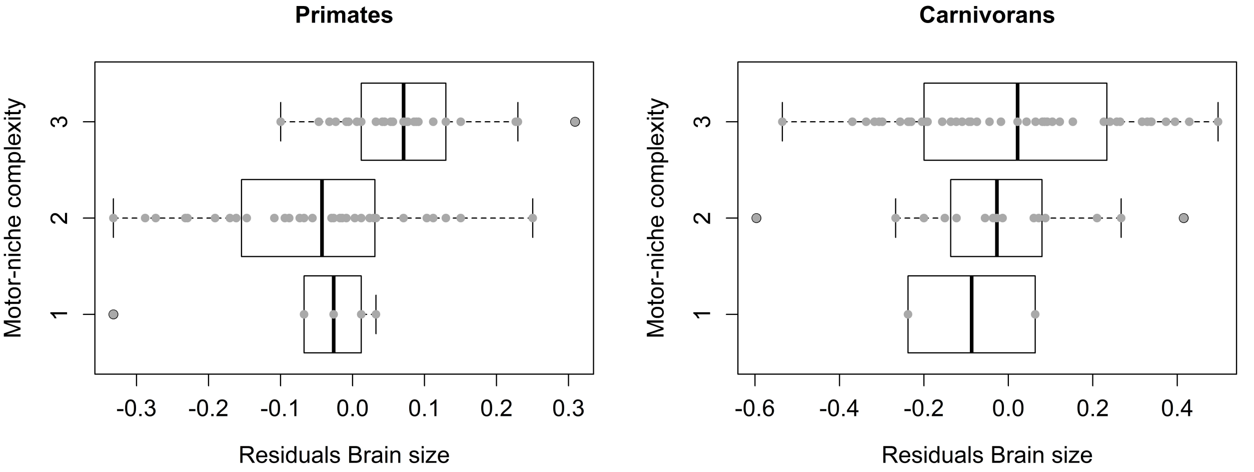


Figure 2.4: Relationships between relative brain size (corrected for body mass) and motor-niche complexity for primates and carnivorans.

Table 2.5: Phylogenetic least-square multiple regression models with motor-niche complexity as the response variable and body mass and brain size as the predictor variables, analyzed separately for the a) 78 primate and b) 65 carnivoran species. Statistical significance ($p<0.05$) is indicated by bold font.

a) **Primates N=78**						
dependent variable	R^2	phylogenetic signal	predictor variables	estimate	**std. error**	p-value
motor-niche complexity	0.12	$\lambda = 0.66$	log body	-0.715	0.224	0.002
			log brain	0.880	0.294	**0.004**

b) **Carnivorans N=65**						
dependent variable	R^2	phylogenetic signal	predictor variables	estimate	**std. error**	p-value
motor-niche complexity	0.00	$\lambda = 0.87$	log body	0.051	0.169	0.761
			log brain	-0.080	0.264	0.764

Knowledge-niche complexity. In primates, the additive knowledge-niche complexity score showed a significant positive correlation with brain size (Table 2.6a; Fig. 2.5). In fact, the PGLS regression continued to show a significant correlation between brain size and the knowledge-niche complexity score even after additionally controlling for possible confounding effects of motorniche complexity or for AFR (SOM Table S4a). These results are consistent with our hypothesis that predicted that species living in complex knowledge- niches have bigger brain sizes. When analyzing the different cognitively challenging elements separately and controlling for the motor-niche dimension, only tool use showed a significant association with relative brain size (SOM Table S4a, Fig. S3). Also, being the only cooperatively hunting primate species in our data set, chimpanzees have a relatively large brain.

For carnivorans, in contrast, no such link between knowledgeniche complexity and relative brain size was found. Neither the additive knowledge-niche complexity score, nor the regression models of the individual cognitive elements showed evidence for a correlation with brain size (Table 2.6b, Fig. 2.5; SOM Table S4b, Fig. S4). Detailed statistics of the regression models of all additional analyses are also shown in the SOM (Table S4a,b).

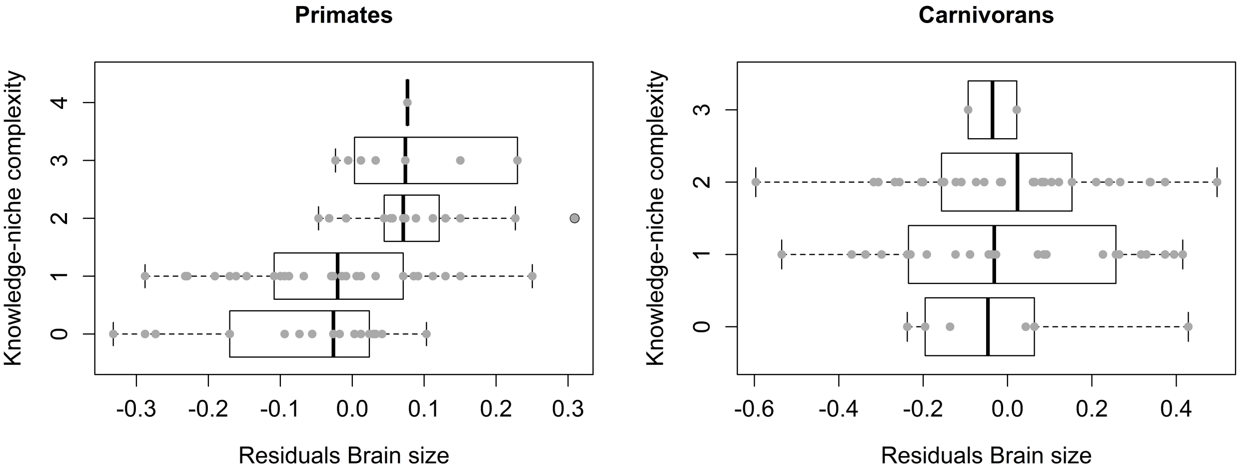


Figure 2.5: Relationships between relative brain size (corrected for body mass) and additive knowledge-niche complexity score for primates and carnivorans.

Table 2.6: Phylogenetic least-square multiple regression models with the additive knowledge-niche complexity score as response variable and body mass and brain size as predictor variables analyzed separately for the a) 78 primate and b) 65 carnivoran species. Statistical significance ($p<0.05$) is indicated by bold font.

a) **Primates N=78**

dependent variable	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
knowledge-niche complexity	0.41	$\lambda = 0.00$	log body	-2.196	0.538	**<0.001**
			log brain	3.600	0.654	**<0.001**

b) **Carnivorans N=65**

dependent variable	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
knowledge-niche complexity	0.02	$\lambda = 0.17$	log body	0.185	0.254	0.471
			log brain	-0.213	0.387	0.584

Discussion

Part I - Life history pathways to complex foraging niches

In the first part, we found that two life history features are consistently correlated with both dimensions of niche complexity: in primates, slow, conservative development, and in carnivorans, provisioning over extended periods of time. Because newly weaned mammals of species living in complex foraging niches generally have not yet reached adult-level feeding skills (Schuppli et al., 2012), both features may help to provide an energetic buffer during periods of learning. Energy deficits caused by failures (and therefore lower net energy intake) during the period of learning may have severe consequences for the still growing juvenile individual because they carry the risk of brain starvation (Janson and van Schaik, 1993; Isler and van Schaik, 2009; Kuzawa et al., 2014). Post-weaning provisioning suppresses these energy deficits not just because it provides the immature animal with energy but also because it reduces the immature animal's required foraging time, and consequently allows it to allocate more time to practicing. Similarly, slow, conservative development reduces the risk of brain starvation and provides the immature animal with a longer prereproductive period during which it can afford to have the reduced foraging efficiency caused by learning. Because reproduction would compete for energy with maintenance, it is postponed until adequate skill levels have been reached. Thus, both mechanisms provide species with enhanced opportunities to learn after weaning. In support of this interpretation, adult-level feeding skills are reached at a relatively later point during ontogeny in those species that get provisioned longer or show an overall slower development (Schuppli et al., 2012).

When we divided niche complexity into a knowledge and a motor dimension we found consistent patterns for both dimensions: a positive correlation with the length of provisioning in carnivorans, and a positive correlation with the pace of development in primates. In terms of motor complexity, this clear finding is in line with our initial prediction that complexmotor patterns need to be practiced over extended periods of time. Species that live in complex motor niches often do not rely exclusively on food requiring complex motor patterns but also forage on less skillintense food items. As one would expect, it has been observed that in these species the different skills ontogenetically develop in the order of their complexity level, as in Japanese monkeys (*Macaca fuscata* [Nakayama et al., 1999; Hanya, 2003]), or in the order of moving from small to large prey in carnivorans and primates (Watt, 1993; Holekamp et al., 1997; Stone, 2006). Furthermore, complex foraging elements seem to be practiced throughout ontogeny (e.g. beach hunting in the bottlenose dolphin, *Tursiops* sp. [Sargeant et al., 2005]).

In terms of knowledge-niche complexity, we found similar correlations for most of the a priori defined cognitively demanding elements (cooperative hunting, diet breadth, extractive foraging and tool use). This finding confirms our initial prediction that acquiring knowledge and understanding requires a long period of learning. In line with our finding, previous studies have shown that all cognitively demanding elements are mastered relatively late in development: tool use in great apes (Lonsdorf, 2006; Meulman and van Schaik, 2013), cooperative hunting in different carnivorans and chimpanzees (Holekamp et al., 1997; Boesch, 2002; Sand et al., 2006) and extractive foraging in various primates (Johnson and Bock, 2004; Gunst et al., 2008; Schuppli et al., 2012).

Knowledge- and motor-niche complexity inevitably overlap since executing one step in the chain of processing steps needed for food acquisition automatically also means being able to coordinate and time all the previous steps needed to get to this step, which has been proposed to explain correlations between brain size measures and tool use (Barton, 2012). Indeed, some of the cognitively demanding elements we used are based on complex, multistep motor patterns. This is especially true for extractive foraging, where it is hard to determine to what extent the observed positive correlation between developmental pace and extractive foraging in primates is based on complex motor patterns that need to be practiced over an extended period of time rather than on cognitive understanding and, therefore, time to learn. This argument predicts a correlation between motor complexity and the knowledge-niche complexity score, which was indeed found in primates. However, when corrected for motor complexity, we still found an independent effect of the pace of development on knowledge-niche complexity. In order to distinguish properly between the motor and knowledge complexity of foraging niches, we will use the relationship of the two dimensions of the foraging- niche with brain size.

Part II - Brain size and foraging-niche complexity

Consistent with our initial prediction, there was no relationship between brain size and the motor dimension of niche complexity in carnivorans. In primates, in contrast, brain size was positively correlated with motor-niche complexity, but after controlling for AFR, this correlation disappeared. Age at first reproduction has been shown to be associated with both brain size (Harvey and Clutton-Brock, 1985; Ross and Jones, 1999; Barrickman et al., 2008) and niche complexity (see results Part I). One interpretation, therefore, is that the correlation between brain size and motor-niche complexity is spurious, because it is, in fact, driven by the duration of development (as in carnivorans, where is driven by the length of provisioning). Alternatively, an extended period of development is indeed the mechanism that allows for the development of a large brain (Barton and Capellini, 2011), which in turn determines motor-niche complexity. Thus, the correlation between motor complexity and brain size in primates could reflect the neural correlates of practice itself or of the sensory motor processes involved in motor skills. At present, we cannot disentangle these possibilities, but the findings imply that complexity in the motor dimension, at least in carnivorans, does not necessarily require cognitive understanding or knowledge but rather training and practice, or, in other words, time. Both life history pathways (extended provisioning and slow development) provide immature animals of both taxa with extensive practice time (see Part I of Discussion).

Also in agreement with our prediction, the analyses in primates provided strong evidence that large brains are associated with a higher complexity in the knowledge dimension of the niche, even after controlling for the effects of the motor-niche. Moreover, in Figure 2.5, which plots knowledge-niche complexity versus relative brain size, all species cluster in the lower-right corner. This shows that, although large-brained species may live in either simple or complex knowledge niches, small-brained species are never found in niches with high knowledge complexity. This finding suggests that living in a foraging-niche with high knowledge complexity is indeed cognitively challenging for a primate. These findings build on work by Barton (2012) and Reader and Laland (2002), who have found that larger brains in primates are associated with enhanced foraging skills and higher frequency of innovation and social learning, usually in the ecological domain. Overall, therefore, it is the cumulative effect of different cognitively challenging elements of a species's niche that underlies the correlation with relative brain size, and thus, cognitive abilities. In fact, the models for the separate elements of the knowledge-niche complexity score do not show strong links with brain size. The effects of brain size disappear as soon as we control for the motor component, except for tool use (see SOM for the different models). Together with the findings from Part I, this implies that neither a diverse diet nor extractive foraging alone is cognitively so challenging that it requires enlarged brain size. However, the combination of all these knowledge elements together does require enhanced cognition in primates.

The coevolution between niche complexity, brain size and developmental slowdown in primates is consistent with the needing-to-learn hypothesis, which states that the age of first reproduction is determined by the number and complexity of skills that have to be learned for adult success (Janson and van Schaik, 1993). However, these findings are also consistent with the idea that larger brains are inevitably connected to extended periods of growth and maturation, due to the developmental costs imposed by growing and maturing a large brain (Barton and Capellini, 2011). The two ideas are related. The slowdown caused by energy tradeoffs creates time to learn more complex skills.

In contrast to primates, brain size has no effect at all on knowledge foraging-niche complexity in carnivorans, neither for the separate a priori defined elements nor for the additive knowledge-niche complexity score. In other words, carnivorans do not need enhanced cognitive abilities to master these elements of their foraging-niche, even though it was found that in carnivorans, diet type is correlated with brain size (Swanson et al., 2012). Together with the fact that most carnivoran species are provisioned as immature animals and the finding that higher knowledge-niche complexity is indeed associated with extended periods of provisioning, this result suggests that, in contrast to primates, successful hunting and foraging in carnivorans is built on intensive practice rather than increased knowledge. Whereas in primates, a slow, conservative development provides not only time to learn but also allows for the development of a large brain and therefore enhanced cognition, carnivorans use a more canalized pathway where provisioning buffers them from the consequences of their own incompetence and so allows them to practice specific skills until they are mastered.

Implications for general mammalian and hominin evolution

We have shown that primates and carnivorans use distinct pathways in order to meet the energetic and time requirements imposed by complex foraging niches: extended periods of provisioning in carnivorans versus a slower overall pace of development in primates. First, this pattern of correlated evolution also implies that only those primate lineages that could somehow afford to develop more slowly and only those carnivoran lineages that could afford longer post-weaning provisioning were able to evolve into a more complex foraging-niche. Thus, each species probably reaches a foraging-niche complexity where the benefits of having this more complex niche (probably especially in terms of starvation avoidance and reduced competition with other species) are balanced by the demographic costs of reduced growth rate (primates) or reproduction (carnivorans).

Our study also showed that, for primates, living in a complex niche is correlated with larger brains and therefore probably requires enhanced cognitive abilities. Again, a scenario of correlated evolution is most plausible: increases in brain size allow species to exploit more complex niches (and therefore qualitatively better resources), which will in the end provide them with the energy needed to support further increases in brain size. The absence of provisioning in the vast majority of all primate species, but the presence of systematic pre- and post-weaning provisioning in many carnivoran species is most likely based on a systematic difference in the feeding biology of the two taxa. Most carnivorans are dependent on food items that are large and difficult to process but energy-rich. Thus, from an energetic perspective, provisioning of food is more effective for them compared to primates, which rely on smaller food items that are generally more easily acquired, albeit not necessarily processed. The observed differences between the two taxa, therefore, seems to be an example of constrained evolution where preexisting life history characteristics predispose species to evolve in certain directions (McKitrick, 1993; Futuyma, 1998).

Across mammals, based on our findings, we predict that opportunities for provisioning or opportunities for low mortality act as limiting factors for the possible evolution of complex niches.We therefore expect that species with high extrinsic mortality (e.g., due to high predation risk) that at the same time rely on resources that cannot be shared will be prevented from evolving into complex niches.

When applied to human hunter-gatherers, our framework might not only explain the general pattern observed across mammals but also the extreme case of the evolution of human life history and intelligence. Human hunter-gatherers occupy by far the most complex motor- and knowledge-niche of all mammals. Thus, hunter-gatherers have a very broad diet composed of food items that require special knowledge to acquire and intensive processing: they rely heavily on extractive foraging, tool use, and cooperative hunting (Kaplan et al., 2000). Accordingly, modern foragers reach adult-level proficiency for the more skill-intensive elements of the diet strikingly late in development and only after years of practice (Kaplan et al., 2000; Gurven et al., 2006).

Obviously, when a lineage shares food and has slow development, evolving into a complex knowledge-niche is more likely. Thus, the most likely explanation for the evolution of a foragingniche complexity far beyond the range of other mammals is that our ancestors, uniquely, combined very slow development and systematic provisioning of immature animals and even adults. With the adoption of systematic hunting, beginning approximately 2.5 million years ago (Dominguez-Rodrigo et al., 2010; Ferraro et al., 2013), our hominin ancestors began to combine a slow primate life history with a carnivoran-like niche. Meat consumption is thought to have provided the necessary energy surplus for the drastic brain size increase and coincides with enhanced technology and social adaptations such as increased levels of cooperation (Milton,1999; Isler and van Schaik, 2012; Ferraro et al., 2013). As big game hunters, early hominins relied on big, energy rich but difficult to process food items which, as in the carnivoran lineage, most likely favored the evolution of prolonged periods of provisioning. This extended provisioning, together with a cooperative breeding system, then provided immature animals with additional time and opportunities to learn ever more complex ecological skills, which allowed the evolution of the unique, technologically driven human niche (Schuppli et al., 2012).

Our study provides support for the view that an ecological challenge, the complexity of the foraging-niche, has shaped the life history and intelligence of the primate lineage. It thus supports the broader hypothesis that environmental factors have played a crucial role in the evolution of life history and intelligence. We did not test social effects on brain size evolution in this study but it is very likely that some of the remaining variance in our data can be explained by social variables, such as group size, as proposed by the social brain hypothesis (Milton, 1988; Dunbar, 1998; Barton, 2012). This general framework is in line with theories suggesting that the coevolution between complex foraging techniques and energetic needs in an increasingly seasonal environment was a crucial element during the evolution of human intelligence (Parker and Gibson, 1977; Byrne, 1997).

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Supplementary Material

Data collection and classification

Data on the different elements of foraging niche complexity were retrieved from various sources, many of them complied in the Animal Diversity Web (Myers et al., 1995).

In primates, for motor-niche complexity and diet breadth we relied on various references given in Table S1. Motor-niche complexity reflects the number of processing steps involved in food acquisition from tearing an item off its substrate until ingestion and is not to be confused with fine hand manipulation. As an example, the gelada baboon (*Theropithecus gelada*) was classified as level 1 of motor-niche complexity as it mainly relies on grazing-like processing, namely pulling grass and tubers out of the soil and bringing them directly to the mouth without any further intermediate processing steps. This is in contrast to most frugivorous species, which rely on additional processing steps such as peeling or core removal, which are thus classified as level 2.
For extractive foraging we followed the compilation of Jaeggi and van Schaik (2011) who used a three point scale which we, in order to make it consistent with the carnivoran data, dichotomized into a binary variable (absent/ present), whereby 1 and 2 by Jaeggi and van Schaik (2011) were coded as present. Species in our data set that were missing in the Jaeggi and van Schaik (2011) compilation were classified according to their definition which is originally based on Gibson (1986), defining extractive foraging as ”feeding on foods that must first be removed from other matrices in which they are embedded or encased” (Gibson, 1986, p 96). Extractive foraging was counted as present only in cases where the extracted food made up a non-incidental and considerable part in a species' diet. Species relying on tubers and roots were classified as extractive foragers in cases where these are actively excavated, whereas pulling out plants with their roots such as grasses or small scrubs was not counted as such.
For tool use we based our classification on Bentley-Condit and Smith (2010), whereby species with tool use in captivity only, in a non-food context only or for which observations were limited to a single example were coded as non-tool users. For species that were not available in Bentley-Condit and Smith (2010), we found no evidence for regular tool use in the literature and we therefore classified them as non-tool-users.

In carnivorans, the classifications into motor-niche complexity, extractive foraging and diet breadth were also based on various references given in Table S1. At the lowest level of motor-niche complexity (level 1) we classified the giant panda (*Ailuropoda melanoleuca*) and the aardwolf (*Proteles cristata*), as ripping off leaves or licking termites off surfaces comprises a single simple processing step. Species that feed predominantly on insects and fruits, such as the European badger (*Meles meles*) or the sloth bear (Melursus ursinus) were classified as level 2 since there is a limited amount of processing involved. All carnivorans hunting for mobile prey (excluding insects) were assigned the highest complexity level (level 3) since this prey needs to be pursued, caught, killed and eventually dissembled before ingestion. We classified carnivoran species as extractive foragers if they cracked bones to access marrow (e.g., spotted hyenas, *Crocuta crocuta*) or broke open hard shells (including eggs) or prey with exoskeletons (e.g., sea otter, *Enhydra lutris*).
For tool use we relied on the classification of Bentley-Condit and Smith (2010), following the same rules as described for primates (see above) and for cooperative hunting on Smith et al. (2012). In carnivorans, for species that were missing in these compilations, literature research showed no evidence for the presence of tool use and they were therefore classified as non-tool users.

In total, data on niche complexity could be retrieved for 65 species of fissiped Carnivora and 78 species of Primates. For these species, morphological and life history data (endocranial volume and body mass of adult females, age at first reproduction and length of provisioning) were taken from published compilations (Isler and van Schaik, 2009, 2012; van Woerden et al., 2014) and complemented by unpublished data compiled from the literature by K. Isler, S. M. Graber and S. A. Heldstab. Additional endocranial volumes (ECV) of adult female museum specimens were measured by S. M. Graber and S. A. Heldstab using glass beads.

Table S1. Data on motor-niche complexity, cooperative hunting, diet breadth, extractive foraging, tool use, knowledge-niche complexity score as well as life history parameters and brain size used for the analyses for the 65 carnivoran and the 78 primate species.

Species	Motor complexity	Cooperative hunting	Diet	Extractive foraging	Tool use	Knowledge score	AFR (d)	Food dependence (d)	Body mass (g)	Brain size (ml)	References foraging niche elements
Carnivorans											
Acinonyx jubatus	3	0	1	0	0	1	865.4	549	43000	111	Caro 1994
Ailuropoda melanoleuca	1	0	0	0	0	0	2278.5	457.5	87500	236	Wei et al. 1999
Alopex lagopus	3	0	1	0	0	1	355.7	165.5	3415	41	Hersteinsson and Macdonald 1996
Canis latrans	3	1	1	0	0	2	374.8	225	9760	89.1	Kitchen et al. 1999
Canis lupus	3	1	1	0	0	2	731.2	365	31100	123.6	Hovens and Tungalaktuja 2005
Canis mesomelas	3	1	1	0	0	2	379.3	270	6600	53.6	Bothma et al. 1984
Caracal caracal	3	0	1	0	0	1	499.6	288.8	9680	47.7	Sunquist and Sunquist 2002
Chrysocyon brachyurus	3	0	1	1	0	2	731.8	213.5	23250	110.3	Rodrigues et al. 2007
Conepatus leuconotus	2	0	1	1	0	2	365.4	152	2010	17.4	Wilson et al. 2009
Crocuta crocuta	3	1	1	1	0	3	1114.4	914.5	57800	154.6	Di Silvestre et al. 2000
Cryptoprocta ferox	3	0	1	0	0	1	1323.4	365	6775	31	Nowak 1999
Cynictis penicillata	2	0	1	0	0	1	724.4	119	571	8.5	Skinner and Smithers 1990
Eira barbara	3	0	1	0	0	1	733.7	200	3500	40.8	Bisbal 1986
Enhydra lutris	2	0	0	1	1	2	1462	210	23600	117.9	Cohn 1998
Felis chaus	3	0	1	1	0	2	612.4	274.5	5050	37.9	Mukherjee et al. 2004
Felis nigripes	3	0	0	0	0	0	613.4	106.75	1100	20.5	Nowak 1999
Felis silvestris	3	0	1	1	0	2	364.7	167.75	4130	25.4	Nowak 1999
Genetta genetta	3	0	1	0	0	1	727.9	126	1820	12.8	Rosalino and Santos-Reis 2002
Gulo gulo	3	0	1	0	0	1	891.6	182.4	10600	71.7	Lofroth et al. 2007
Helogale parvula	3	0	1	1	0	2	505.7	153	267	4.2	Wilson et al. 2009
Herpestes ichneumon	3	0	1	1	0	2	610.7	365	3265	19.6	Wilson et al. 2009
Hyaena hyaena	2	0	1	1	0	2	1003.2	365	36300	103.1	Wilson et al. 2009
Ictonyx striatus	3	0	1	0	0	1	365.1	126	713	8	Wilson et al. 2009
Leopardus pardalis	3	0	1	0	0	1	993.6	213.5	10750	63.2	Wilson et al. 2009
Leptailurus serval	3	0	1	0	0	1	895.3	200	10400	54	Bowland and Perrin 1993
Lontra canadensis	3	0	1	1	0	2	792	182.4	7850	52.3	Wilson et al. 2009
Lutra lutra	3	0	1	1	0	2	974.6	238	6750	36.6	Heggberget and Moseid 1994
Lycaon pictus	3	1	1	0	0	2	729.5	391	22050	133	Wilson et al. 2009
Lynx lynx	3	0	1	0	0	1	739.6	304	17200	88.6	Schmidt et al. 2009
Lynx rufus	3	0	1	0	0	1	731.6	243.2	7500	61.8	Neale and Sacks 2001
Martes pennanti	3	0	1	1	0	2	577.9	137.25	2250	30.7	Slauson et al. 2011
Meles meles	2	0	1	1	0	2	574.4	183	10100	44	Sidorovich et al. 2011

to be continued

Species	Motor complexity	Cooperative hunting	Diet	Extractive foraging	Tool use	Knowledge score	AFR (d)	Food dependence (d)	Body mass (g)	Brain size (ml)	References foraging niche elements
Melursus ursinus	2	0	1	1	0	2	1215.8	547.5	99750	272.5	Joshi et al. 1997
Mephitis mephitis	2	0	1	1	0	2	376.2	84	1790	10.4	Wilson et al. 2009
Mustela frenata	3	0	1	1	0	2	189.1	84	165	4	Wilson et al. 2009
Mustela nivalis	3	0	1	1	0	2	156.1	73.5	60	2.3	Tapper 1979
Mustela putorius	3	0	1	0	0	1	353.1	91.5	689	6	Wilson et al. 2009
Mustela sibirica	3	0	1	0	0	1	365.2	91.5	395	5.7	Nowak 1999
Nasua narica	2	0	1	1	0	2	790.5	152	3700	39.4	Wilson et al. 2009
Neofelis nebulosa	3	0	0	0	0	0	881.9	304	19490	72	Wilson et al. 2009
Nyctereutes procyonoides	3	0	1	1	0	2	364.7	121	4020	28.5	Sidorovich et al. 2008
Otocyon megalotis	2	0	1	1	0	2	367	197.6	4075	30.3	Klare et al. 2011
Panthera leo	3	1	1	0	0	2	1418.8	775.2	124000	211.3	Wilson et al. 2009
Panthera onca	3	0	1	0	0	1	1012.1	501.6	77700	167.7	Wilson et al. 2009
Panthera pardus	3	0	1	0	0	1	1033.6	365	31500	129.8	Hayward et al. 2006
Panthera tigris	3	0	0	0	0	0	1346.9	577.6	130000	258.1	Wilson et al. 2009
Parahyaena brunnea	2	0	1	1	0	2	1157.3	427	39300	118.1	Maude 2005
Potos flavus	2	0	1	0	0	1	928.5	121.6	2800	27.1	Kays 1999
Procyon lotor	2	0	1	1	0	2	603.4	140	5620	41.9	Wilson et al. 2009
Proteles cristatus	1	0	0	0	0	0	747.5	122	8820	41.5	Matsebula et al. 2009
Pteronura brasiliensis	3	0	0	0	0	0	798	288.8	24000	104.5	Carter and Rosas 1997
Puma concolor	3	0	1	0	0	1	1006.6	304	42700	119.6	Wilson et al. 2009
Suricata suricatta	2	0	1	0	0	1	738.4	90	725.5	10.3	Doolan and Macdonald 1996
Uncia uncia	3	0	1	0	0	1	1374.9	547.2	32500	111.2	Wilson et al. 2009
Urocyon cinereoargenteus	3	0	1	1	0	2	361.4	122	4010	35.8	Neale and Sacks 2001
Urocyon littoralis	2	0	1	0	0	1	365.2	152	1896	29.7	Garcelon et al. 1999
Ursus americanus	2	0	1	1	0	2	1734.5	503.25	84700	221.7	Beeman and Pelton 1980
Ursus arctos	3	0	1	1	0	2	1928.3	645	182000	340.8	Munro et al. 2006
Ursus maritimus	3	0	1	1	1	3	2128.9	881.6	225000	429.9	Stirling and McEwan 1975
Viverricula indica	3	0	1	0	0	1	371.4	127.5	2660	17.4	Chuang and Lee 1993
Vormela peregusna	3	0	1	0	0	1	365	64.5	447.5	5.8	Ben-David et al. 1991
Vulpes chama	3	0	1	0	0	1	325.7	152	2955	35.8	Nel 1984
Vulpes rueppellii	3	0	1	1	0	2	356.9	121.6	1575	25.3	Wilson et al. 2009
Vulpes velox	3	0	1	0	0	1	361.2	152	2345	31.3	Andersen et al. 2003
Vulpes vulpes	3	0	1	0	0	1	356.3	225.5	4210	42.3	Johnson 1970

to be continued

Species	Motor complexity	Cooperative hunting	Diet	Extractive foraging	Tool use	Knowledge score	AFR (d)	Food dependence (d)	Body mass (g)	Brain size (ml)	References foraging niche elements
Primates											
Alouatta caraya	2	0	0	1	0	1	1350.5	325	4240	47.5	Di Fiore and Campbell 2007
Alouatta palliata	2	0	1	0	0	1	1460	365	5350	49.4	Di Fiore and Campbell 2007
Alouatta seniculus	2	0	1	0	0	1	1898	380	5210	53.5	Di Fiore and Campbell 2007
Arctocebus aureus	2	0	0	0	0	0	438	115	200	5.7	Charles-Dominique 1974
Arctocebus calabarensis	2	0	0	0	0	0	401.5	115	309	6.8	Charles-Dominique 1974
Ateles paniscus	2	0	1	0	0	1	1825	1094	8070	107	Di Fiore and Campbell 2007
Avahi laniger	1	0	0	0	0	0	949	153	1207	9.2	Harcourt 1991
Cacajao calvus	2	0	1	0	0	1	1314	638	2880	71.7	Norconk 2007
Callimico goeldii	3	0	1	0	0	1	547.5	67	483.5	11	Porter 2001
Callithrix jacchus	3	0	1	1	0	2	620.5	182.5	320	7.9	Digby et al. 2007
Cebus albifrons	3	0	1	1	1	3	1460	264	2290	63.8	Defler 1979
Cebus apella	3	0	1	1	1	3	2445.5	265	2500.7	62	Mittermeier and van Roosmalen 1981
Cebus capucinus	3	0	1	1	1	3	2190	517	2436.5	66.8	Rose 1994
Cebus nigritus	3	0	1	1	0	2	2555	450	2215	61.9	Izar 2004
Cebus olivaceus	3	0	1	1	1	3	2190	547	2633.3	67.7	Miller 1992
Cercocebus atys	2	0	1	0	0	1	1715.5	126	6200	83.8	Rutte 1998
Cercopithecus ascanius	3	0	1	1	0	2	1825	577.5	2901	54.7	Enstam and Isbell 2007
Cercopithecus campbelli	2	0	1	0	0	1	1277.5	365	2544.4	53	Enstam and Isbell 2007
Cercopithecus cephus	2	0	1	0	0	1	1825	365	2880	58.6	Enstam and Isbell 2007
Cercopithecus diana	2	0	1	0	0	1	1971	365	3900	55.3	Enstam and Isbell 2007
Cercopithecus mitis	3	0	1	1	0	2	2372.5	316	4628	63.6	Enstam and Isbell 2007
Cercopithecus neglectus	2	0	1	0	0	1	1825	365	4130	58.8	Enstam and Isbell 2007
Chlorocebus pygerythrus	2	0	1	0	0	1	1861.5	259	3575.8	57.8	Enstam and Isbell 2007
Chlorocebus sabaeus	2	0	1	0	0	1	1460	165	3700	57.3	Galat and Galat-Luong 1977
Colobus angolensis	2	0	1	0	0	1	2190	365	7570	69.8	Fashing 2007a
Colobus guereza	1	0	1	0	0	1	1752	334	7505.6	70.1	Fashing 2007b
Colobus polykomos	1	0	0	0	0	0	2007.5	365	6708.9	68.5	DaSilva 1989
Daubentonia madagascariensis	3	0	1	1	0	2	1277.5	205	2555	43.2	Sterling 1994
Eulemur fulvus	2	0	1	0	0	1	985.5	183	2291.7	23.9	Rasmussen 1999
Eulemur macaco	2	0	0	0	0	0	803	135	2350	21.9	Birkinshaw 2001
Eulemur mongoz	3	0	1	1	0	2	912.5	152	1212.4	17.3	Rasmussen 1999
Galago moholi	2	0	0	0	0	0	438	84	148.4	3.6	Harcourt 1986
Gorilla gorilla	2	0	0	1	0	1	3723	1680	71500	418.4	Remis et al. 2001
Hapalemur griseus	2	0	0	0	0	0	1204.5	121	709	13.3	Overdorff et al. 1997

to be continued

Species	Motor complexity	Cooperative hunting	Diet	Extractive foraging	Tool use	Knowledge score	AFR (d)	Food dependence (d)	Body mass (g)	Brain size (ml)	References foraging niche elements
Lemur catta	2	0	1	0	0	1	1168	179	2210	21.3	Kelley 2011
Leontopithecus rosalia	3	0	0	1	0	1	1314	91	609	12.4	Digby et al. 2006; Miller and Dietz 2006
Lepilemur mustelinus	2	0	0	0	0	0	584	75	804	8	Thalmann 2001
Lophocebus albigena	2	0	1	0	0	1	2190	213	6010	87.5	Pouslsen et al. 2001
Loris lydekkerianus	2	0	0	0	0	0	547.5	145	273	6.1	Nekaris and Rasmussen 2003
Loris tardigradus	2	0	0	0	0	0	511	135	192.5	5.3	Nekaris and Rasmussen 2003
Macaca fascicularis	3	0	1	1	1	3	1898	231	3517.9	58.8	Thierry 2007
Macaca fuscata	3	0	1	1	1	3	2226.5	195	8030	93.4	Thierry 2007
Macaca mulatta	3	0	0	1	0	1	1825	192	5670.5	81.4	Goldstein and Richard 1989
Macaca nemestrina	3	0	1	1	0	2	1423.5	237	6539.2	94.7	Caldecott 1986
Macaca nigra	3	0	0	1	0	1	1971	214	5470	77.5	O'Brien 1997
Macaca radiata	3	0	1	1	0	2	1642.5	365	3855.7	68.1	Krishnamani 1994
Macaca silenus	3	0	1	1	1	3	1788.5	456	6100	75.3	Kumar 1987
Macaca sylvanus	3	0	1	1	0	2	1752	213	9625	89.7	Thierry 2007
Mandrillus sphinx	2	0	1	0	0	1	1825	307	12800	131.3	Hoshino 1985
Microcebus murinus	3	0	1	0	0	1	657	49	65.1	1.5	Génin 2001
Nasalis larvatus	2	0	1	0	0	1	1825	456	9729.6	81.9	Kirkpatrick 2007
Nycticebus coucang	2	0	1	0	0	1	547.5	183.2	652.5	9.7	Wiens et al. 2006
Otolemur crassicaudatus	2	0	1	0	0	1	657	134	1150	11.4	Crompton 1984
Otolemur garnettii	2	0	0	0	0	0	584	140	1188	10.5	Harcourt and Nash 1986
Pan paniscus	3	0	1	1	0	2	5183	1642.5	33200	315	Stumpf 2007
Pan troglodytes	3	1	1	1	1	4	4854.5	1643	40366.7	344.4	Stumpf 2007
Papio anubis	3	0	1	1	1	3	2518.5	420	13300	149.9	Hill and Dunbar 2002
Papio cynocephalus	3	0	1	1	0	2	2190	456	12000	144.3	Hill and Dunbar 2002
Papio hamadryas	3	0	1	1	0	2	2226.5	480	10300	133.5	Hill and Dunbar 2002
Papio ursinus	3	0	1	1	1	3	2482	502	14800	159.3	Hill and Dunbar 2002
Pithecia monachus	2	0	0	0	0	0	1095	365	2292.7	34.7	Soini 1986
Pithecia pithecia	3	0	1	1	0	2	1460	150	1639	30.3	Norconk 2007
Pongo abelii	3	0	1	1	1	3	5621	2555	41148	334.1	Morrogh-Bernard et al. 2009
Pongo pygmaeus	3	0	1	1	1	3	5730.5	2008	36947.6	326	Morrogh-Bernard et al. 2009
Presbytis thomasi	2	0	1	0	0	1	1971	579	6350.4	62.4	Sterck 1995
Propithecus diadema	2	0	1	0	0	1	1934.5	183	6130	37	Irwin 2008
Propithecus edwardsi	2	0	0	0	0	0	1825	365	5790	36.1	Arrigo-Nelson 2006

to be continued

Species	Motor complexity	Cooperative hunting	Diet	Extractive foraging	Tool use	Knowledge score	AFR (d)	Food dependence (d)	Body mass (g)	Brain size (ml)	References foraging niche elements
Pygathrix nemaeus	1	0	0	0	0	0	1752	330	8440	91.6	Lippold 1998
Saguinus fuscicollis	3	0	1	1	0	2	985.5	91	350.5	8	Garber 1993
Saguinus geoffroyi	2	0	1	0	0	1	730	75	516.9	9.8	Garber 1980
Saguinus midas	2	0	1	0	0	1	730	70	535	9.5	Mittermeier and van Roosmalen 1981
Saguinus mystax	2	0	0	0	0	0	474.5	90	584	9.9	Peres 1993
Saimiri sciureus	3	0	1	1	0	2	1423.5	330	742	22.7	Lima and Ferrari 2003
Tarsius bancanus	3	0	0	0	0	0	584	76	110.7	3.1	Gursky 2007
Theropithecus gelada	1	0	0	0	0	0	1460	450	11700	120.2	Hunter 2001
Trachypithecus obscurus	2	0	1	0	0	1	1642.5	365	6764.8	57.2	Kirkpatrick 2007
Trachypithecus vetulus	2	0	1	0	0	1	1569.5	228	5103	57.8	Kirkpatrick 2007
Varecia variegata	2	0	1	0	0	1	839.5	135	3575	29.2	Morland 1991

Additional Results

In order to get a more detailed picture, we analyzed the correlations of the two life history factors and brain size with the different knowledge-niche elements separately. Also, we additionally controlled for possibly confounding variables to ascertain the robustness of all our results.

Life history pathways and foraging-niche complexity

When looking at the effects of the two life-history parameters on the different knowledge-niche elements separately, we found that in primates the age at first reproduction was significantly positively correlated with diet breadth, extractive foraging and tool use. Also, chimpanzees as the only cooperatively hunting primate species in our data set have a relatively late age at first reproduction (Table S2a; Fig. S1).

In carnivorans, we found a significant positive correlation between the length of provisioning and diet breadth, and a trend for a positive correlation between the length of provisioning and cooperative hunting. For extractive foraging, no effect was apparent, whereas for tool use, sample size was too small for statistical testing (Table S2b; Fig. S2).

Since we found a positive correlation between knowledge-niche complexity and motor-niche complexity in primates (but not in carnivorans), we added motor-niche complexity as a factor in our regression models for primates, in order to control for any possible confounding effects. However, this did not change the direction of the effect or the significance level of the results (Table S2a).

Table S2.Relation between life history and knowledge-niche elements as well as controlling for possible confounding effect of motor-niche complexity. Phylogenetic least-square (PGLS) and phylogenetic logistic (PLR) multiple regression models with the knowledge-niche elements (diet breadth, extractive foraging and tool use) and the additive knowledge-niche complexity score as response variables and body mass, age at first reproduction (AFR), length of provisioning and motor-niche complexity as predictor variables for the 78 primate species (a). Phylogenetic least-square and phylogenetic logistic multiple regression models with the knowledge-niche elements (diet breadth, extractive foraging and cooperative hunting) as response variables and body mass, age at first reproduction and length of provisioning as predictor variables for the 65 carnivoran species (b). Statistical significance ($p<0.05$) is indicated by bold font.

a) **Primates N=78**

dependent variable	method	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
diet breadth	PGLS	0.15	$\lambda = 0.21$	log body	-0.318	0.440	0.472
				log AFR	3.394	1.090	**0.003**
				log provisioning	-0.819	0.671	0.226
		0.19	$\lambda = 0.29$	log body	-0.068	0.441	0.878
				motor-niche complexity	0.571	0.228	**0.014**
				log AFR	1.619	1.097	0.144
extractive foraging	PLR	-	$\alpha = 0.07$	log body	-1.166	0.497	**0.019**
				log AFR	11.065	3.089	**0.000**
				log provisioning	-0.185	1.468	0.900
		-	$\alpha = 0.01$	log body	1.535	0.905	0.090
				motor-niche complexity	10.190	3.862	**0.008**
				log AFR	6.804	6.453	0.292
tool use	PLR	-	$\alpha = 0.01$	log body	-0.596	0.482	0.216
				log AFR	11.693	3.666	**0.001**
				log provisioning	-0.623	1.228	0.612
		-	$\alpha = 0.0002$	log body	0.031	0.155	0.842
				motor-niche complexity	0.768	0.264	0.004
				log AFR	2.184	1.125	0.052
knowledge-niche compl.	PGLS	0.73	$\lambda = 0.00$	log body	0.229	0.222	0.305
				motor-niche complexity	1.109	0.117	**<0.001**
				Log AFR	1.142	0.541	**0.038**

b) **Carnivorans N=65**

dependent variable	method	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
diet breadth	PGLS	0.12	$\lambda = 0.07$	log body	-0.137	0.114	0.233
				log AFR	-0.407	0.251	0.110
				log provisioning	0.587	0.273	**0.035**
extractive foraging	PLR	-	$\alpha = 0.07$	log body	0.006	0.361	0.987
				log AFR	-0.535	0.831	0.520
				log provisioning	0.273	0.794	0.732
cooperative hunting	PLR	-	$\alpha = 0.01$	log body	3.310	2.620	0.207
				log AFR	-15.492	7.779	**0.046**
				log provisioning	8.899	4.986	0.074

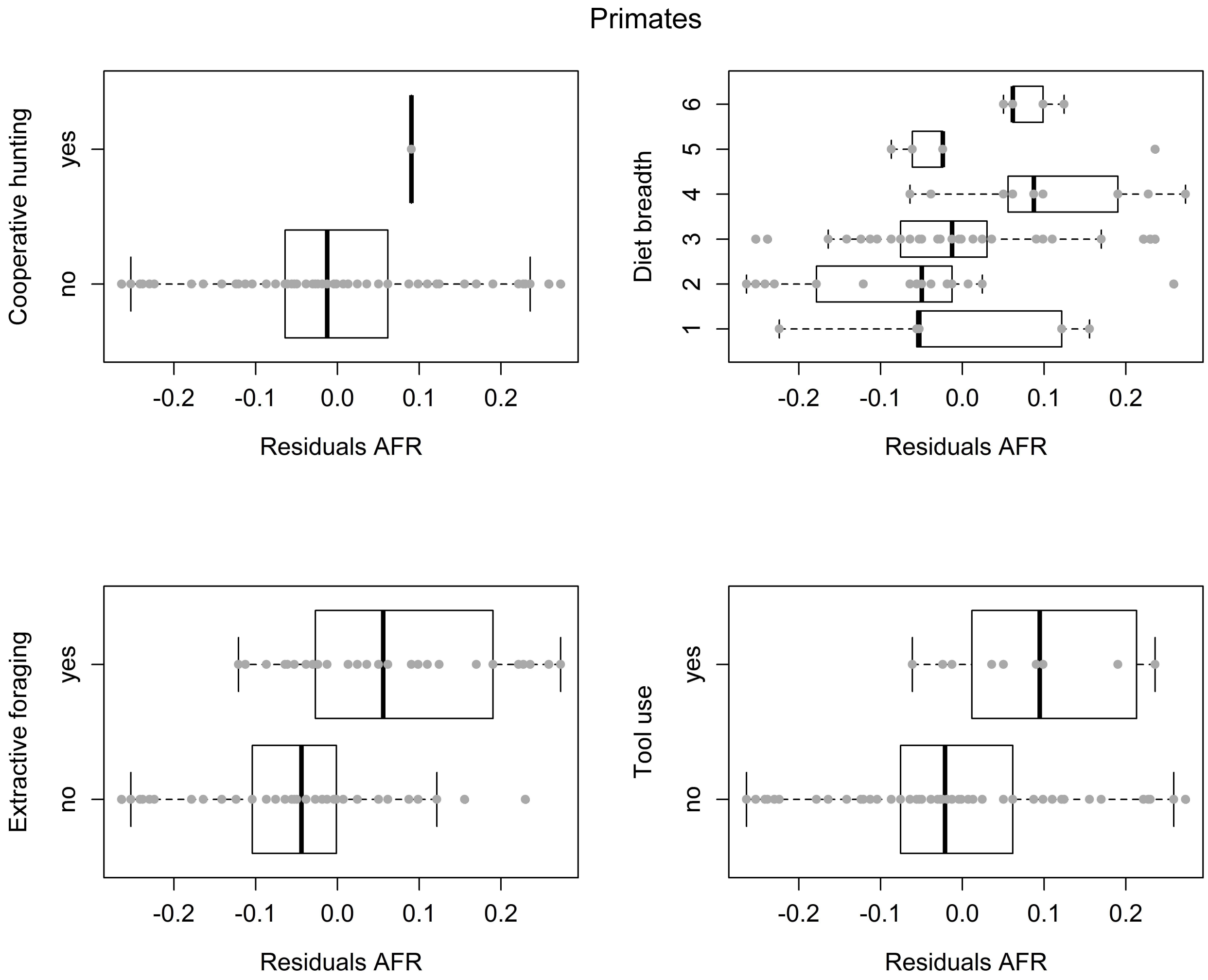

Figure S1. Relationships between pace of development (age at first reproduction corrected for body mass) and the different elements of knowledge-niche complexity in primates.

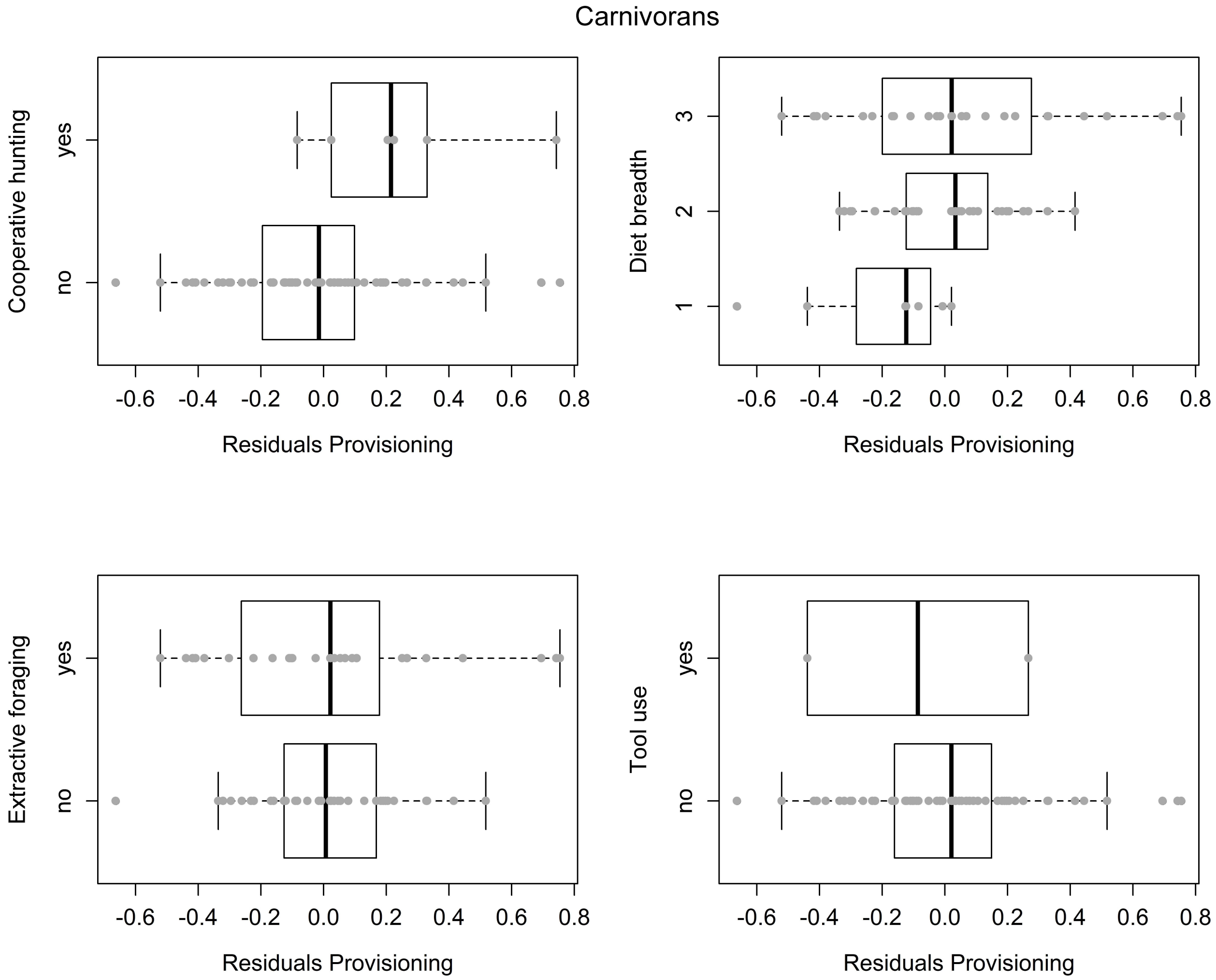

Figure S2. Relationships between length of provisioning (corrected for body mass) and the different elements of knowledge-niche complexity in carnivorans.

Brain size and foraging-niche complexity

In primates, age of fist reproduction (AFR) has been shown to be correlated with both brain size (Harvey and Clutton-Brock, 1995; Ross and Jones, 1999; Barrickman et al., 2008) and motor-niche complexity (see results Part I). We therefore repeated our analysis on the effects of brain size on motor-niche complexity controlling for AFR by adding it as a factor to the regression model. The effect of brain size on motor-niche complexity then disappeared (Table S3a). This suggests that the correlation between brain size and motor-niche complexity in primates is spurious and driven by the duration of development. Alternatively, this result can be interpreted as evidence that an extended period of development is indeed the mechanism that allows for the development of a large brains (Barton and Capellini, 2011). In carnivorans, adding the length of provisioning as an additional factor did not change the results (Table S3b).

When looking at the effects of brain size on the different knowledge-niche elements separately, we found that in primates, diet breadth, extractive foraging and tool use were significantly correlated with brain size. In line with our prediction, as the only cooperatively hunting primates, chimpanzees are highly enzephalized (Table S4a). Controlling for possible confounding effects of motor-niche complexity (since motor- and knowledge-niche complexity have been shown to be correlated in primates) did not affect the correlation between brain size and the overall knowledge, but of the individual knowledge elements only tool use remained significantly correlated with brain size (Table S4a). Adding AFR as an additional factor to the regression model (since it has been shown to be correlated with both brain size (Harvey and Clutton-Brock, 1995; Ross and Jones, 1999; Barrickman et al., 2008) and knowledge-niche complexity (see results Part I) also did not affect the correlation between the additive knowledge-niche complexity score and brain size. All correlations between the individual knowledge elements and brain size remained significant with the exception of diet breadth (Table S4a, Fig. S3).

In carnivorans, in line with the absence of a correlation between the overall knowledge-niche complexity score and brain size, none of the knowledge-niche elements was correlated with brain size either (Table S4b, Fig. S4). Adding the length of provisioning as an additional factor to the model (since it has been shown to be correlated with knowledge-niche complexity in carnivorans) mostly did not change the results. Only in the case of cooperative hunting did a significant positive correlation with brain size emerge. (Table S4b).

Table S3. Relation between brain size and motor-niche complexity - controlled for age at first reproduction or length of provisioning. Phylogenetic least-square (PGLS) multiple regression models with motor-niche complexity as response variable and body mass, age at first reproduction (AFR) and brain size as predictor variables for the 78 primate species (a). Phylogenetic least-square multiple regression models with motor-niche complexity as response variable and body mass, length of provisioning and brain size as predictor variables for the 65 carnivoran species (b). Statistical significance ($p<0.05$) is indicated by bold font.

a) **Primates N=78**

dependent variable	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
motor-niche complexity	0.22	$\lambda = 0.83$	log body	-0.523	0.229	**0.025**
			log AFR	0.897	0.246	**<0.001**
			log brain	0.287	0.331	0.389

b) **Carnivorans N=65**

dependent variable	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
motor-niche complexity	0.15	$\lambda = 0.80$	log body	-0.083	0.164	0.616
			log provisioning	0.571	0.174	**0.002**
			log brain	-0.164	0.250	0.515

Table S4. Relation between brain size and knowledge-niche elements - controlled for age at first reproduction, length of provisioning and the possibly confounding effect of motor complexity. Phylogenetic least-square (PGLS) and phylogenetic logistic (PLR) multiple regression models with the knowledge-niche elements (diet breadth, extractive foraging and tool use) and additive knowledge-niche complexity score as response variables and body mass, age at first reproduction (AFR), motor-niche complexity and brain size as predictor variables for the 78 primate species (a). Phylogenetic least-square and phylogenetic logistic multiple regression models with the knowledge-niche elements (diet breadth, extractive foraging and cooperative hunting) and additive knowledge-niche complexity score as response variables and body mass, length of provisioning, and brain size as predictor variables for the 65 carnivoran species (b). Statistical significance ($p<0.05$) is indicated by bold font.

a) **Primates N=78**

dependent variable	method	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
diet breadth	PGLS	0.24	$\lambda = 0.00$	log body	-0.659	0.324	**0.045**
				log brain	1.213	0.391	**0.003**
		0.27	$\lambda = 0.00$	log body	-0.621	0.319	0.055
				log AFR	0.915	0.486	0.064
				log brain	0.744	0.458	0.108
		0.30	$\lambda = 0.00$	log body	-0.239	0.355	0.503
				motor-niche complexity	0.559	0.224	**0.015**
				log brain	0.683	0.433	0.119
extractive foraging	PLR	-	$\alpha = 0.06$	log body	-3.264	1.106	**0.003**
				log brain	4.934	1.416	**<0.001**
		-	$\alpha = 0.07$	log body	-3.184	1.100	**0.004**
				log AFR	3.343	1.375	**0.015**
				log brain	3.275	1.418	**0.021**
		-	$\alpha = 0.01$	log body	2.052	2.217	0.355
				motor-niche complexity	9.817	3.149	**0.002**
				log brain	0.278	2.508	0.912
tool use	PLR	-	$\alpha = 0.61$	log body	-3.600	1.432	**0.012**
				log brain	6.092	2.177	**0.005**
		-	$\alpha = 0.02$	log body	-2.727	1.140	**0.017**
				log AFR	2.048	1.360	0.132
				log brain	3.767	1.586	**0.018**
		-	$\alpha = 0.0009$	log body	-1.601	0.724	**0.027**
				motor-niche complexity	1.324	0.638	**0.038**
				log brain	2.873	1.019	**0.005**
knowledge-niche compl.	PGLS	0.48	$\lambda = 0.00$	log body	-2.051	0.512	**<0.001**
				log AFR	2.429	0.788	**0.003**
				log brain	2.282	0.753	**0.003**
		0.74	$\lambda = 0.00$	log body	-0.394	0.403	0.332
				motor-niche complexity	1.100	0.112	**<0.0001**
				log brain	1.318	0.493	**0.009**

to be continued

b) **Carnivorans N=65**

dependent variable	method	R^2	phylogenetic signal	predictor variables	estimate	std. error	p-value
diet breadth	PGLS	0.03	$\lambda = 0.19$	log body	0.107	0.238	0.654
				log brain	-0.257	0.362	0.480
		0.10	$\lambda = 0.27$	log body	-0.033	0.246	0.894
				log provsioning	0.599	0.273	**0.032**
				log brain	-0.332	0.356	0.355
extractive foraging	PLR	-	$\alpha = 0.098$	log body	0.695	0.723	0.337
				log brain	-1.118	1.101	0.310
		-	$\alpha = 0.07$	log body	0.925	0.776	0.233
				log provisioning	-0.166	0.819	0.839
				log brain	-1.397	1.117	0.211
cooperative hunting	PLR	-	$\alpha = 0.09$	log body	0.142	1.520	0.926
				log brain	0.549	2.396	0.819
		-	$\alpha = 0.01$	log body	-7.380	3.249	**0.023**
				log provisioning	7.673	3.523	**0.029**
				log brain	9.310	4.202	**0.027**
knowledge-niche complexity	PGLS	0.13	$\lambda = 0.29$	log body	0.000	0.260	0.999
				log provisioning	0.802	0.287	**0.007**
				log brain	-0.308	0.377	0.417

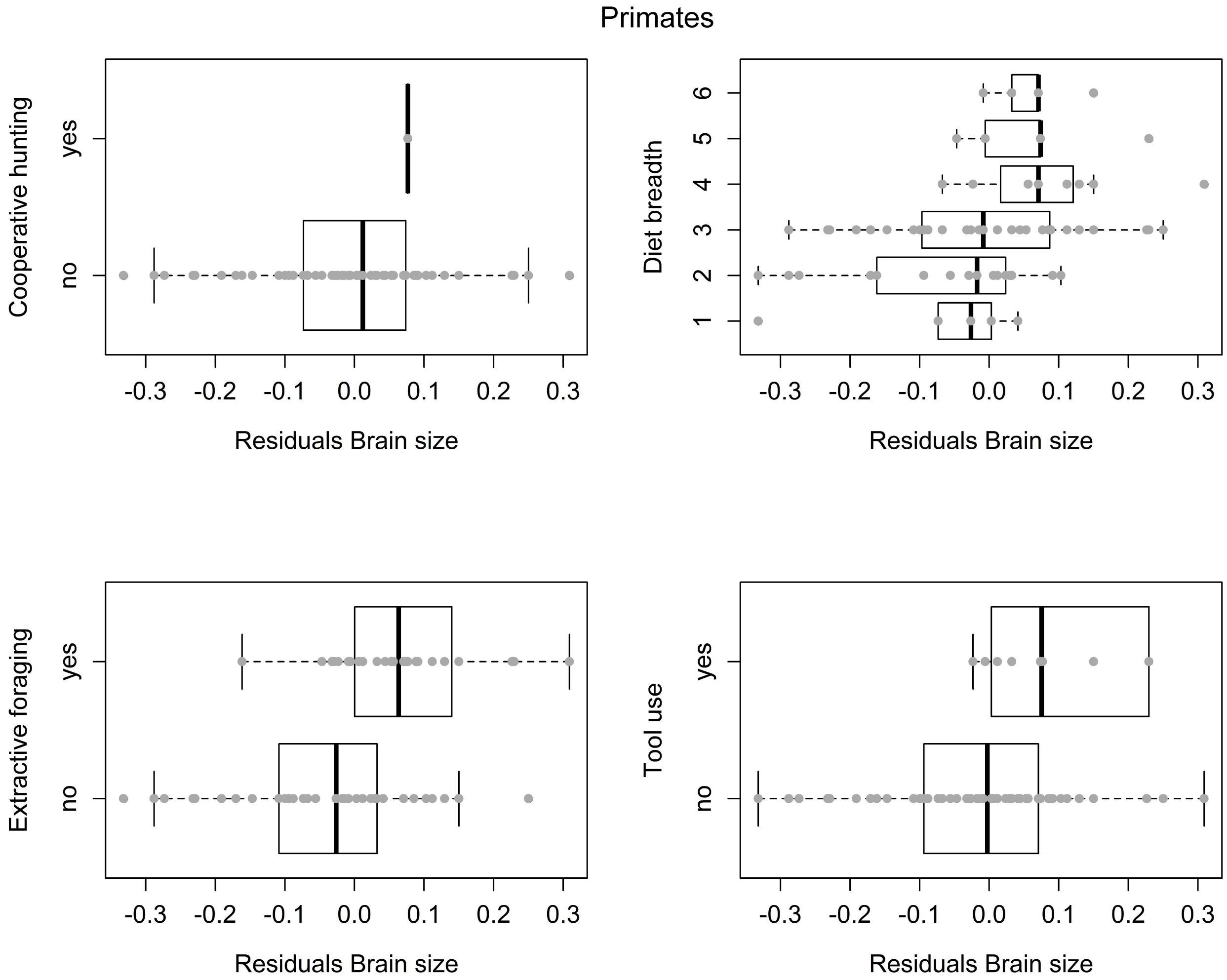

Figure S3. Relationships between relative brain size (corrected for body mass) and the different elements of knowledge-niche complexity in primates.

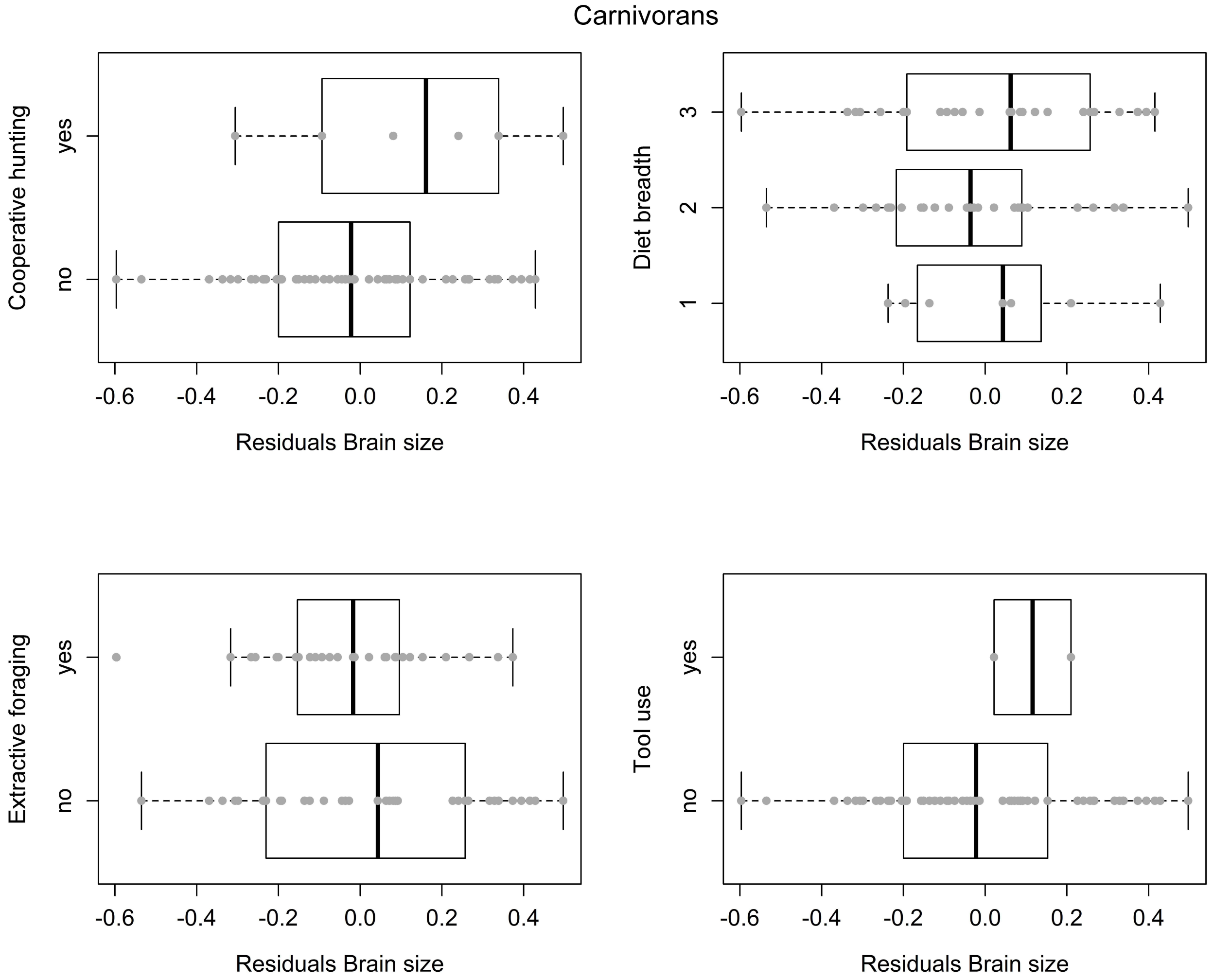

Figure S4. Relationships between relative brain size (corrected for body mass) and the different elements of knowledge-niche complexity in carnivorans.

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Chapter 3

Extended opportunities for skill learning enable the evolution of intelligence - a comparative study in birds

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Abstract

The cultural intelligence hypothesis proposes that extended opportunities for social learning ultimately favor the evolution of intelligence, and thus increased brain size. To date, no study has tested its key prediction: that increased opportunities for socially mediated learning during development are associated with greater individual learning ability, and thus larger relative brain size. We systematically tested this prediction using phylogenetic comparative methods across a large sample of bird species (N = 634). As predicted, we find that both a longer period of post-fledging parent-offspring association and a larger number of role models were associated with a higher degree of encephalization. Our findings suggest that the high levels of cooperation in long-term monogamous pair bonds imply increased social tolerance by parents, allowing for more learning opportunities by the offspring. These conditions ultimately enable the evolution of intelligence. Because this pattern was not found for non-passerine orders, a fundamental difference may exist in the need for skill learning between the two main avian lineages, linked to vulnerability to starvation. This confirmation of the cultural intelligence hypothesis emphasizes the importance of opportunities for learning during development in the evolution of cognition.

Introduction

In many birds and mammals, feeding skills are not simply innate or developmentally canalized, but are instead acquired during development through learning and practice. Thus, individuals gradually increase their food-capturing abilities and expand their diet breadth as they develop (reviewed by Wunderle 1991; Marchetti and Price 1989), and only start reproducing once adult-level skill competence is reached (Schuppli et al. 2012). Non-food related skills similarly need practice before adult proficiency is reached, as shown by studies on the role of experience in predator recognition or the effectiveness of helping in cooperative breeders (Lawton and Guindon 1981, Poiani 1993, Komdeur 1996, Griesser and Suzuki 2016). Although alternative or complementary explanations for age differences in behavior and efficiency invoke morphological constraints or nutritional requirements, the majority of studies ascribe age-related changes in foraging behavior and efficiency to lack of experience (Marchetti and Price 1989).

Skill acquisition relies on an array of learning categories ranging from purely individual exploration, practice and learning to fully social, observational learning (Heyes 2012). Purely individual (asocial) learning is based on the mechanism of private trial-and-error without any social inputs, whereas observational learning implies close social contact, allowing for imitation or emulation (van Schaik et al. 2017). Protracted association with parents (i.e. family living: Ekman and Griesser 2002) and other caretakers provides young with extended opportunities for skill learning. A recent study in Siberian jays (*Perisoreus infaustus*) has shown that naïve individuals copy the mobbing behavior of role models, particularly from related caretakers (Griesser and Suzuki 2016). However, family living also allows for various intermediate possibilities of socially buffered learning, which may be of great importance (van Schaik et al. 2017). Thus, caretakers work as an energetic buffer in terms of providing increased vigilance and/or provisioning, ultimately allowing for more extensive individual learning. We can call this protected and supported individual learning, respectively (Heinsohn 1987, Alonso and Alonso 1993, Yoerg 1998, Gamero and Kappeler 2015, van Schaik et al. 2017). The social component of protected and supported individual learning eases the time and energetic compromises otherwise imposed by skill learning. Since in practice parental and allomaternal care most commonly encompass predator protection as well as provisioning, the two mechanisms are non-exclusive and most likely co-occur in most species. These various, complementary forms of social learning thus offer extended opportunities for skill learning in species with extended parent-offspring association.

Given the widespread reliance on skill learning, it follows that where individuals have more opportunities to learn (be it individual, social, or supported or protected), they should be able to assemble the adult skill set faster or acquire a larger skill set (van Schaik and Burkart 2011; Schuppli and Graber et al. 2016). Consistent with this prediction, comparative work in primates and carnivorans has shown that a slow pace of development and longer periods of provisioning, by offering a greater abundance of opportunities for individual and social learning, co-occur with more complex foraging niches (Schuppli et al. 2012; Schuppli and Graber et al. 2016). Moreover, in great ape species with a fission-fusion social system (chimpanzees and orangutans), the percentage of time in association with other individuals than the mother, which reflects the abundance of opportunities for social or protected learning, is positively correlated with a population's repertoire of complex cultural variants (van Schaik 2003, Whiten and van Schaik 2007).

Among birds, no systematic comparative studies have so far examined whether variation in opportunities for learning (i.e. the duration of post-fledging association with caretakers, as well as their number) is linked to variation in skill sets or niche complexity. This absence may be related to two problems. First, direct estimates on the size of the repertoire of learned skills, especially in wild populations of birds, are difficult to acquire, because skill sets in birds encompass a broad range of dimensions including breeding, parenting/alloparenting, predator avoidance, foraging, piracy behavior and habitat selection (Schuppli et al. 2012). Second, within these dimensions there is an enormous intraspecific variability e.g. for foraging in terms of foraging sites, search methods/patterns, food recognition/selection, prey capture and handling techniques. While this variability implies a major role of skill learning, it hampers the determination and quantification of the degree of skill complexity, and thus species comparisons. Nevertheless, there is some evidence for birds suggesting that more complex skills require more time to learn and that adult levels are reached later in development. Thus, in white-breasted mesites (Gamero and Kappeler 2015) and Eurasien dippers (Yoerg 1998) young with a slower acquisition of adult-level feeding efficiency and more complex foraging techniques (in the dipper case, diving for large prey in contrast to catching stationary larvae) disperse at later ages. These findings suggest that longer parent-offspring associations are linked to higher levels of learned skills - either in terms of handling efficiency or complexity.

Skill learning and the evolution of intelligence

Because having a greater number of skills or more complex skills is advantageous by providing behavioral flexibility in diverse or changing environments (Wright et al. 2010), it should positively affect fitness (e.g. Sol et al. 2002). Selection will thus generally favor increases in the size of the repertoire of learned skills. And since various studies in both birds and primates have shown that a species' social and asocial learning (or innovation) abilities are correlated (Lefebvre et al. 1996, Lefebvre 2000, Lefebvre and Giraldeau 1996, Reader and Laland 2002), selection will generally favor increases in skills when opportunities for skill learning are abundant, whether they are learned individually through protected/supported learning or through social learning.

These data and arguments are consistent with the cultural intelligence hypothesis (CIH) (Whiten and van Schaik 2007, van Schaik and Burkart 2011), which suggests that systematic opportunities for cultural (i.e. social) acquisition of complex skills are a precondition for selection for increased intelligence, we predict that the abundance of opportunities for skill learning, either individually, through protected/supported individual learning, or social observational learning, will be an enabling factor in the evolution of intelligence, i.e. the ability to innovate, behave flexibly and learn rapidly. Thus, the key prediction is that intelligent species should be those where long-term, close proximity with tolerant role models is possible.

A systematic test of the correlation between the reliance on extended skill learning and intelligence has not yet been conducted (beyond an ad hoc attempt by van Schaik et al. 2012). Birds show great variation in life history, innovation propensity and brain size. Furthermore, studies have found species with higher behavioral flexibility (as indexed by innovation repertoires or learning ability) have larger relative brain size (e.g. Overington et al. 2009; Ducatez et al. 2015) and are better social learners (Sasvari 1985). Birds are therefore an excellent taxon to test the main prediction of our hypothesis that more intelligent species show higher incidence of social learning (or opportunities for it).

The present study therefore examined the interspecific correlation between the abundance of opportunities for skill learning in birds. We used (relative) brain size as a proxy of general cognitive abilities in the comparative analyses reported below. Although domain-general cognitive abilities have been measured in few species, comparative work in primates suggests that they are closely related to brain size (Deaner et al. 2007; Reader et al. 2011; Graber et al. in review). Likewise, high innovation frequencies, representative for individual learning and thus intelligence, show correlated evolution with brain size in birds (e.g. Lefebvre et al. 1997, Timmermans et al. 2000, Sol et al. 2016).

We use both the duration offspring stay with the parents/caretakers and the absolute number of caretakers as a proxy measure for opportunities for skill learning.
First, prolonged juvenile dependence offers more time to learn, and indeed has been associated with learning-intensive foraging techniques in New Caledonian crows (Hunt et al. 2012). Second, alloparental caretakers during breeding, which in the majority of cases are related to the offspring, show high levels of social tolerance and thus offer the best opportunities for skill acquisition through social learning (van Schaik 2010). Indeed, Griesser and Suzuki (2016) recently showed that offspring are more likely to learn socially from related than unrelated caregivers. Furthermore, a larger number of caretakers alleviates the time needed for vigilance and/or feeding offering more time for individual learning and exploration (i.e. protected and supported individual learning).

So far, most comparative research in primates and birds has mainly focused on testing the social brain hypothesis, which predicts that managing a complex social environment requires enhanced cognitive abilities and thus ultimately drives the evolution of encephalization (Dunbar 1998). In primates, social group size as a representative of social complexity seems to play some role in the evolution of intelligence (e.g. Dunbar 1998). In birds, however, there is no evidence for an effect of the absolute number of associates (flock size: Beauchamp and Fernandez-Juricic 2004), but rather the type and strength of the pair bonds. Emery et al. (2007) and Shultz and Dunbar (2010) found that the most encephalized species are those with multi-year pair bonds, and suggested that the higher degrees of coordination and cooperation associated with long-term monogamy require high levels of cognition. To preclude that our measures of opportunities for social learning (where social tolerance is abundant, high levels of cooperation are more likely) are not simply reflecting the social brain effect in terms of long-term pair bonding, one needs to additionally account for the effect of long-term pair bonds when testing the cultural intelligence hypothesis.

We use a comparative sample of 634 bird species to test for correlated evolution between relative brain size and the total number of caretakers as well as time of post-fledging caretaker-offspring association. We predict that the increasing number of tolerant role models (i.e. caretakers) and the length of post-fledging caretaker-offspring association are correlated with relative brain size. We additionally control for the effects of long-term pair bonds in order to account for the social brain hypothesis as an alternative explanation.
We tested the prediction both for all birds and for particular lineages. In particular, we were interested in the contrast between passerines and non-passerines, not only because of fundamental phylogenetic differences but also because passerines are generally smaller and have a higher basal metabolic rate (Londono et al. 2015, Bech et al. 2016), which should make them more likely to use cognitive buffering rather than physiological buffering (Navarrete et al. 2011) in response to food shortage, which in turn may influence their brain size and how brain size is linked to post-fledging association.

Material and Methods

Data

We used measurements of total relative brain size as a proxy for intelligence. First, among mammals the cognitive process involved in general problem solving comprises multiple brain parts simultaneously (Barton 2006, Anderson 2010) and thus correlates with overall brain size (Deaner et al. 2007). It is justified to make this assumption for birds as well because Sol et al. (2005) found a strong correlation between innovation propensity (an expression of intelligence) and overall relative brain size in this lineage. Second, as in mammals (Bennett and Harvey 1985a, Finlay et al. 2001), changes in size of individual brain parts among bird species are correlated among each other as well as with changes in overall brain size (Iwaniuk et al. 2004).

All the data on a total of 634 avian species (347 non-passerines, 287 passerines) were retrieved from the literature. Brain size and body mass were based on an established data base by K. Isler originally compiled from various sources (Mlikovski 1989a, 1989b, 1989c, 1990; Iwaniuk and Nelson 2003; Schönwetter 1960-1978). Life history data on development mode, length of post-fledging caretaker-offspring association and total number of caretakers were retrieved from the major handbooks of birds (Del Hoyo et al. 2011, the Poole 2005, Higgins et al. 2007, Maclean and Robert 1985).
Development mode at birth was dichomotized into precocial and altricial, in each case including semi-precocial and semi-altricial species. Long-term pair-bonding data was taken from Shultz and Dunbar 2010, where they are defined as ”high probability of persistence across breeding seasons”. We dichomotized their variable (3 levels: non-pair, short-pair and long-pair) into a binary variable (2 levels: long-pair vs. non/short pair).
As estimates of the abundance of opportunities for extended skill learning we used two main measures: (1) the length of post-fledging caretaker-offspring association, represented by the period from when hatchlings leave the nest until dispersal; and (2) the total number of caretakers who contribute to feeding and protection of hatchlings and fledglings (including breeding pair). If a species was described to a facultative cooperative breeder, the number of helpers (caretakers in addition to breeding pair) was halved and added to the breeding pair (total number of caretakers = 2 + 0.5 * number of helpers).

Analyses

Analyses were run for the total sample of 634 species as well as for passerines (N=287) and non-passerines (N=347) separately. If additionally accounting for long-term pair bonding, the analyses were repeated on a reduced sample, since the data of Shultz and Dunbar 2010 overlap only for N=56, and N=28 for passerines and non-passerines species, respectively.
Due to the fundamental difference in the phylogenetic history of the passerines and non-passerines (Jetz et al. 2012), a phylogenetic analysis including all species might lead to misleading results. In fact, the phylogenetic signal, i.e. the degree to which interspecific variation in trait values is correlated with phylogenetic distance (lambda [λ], Pagel 1999), in the traits included in our analyses are very different for passerines and non-passerines, and thus might also be for the residual errors in models (Table 3.1). In passerines most diversification happened relatively recent in evolutionary time, thus, trait similarities between species are to a higher degree assignable to their long path of shared evolutionary history (i.e. moderate/high phylogenetic signals), whereas in non-passerine species the opposite is the case, i.e. early diversification, briefly shared evolutionary histories and minimal phylogenetic signals.

Table 3.1: Phylogenetic signal (lambda) for body mass, brain size, post-fledging caretaker-offspring association (PFA), number of caretakers and the product thereof (total PFA), for passerines and non-passerine species. P-values based on likelihood ratio test, lambda significantly different from 0.0. Calculated using the phylosig function in R package phytools (Revell 2012).

Clade	**body mass**	**brain size**	**PFA**	**# caretakers**	**total PFA**
Passerines (N=287)	0.87 ($p<0.001$)	0.84 ($p<0.001$)	0.46 ($p<0.001$)	0.24 ($p=0.021$)	0.30 ($p=0.002$)
Non-passerines (N=347)	0.00 ($p=1.00$)	0.00 ($p=1.00$)	0.00 ($p=1.00$)	0.059 ($p=0.08$)	0.00 ($p=1.00$)

We used phylogenetic least-square (PGLS) regression including the estimation of phylogenetic signal lambda for the analyses (caper, Orme et al. 2013). Because both brain size and length of post-fledging association are known to correlate with body mass and development mode (Bennett and Harvey 1985b, Iwaniuk and Nelson 2003), all analyses accounted for these effects using multiple regression models. The interaction term between the length of post-fledging association and number of caretakers was only included in a model if significant.

The natural Log transformation was applied to continuously varying variables in order to obtain normally distributed model residuals. All analyses and graphs were performed in the R programming language (R development core team 2014).

The relationship between brain size and opportunities for extended learning in terms of total number of caretakers and length of the post-fledging association period might (besides long-term pair bonding) be accounted for by several other factors, which have been suggested to be associated with brain size: migration, annual fecundity, breeding latitude. The statistical models controlling for and further details on these potential confounding effects are given in the supplementary material.

Results

For birds in general, the length of post-fledging association and the total number of caretakers show significantly positive effects on brain size after controlling for body mass and development mode (Table 3.2a: models A,B; Fig. 3.1A,B), consistent with our prediction. In the model including both measurements of opportunities for extended learning, the effect of the number of tolerant role models significantly affects encephalization (Table 3.2a: model C), but the effect of length of post-fledging association disappears. Even though the variance inflation factor does not indicate severe multicollinearity (e.g. Hair et al. 1998), the two factors might still partly cancel each other out. The interaction term was not significant, and thus not included in the model. We see a similar pattern if we additionally control for the effect of long-term pair-bonding in a reduced sample (Table 3.3a). Here, however, the effect of number of caretakers disappears most likely due to extremely reduced variation.

Including only passerine species, the models show equivalent, but even stronger patterns (Table 3.2b, model A-C; Fig. 3.1A,B). In this case, in the model including both estimates of opportunities for skill learning additionally yields a significant negative interaction effect (Table 3.2b: model C). In other words, the effect of the length of post-fledging association on relative brain size is more pronounced in species with fewer caretakers, suggesting a compensatory pattern between number of role models and time spent with them. Also if we additionally control for long-term pair bonding, the effect of the length of post-fledging association remains, but also here the effect of the number of caretakers disappears, again most likely due to extremely reduced variation (Table 3.3b). In non-passerine species, interestingly, no significant effects were found (Table 3.2c and 3.3c: model A-C; Fig. 3.1A,B).

All the analyses were repeated without controlling for body mass and development mode. The results were retained. The robustness of our results was further underlined by the effects of including the various potentially confounding effects of annual fecundity, migration and breeding latitude. These analyses all produce the same basic result: more post-fledging association shows correlated evolution with larger relative brain size (Tables S1-S3 in the supplementary material).

Figure 3.1: Interspecific relationships between residuals Ln brain size and A) residuals Ln postfledging caretaker-offspring association, B) residuals total number of caretakers for the passerine (red) and non-passerine (blue) species. Corresponding residuals are based on non-phylogenetic multiple regression models with Ln body mass and development mode as predictor variables.

Table 3.2: Multiple PGLS regression models for a) all species, b) passerine species only, and c) non-passerines species only, with Ln brain size as response and Ln length of postfledging caretaker-offspring association (Ln PFA) (model A), total number of caretakers (# caretakers) (model B), and both, Ln length of postfledging association (Ln PFA) and total number of caretakers (caretakers) with corresponding interaction (model C) as predictor variables. All models additionally include Ln body mass as a covariate and the ones including all species and the non-passerines additionally control for development mode (altricial vs. precocial). Interaction effects are only included if significant. Given are the Akaike information criterion (AIC), coefficient of determination (R^2) and the phylogenetic signal (λ) as well as the estimates and p-values for each model. P-values reaching a significance level lower than 5% are indicated in bold.

				Ln PFA		**# caretakers**		**interaction**	
Model	**AIC**	R^2	λ	estimate	p-value	estimate	p-value	estimate	p-value
a) all species (N=634)									
model A	-462.9	0.89	0.90	0.013	**0.050**	-	-	-	-
model B	-466.8	0.89	0.91	-	-	0.017	**0.006**	-	-
model C	-466.4	0.89	0.91	0.009	0.213	0.015	**0.020**	-	-
b) passerines (N=287)									
model A	-273.0	0.90	0.78	0.029	**0.002**	-	-		
model B	-269.5	0.89	0.82	-	-	0.015	**0.016**		
model C	-276.8	0.89	0.82	0.066	**0.001**	0.125	**0.009**	-0.020	**0.015**
c) non-passerines (N=347)									
model A	-214.0	0.89	0.92	0.004	0.628	-	-	-	-
model B	-214.1	0.89	0.92	-	-	0.013	0.534	-	-
model C	-212.2	0.89	0.92	0.003	0.744	0.011	0.611	-	-

Table 3.3: Multiple PGLS regression models for a) all species, b) passerine species only, and c) non-passerines species only, with Ln brain size as response and Ln length of post-fledging caretaker-offspring association (Ln PFA) (model A), total number of caretakers (caretakers) (model B), and both, Ln length of post-fledging association (Ln PFA) and total number of caretakers (#caretakers) with corresponding interaction (model C) as predictor variables additionally controlling for long-term pair bonding (models A.2, B.2, C.2). All models additionally include Ln body mass as a covariate and the ones including all species and the non-passerines additionally control for development mode (altricial vs. precocial). No interaction effects included because non-significant. Given are the Akaike information criterion (AIC), coefficient of determination (R^2) and the phylogenetic signal (λ) as well as the estimates and p-values for each model. P-values reaching a significance level lower than 5% are indicated in bold.

				Ln PFA		**# caretakers**		**pair-bonding**	
Model	**AIC**	R^2	λ	estimate	p-value	estimate	p-value	estimate	p-value
a) all species (N=56)									
model A.1	-7.8	0.93	0.86	0.093	**0.013**	-	-	-	-
model A.2	-15.1	0.94	0.81	0.092	**0.009**	-	-	0.202	**0.003**
model B.1	-1.4	0.92	0.86	-	-	0.027	0.546	-	-
model B.2	-7.9	0.93	0.82	-	-	0.021	0.615	0.206	**0.005**
model C.1	-6.6	0.93	0.85	0.113	**0.011**	-0.043	0.390	-	-
model C.2	-14.4	0.94	0.8	0.116	**0.006**	-0.050	0.285	0.205	**0.003**
b) passerines (N=28)									
model A.1	-14.5	0.94	0.83	0.078	*0.058*	-	-	-	-
model A.2	-20	0.96	0.64	0.084	**0.033**	-	-	0.201	**0.010**
model B.1	-12	0.94	0.7	-	-	0.047	0.294	-	-
model B.2	-16.6	0.95	0.5	-	-	0.049	0.216	0.198	**0.016**
model C.1	-12.5	0.94	0.83	0.077	0.129	0.001	0.983	-	-
model C.2	-18	0.96	0.64	0.084	*0.092*	-0.001	0.991	0.201	**0.012**
c) non-passerines (N=28)									
model A.1	2.4	0.92	0.9	0.076	0.233	-	-	-	-
model A.2	2.3	0.92	0.89	0.059	0.358	-	-	0.162	0.203
model B.1	3.8	0.91	0.93	-	-	-0.023	0.816	-	-
model B.2	2.4	0.92	0.94	-	-	-0.089	0.395	0.229	0.098
model C.1	3.5	0.92	0.9	0.104	0.156	-0.093	0.408	-	-
model C.2	2.2	0.93	0.91	0.094	0.181	-0.146	0.200	0.212	0.113

Discussion

Our results show that in birds in general, and passerines in particular, species in which offspring stay longer with their parents and are surrounded by more tolerant role models (i.e. have increased levels of opportunities for skill learning) show larger relative brain sizes. This confirms the prediction based on the cultural intelligence hypothesis: opportunities for learning enable selection on increased skill levels and thus increased brain size when the possession of extra skills increases fitness and thus is not prevented by high degrees of unavoidable mortality.

It could be argued that this result is an artifact. A first possible objection could be that we have not in fact tested the cultural intelligence hypothesis, but rather the social brain hypothesis. In avian species, the social brain hypothesis claims the cognitive demands of managing stable social relationships in terms of long-term pair bonds to drive the evolution of enlarged brains (Shultz and Dunbar 2007; Emery et al. 2007; Shultz and Dunbar 2010). Nonetheless, our results showed, that even after additionally including the effect of long-term pair bonds into a regression model, the duration of post-fledging parent-offspring association still significantly affects encephalization. These findings suggest an association between relative brain size and both long-term pair-bonds and extended post-fledging association of offspring. We therefore propose that the high level of cooperation in long-term monogamous and cooperatively breeding species allows for higher degrees of social tolerance which in turn allows for the social acquisition of learning-intensive skills. Furthermore, in addition to the stable and socially tolerant environment afforded by the family group, the duration of this association provides time for skill learning and shows correlated evolution with intelligence.

A second alternative interpretation is that immatures in species with longer post-fledging associations perhaps merely receive longer periods of provisioning, and thus have more favorable energy budgets to support brain growth, as proposed by the Maternal Energy Hypothesis (Martin 1996). However, even though the beneficial effects of provisioning are not to be dismissed, the pattern is retained when we control for a species' development mode (altricial young are provisioned, whereas precocial ones are not).

Finally, the relationship between brain size and opportunities for extended learning in terms of total number of caretakers and length of the post-fledging association period might be due to the effects of various confounding variables: migration (Sol et al. 2005), annual fecundity (Isler and van Schaik 2009) and breeding latitude (Covas 2012) (details see supplementary material). However, even after additionally taking those factors into account, the effects of opportunities for skill learning on relative brain size remained (supplementary information: Tables S1-S3).

Given that our findings are robust, their implications in relation to the cultural intelligence hypothesis presumes that birds learn their skills at least partly through social learning as broadly defined here and that more role models and more time in association with them actually leads to more opportunities for doing so. This conclusion may be surprising for birds, because it has been argued that birds do not learn socially in nature or that they do not use the opportunities for social learning offered by living in groups. Here, we address these concerns.

First, it has been suggested that in general social transmission is far more prevalent in primates than in birds (Lefebvre and Bouchard 2003). However, a great number of cross-fostering experiments and studies in captive and wild populations have shown that birds learn behavioral patterns in nest defense, predator recognition, vocal repertoire, mate choice and feeding niche through social transmission (Norton-Griffiths 1968; Curio 1978; Farabaugh et al. 1994; Slagsvold et al. 2002; Slagsvold and Hansen 2001; Slagsvold and Wiebe 2007; Slagsvold and Wiebe 2011; Werner and Sherry 1987;

Midford et al. 2000; Boogert et al. 2008; Aplin et al. 2013, 2015; Farine et al. 2015; Griesser and Suzuki 2016). Moreover, every experiment that examined whether birds can engage in imitation found evidence in favor of it (Lefebvre and Bouchard 2003), begging the question why birds would be so good at observational forms of social learning, if they did not use it in practice. Taken together, these findings not only provide strong evidence that birds need to acquire their skills, but more importantly, also that they often do so through social learning. Although we are not able to distinguish whether the immatures rely more on supported, protected or observational learning, all depend on social mediation. In fact, purely individual acquisition of skills without any contact to role models is dangerous and time-consuming and thus makes skill acquisition far less efficient in contrast to any form of socially mediated learning (e.g. Midford et al. 2000). As a result, immatures of many species prefer social learning (van Schaik and Burkart 2011, van Schaik et al. 2017).
Second, the CIH presumes higher degrees of social learning in species with a higher number of tolerant role models and/or longer associations with them (i.e. extended opportunities for it). The fact that many studies found that social learning is not necessarily more abundant in more social species, in birds as well primates (Lefebvre and Bouchard 2003, Lefebvre et al. 1996, Templeton et al. 1999, Reader and Lefebvre 2001), appears to argue against this assumption. However, increasing flock size or group size are not adequate measures of opportunities for social learning because individuals in such aggregations are not necessarily related or socially tolerant, and thus are not expected to learn socially from each other. In fact, social learning is only expected where close social contact to tolerant role models are prevalent, such as within cooperatively breeding family groups. Indeed, a study in two Corvids showed that the species which breeds cooperatively and shows many prosocial interactions (*Gynmnorhinus cyanocephalus*) learns more efficiently in a social compared to an asocial environment, whereas the less social species (*Nucifraga columbiana*) did not show a difference between the two learning conditions (Templeton et al. 1999).

We therefore think that both the comparative evidence and a revised interpretation of the behavioral studies indicate that birds learn socially from one another, especially from tolerant role models, and that elongated periods of post-fledging protection and provisioning, i.e. family living, represents an optimal environment for socially mediated skill learning. If more skills imply higher fitness, selection should favor larger brains where opportunities for social learning are more abundant. In concordance with this prediction of the cultural intelligence hypothesis, our results suggest that the abundance of such conditions favor the evolution of increased encephalization. Whereas we find evidence across birds in general and particularly across passerine species, no such pattern is found across non-passerine orders. This discrepancy in findings may be explained by a major difference between these two phylogenetically clearly distinct clades (Jetz et al. 2012) in the need for skill acquisition (based on differences in metabolism) and thus opportunities for socially mediated learning. Even though past studies provide non-conclusive evidence on differences in basal metabolic rates (Lasiewski and Dawson 1967, Reynolds and Lee 1996, McKechnie and Wolf 2004), the latest, more comprehensive studies clearly show higher BMR in passerines compared to non-passerines, independent of breeding latitude (Londoño et al. 2015, Bech et al. 2016). Additionally, our sample clearly shows smaller body mass in passerine compared to the non-passerine orders (supplementary material: Table S4): the average non-passerine is 30 times heavier than the average passerine. High metabolism relative to body size plus small body size implies high vulnerability to starvation, especially in highly seasonal environments. Therefore, passerine species potentially are in the need of more complex and learning-intensive skills in order to overcome seasonally lean periods, because alternative strategies such as fat storage are unfavorable in avian species (Heldstab et al. 2016).

This difference in need is indeed reflected in their social organization. Across our sample of 634 species, passerine species tend to have a larger number caretakers, i.e. larger number of tolerant role models offering opportunities for social learning (supplementary information: Table S4). Taken together, based on metabolic differences, non-passerine species may be less sensitive to starvation and thus, have less need for seasonal buffering, and thus for the acquisition of a broad and flexible skill repertoire (based on strong innate learning ability), which is reflected in decreased opportunities for social learning. However, this line of argumentation is currently speculative and the discrepancy in our findings as well as general differences between passerine and non-passerine species certainly needs further investigations.

In conclusion, as predicted by the evolutionary version of the cultural intelligence hypothesis we find that there is strong correlated evolution between encephalization and opportunities for socially mediated learning in terms of both the number of tolerant role models and time in association with them. This effect is most pronounced in passerines, arguably because they are far more sensitive to starvation risk.

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Supplementary Material

The relationship between brain size and opportunities for extended learning in terms of total number of caretakers and length of the post-fledging association period might alternatively be accounted for by several other factors: migration, annual fecundity and breeding latitude.
First, several studies have shown that migrating species have smaller relative brain sizes compared to resident species, perhaps because long-distance migration does not allow them to have energetically expensive large brains (Sol et al. 2005, Sol et al. 2010, Winkler et al. 2004), though perhaps also because they might be time-constrained in the post-fledging parent-offspring period. We therefore included migration tendency as a confounding variable. We classified species as resident if they are sedentary and or do local movements, whereas migratory species include those with regional movements and long distance migration (based on minimal movement distances). A second potential confounder is annual fecundity. According to the expensive brain framework (Isler and van Schaik 2009) and basic life history theory (e.g. Flatt and Heyland 2011), production shows not only a cross-species trade-off with brain size but also the amount of (allo-)parental care and the length of caretaker-offspring association. Additionally, we accounted in our analyses for the effects of breeding latitude since reproductive life histories (Covas 2012) and brain size through stronger cognitive buffer effects at high latitudes (Garamszegi and Lucas 2005) might confound the predicted relationship between opportunities for extended skill learning and brain size. We calculated annual fecundity as the product of clutch size and number of clutches per year; breeding latitude represents the northernmost latitude in the breeding range given in Botero et al. (2013).

Given that these factors may influence the length of post-fledging association as well as brain size, we controlled therefore by additionally including them into the phylogenetic regression models displayed in the Tables S1 - S3. Because data on annual fecundity and breeding latitude were not available for the total set of 634 species, the analyses from the main text are repeated in these cases with the subsamples of N=534 and N=469, respectively, in order to show that the main effects of length of post-fledging association and number of caretakers also hold in these subsamples. The interaction between length of post-fledging association and number of caretakers are only included in the model if significant ($p < 0.05$).

Table S1. Multiple PGLS regression models for a) all species, b) passerines and c) non-passerines species with Ln brain size as response and Ln length of post-fledging caretaker-offspring association (Ln PFA) (model A), total number of caretakers (# caretakers) (model B), both, Ln length of post-fledging association (Ln PFA) and total number of caretakers (#caretakers) with corresponding interaction (model C) as predictor variables additionally controlling for Ln annual fecundity (models A.2, B.2, C.2). All models additionally include Ln body mass as a covariate and the ones over all species/non-passerines additionally control for development mode (altricial vs. precocial). Given are the Akaike information criterion (AIC), coefficient of determination (R^2) and the phylogenetic signal (λ) as well as the estimates and p-values. P-values reaching a significance level lower than 5% are indicated in bold.

				Ln annual fecundity		**Ln PFA**		**# caretakers**		**interaction**	
Model	**AIC**	R^2	λ	estimate	p-value	estimate	p-value	estimate	p-value	estimate	p-value
a) all species (N=534)											
model A.1	-403.0	0.89	0.89	-	-	0.020	**0.021**	-	-	-	-
model A.2	-401.2	0.89	0.89	-0.006	0.736	0.019	**0.024**	-	-	-	-
model B.1	-404.0	0.89	0.90	-	-	-	-	0.016	**0.013**	-	-
model B.2	-402.8	0.89	0.89	-0.015	0.383	-	-	0.017	**0.010**	-	-
model C.1	-404.7	0.89	0.89	-	-	0.015	0.104	0.013	0.058	-	-
model C.2	-403.1	0.89	0.89	-0.012	0.514	0.014	0.130	0.014	**0.048**	-	-
b) passerines (N=254)											
model A.1	-240.7	0.90	0.77	-	-	0.029	**0.005**	-	-	-	-
model A.2	-238.8	0.90	0.78	0.008	0.716	0.030	**0.005**	-	-	-	-
model B.1	-238.7	0.89	0.82	-	-			0.015	**0.019**	-	-
model B.2	-236.8	0.89	0.82	-0.007	0.767			0.016	**0.019**	-	-
model C.1	-244.2	0.90	0.82			0.067	**0.003**	0.130	**0.011**	-0.020	**0.019**
model C.2	-242.2	0.90	0.82	-0.005	0.823	0.067	**0.003**	0.131	**0.012**	-0.020	**0.019**
c) non-passerines (N=280)											
model A.1	-184.2	0.90	0.91			0.017	0.211			-	-
model A.2	-183.8	0.90	0.90	-0.033	0.209	0.016	0.256			-	-
model B.1	-182.6	0.89	0.91					0.000	0.987	-	-
model B.2	-182.5	0.90	0.90	-0.036	0.174			-0.001	0.953	-	-
model C.1	-182.4	0.90	0.91			0.019	0.187	-0.010	0.666	-	-
model C.2	-182.0	0.90	0.91	-0.033	0.209	0.017	0.224	-0.010	0.662	-	-

Table S2. Multiple PGLS regression models for a) all species, b) passerines and c) non-passerines species with Ln brain size as response and Ln length of postfledging caretaker-offspring association (Ln PFA) (model A), total number of caretakers (caretakers) (model B), both, Ln length of postfledging association (Ln PFA) and total number of caretakers (caretakers) with corresponding interaction (model C) as predictor variables additionally controlling for migration. All models additionally include Ln body mass as a covariate and the ones over all species/non-passerines additionally control for development mode (altricial vs. precocial). Given are the Akaike information criterion (AIC), coefficient of determination (R^2) and the phylogenetic signal (λ) as well as the estimates and p-values. P-values reaching a significance level lower than 5% are indicated in bold.

				migration		**Ln PFA**		**# caretakers**		**interaction**	
Model	**AIC**	R^2	λ	estimate	p-value	estimate	p-value	estimate	p-value	estimate	p-value
a) all species (N=634)											
model A	-464.2	0.89	0.90	-0.028	0.072	0.011	0.123	-	-	-	-
model B	-468.9	0.89	0.91	-0.030	**0.045**	0.017	**0.008**	-	-	-	-
model C	-467.6	0.89	0.91	-0.027	0.073	0.006	0.389	0.015	**0.020**	-	-
b) passerines (N=287)											
model A	-294.9	0.90	0.79	-0.105	**0.000**	0.019	**0.038**	-	-	-	-
model B	-295.3	0.90	0.82	-0.110	**0.000**	-	-	0.013	**0.032**	-	-
model C	-298.8	0.90	0.82	-0.103	**0.000**	0.053	**0.007**	0.118	**0.010**	-0.018	**0.018**
c) non-passerines (N=347)											
model A	-215.0	0.89	0.92	0.036	*0.083*	0.008	0.388	-	-	-	-
model B	-214.9	0.89	0.92	0.033	*0.099*	-	-	0.016	0.434	-	-
model C	-213.4	0.89	0.92	0.036	*0.079*	0.007	0.493	0.012	0.565	-	-

Table S3. Multiple PGLS regression models for a) all species, b) passerines and c) non-passerines species with Ln brain size as response and Ln length of postfledging caretaker-offspring association (Ln PFA) (model A), total number of caretakers (# caretakers) (model B), both, Ln length of postfledging association (Ln PFA) and total number of caretakers (caretakers) (model C) as predictor variables additionally controlling for northern breeding latitude (models A.2, B.2, C.2). All models additionally include Ln body mass as a covariate and the ones over all species/non-passerines additionally control for development mode (altricial vs. precocial). Given are the Akaike information criterion (AIC), coefficient of determination (R^2) and the phylogenetic signal (λ) as well as the estimates and p-values. P-values reaching a significance level lower than 5% are indicated in bold.

				N lat breeding		**Ln PFA**		**# caretakers**	
Model	**AIC**	R^2	λ	estimate	p-value	estimate	p-value	estimate	p-value
a) all species (N=469)									
model A.1	-309.4	0.87	0.88	-	-	0.027	**0.002**	-	-
model A.2	-308.4	0.87	0.88	0.000	0.306	0.030	**0.001**	-	-
model B.1	-304.1	0.87	0.89	-	-	-	-	0.025	**0.046**
model B.2	-302.3	0.87	0.89	0.000	0.713	-	-	0.026	**0.044**
model C.1	-308.4	0.87	0.88	-	-	0.024	**0.012**	0.014	0.306
model C.2	-307.5	0.87	0.88	0.000	0.296	0.027	**0.007**	0.014	0.296
) passerines (N=221)									
model A.1	-196.6	0.87	0.74	-	-	0.036	**0.002**	-	-
model A.2	-196.2	0.87	0.73	-0.001	0.214	0.029	**0.022**	-	-
model B.1	-193.2	0.86	0.78	-	-	-	-	0.035	**0.016**
model B.2	-196.2	0.87	0.76	-0.001	**0.025**	-	-	0.033	**0.024**
model C.1	-196.7	0.87	0.74	-	-	0.030	**0.017**	0.022	0.150
model C.2	-196.6	0.87	0.74	-0.001	0.169	0.021	0.119	0.024	0.120
c) non-passerines (N=248)									
model A.1	-123.7	0.88	0.91	-	-	0.025	*0.063*	-	-
model A.2	-126.4	0.88	0.91	0.001	**0.032**	0.030	**0.028**	-	-
model B.1	-120.4	0.88	0.91	-	-	-	-	0.010	0.668
model B.2	-122.1	0.88	0.91	0.001	*0.058*	-	-	0.018	0.439
model C.1	-121.8	0.88	0.92			0.026	*0.068*	-0.006	0.810
model C.2	-124.4	0.88	0.91	0.001	**0.033**	0.030	**0.039**	0.001	0.950

Table S4. Mean body mass (median in brackets) and mean number of caretakers for passerines (N=287) and non-passerine (N=347) species.

	Passerines	**Non-passerines**
Body mass	1623.41 (531.4)	53.2 (22.7)
Caretakers	2.436	1.880

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Chapter 4

Seasonality constrains brain size evolution among non-primate mammals

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Abstract

The expensive brain hypothesis claims that a high degree of experienced seasonality imposes an energetic challenge, and thus acts as an evolutionary constraint on brain size. In contrast, but not mutually exclusive, the cognitive buffer hypothesis claims that species with larger brains, which therefore show increased cognitive and behavioural flexibility, are better at dealing with lean periods in seasonal habitats. So far, the concomitant effects of the two hypotheses have only been systematically tested within primate lineages (anthropoids and lemurs). However, to test the generality of the underlying evolutionary patterns of brain size evolution, a broader mammalian comparison is needed. Here we test the two hypotheses on brain size evolution in a sample of 41 non-primate mammals and compare them with the primate findings. We find that species experiencing higher degrees of seasonality in diet composition show smaller relative brain sizes, which is also the pattern found across primates. However, we find only weak evidence for the cognitive buffer hypothesis, comparable to lemurs and in contrast to anthropoid primates. In conclusion, current evidence suggests that energetic and thus ecological constraints play a crucial role in mammalian brain size evolution, but that cognitive buffering seems to be less pervasive. We find tentative evidence that cognitive buffering is more likely in large-brained mammals.

Introduction

The immense variation in brain size across species has long inspired evolutionary speculation. Many theories have been proposed, particularly for primates, eventually trying to explain what factors led to the most encephalized (i.e. brain size or neuron numbers relative to body mass) lineage within the animal kingdom. A large brain entails not only fitness benefits through increased cognitive abilities (Deaner et al. 2007) but also implies high energetic costs of production (Striedter 2005) and maintenance (Niven and Laughlin 2008), as well as delayed development (Isler et al. 2008, Isler 2011), with negative fitness consequences. Nonetheless, most theories focus on either the cost or the benefit perspective.

The cognitive buffer hypothesis (Allman et al. 1993, Sol 2009, Sayol et al. 2016) emphasizes the benefit perspective. It suggests that large brains are beneficial in terms of enhanced cognitive flexibility, which allows individuals to better deal with changing ecological conditions, ultimately increasing fitness. Therefore, the hypothesis predicts that larger-brained species are able to respond more flexibly to seasonal changes in the environment. Fallback foods (e.g. underground storage organs, roots, tubers) may not be easy to find and often demand complex and coordinated processing techniques (Kaplan et al. 2000, Johnson and Bock 2004, Marshall and Wrangham 2007, Melin et al. 2014, Heldstab et al. 2016). Switching to alternative food resources during lean periods of the preferred foods minimizes fluctuations in the energetic input relative to fluctuations in environmental productivity (e.g. Nagy and Gruchacz 1994: *D. merriami*; Sidorovich et al. 2008: *N. procyonoides*; Melin et al. 2014: *C. capucinus*) and thus ultimately increases survival and longevity (Allman et al. 1993, Sol 2009).

The expensive brain hypothesis (Isler and van Schaik 2009) emphasizes the costs of brains. It claims that an evolutionary increase in brain size is either constrained by the energy allocation to other functions (e.g. growth, reproduction; Isler and van Schaik 2009) or by the total energetic input (Isler 2011, Isler et al. 2008, Pontzer et al. 2016). Brain tissue is one of the most expensive somatic tissues, needing a continuously high supply of energy (Mink et al. 1981; Rolfe and Brown 1997, Bauernfeind et al. 2014), and thus is very sensitive to periods of starvation. Seasonality, in terms of annual periodicity in climate and environmental productivity, may lead to periods of severe food scarcity. In that respect, the expensive brain hypothesis suggests that in highly seasonal habitats where the nutritional demands during the lean season cannot be fulfilled by finding alternative food resources and thus the costs of increased brain size cannot be offset, the degree of experienced seasonality is likely to act as energetic constraint on brain size.

Recent work across primates has found support for both the expensive brain as well as the cognitive buffer hypothesis (van Woerden et al. 2010, 2012, 2014). This work systematically distinguished between experienced seasonality (i.e. annual variability in caloric composition of the diet = energetic input) and environmental seasonality (i.e. annual variability in environmental productivity). It showed, first, that species experiencing higher degrees of seasonality evolved relatively smaller brains, across both anthropoids and lemurs (see also Taylor and van Schaik 2007). Second, in anthropoids, but only to a lesser degree in lemurs, larger-brained species are better at keeping their experienced seasonality constant relative to the seasonality in the environment, supporting the notion of cognitive buffering.

Taken together, whereas the expensive brain pattern seems to be ubiquitously applicable across the entire primate lineage, the cognitive buffer hypothesis applies primarily to anthropoids. In order to disentangle whether the more encephalized anthropoids are special or whether lemurs represent the exception, and thus eventually understand the importance of seasonality in the evolution of our own species' unmatched degree of cognition, these patterns need to be evaluated in a broader comparative context that also includes non-primate mammals. Outside the primate clade, comparative tests of the two hypotheses, particularly in relation to seasonality, is very limited. The only other mammalian study, focusing on marsupials, found a negative relationship between environmental seasonality and relative brain size, implying a lack of buffering and supporting the cost perspective of brain size evolution (Weisbecker et al. 2015). Among birds, the opposite was found: several studies have shown that species living in in harsher and more seasonal habitats tend to have larger brains, implying cognitive buffering (Schuck-Paim et al. 2008, Vincze 2016, Sayol et al. 2016).

These studies found clear effects of environmental seasonality, which permits unambiguous conclusions. However, an absence of an effect of environmental seasonality would not allow us to reject the cognitive buffering or expensive brain hypothesis, because the combination of the two effects might balance out. Thus, only if the annual variability in the actual experienced seasonality followed the fluctuations in environmental productivity, i.e. if there was no buffering, would it be justified to use external, environmental indicators to test seasonality's relationship with brain size. It is therefore best to use the distinction between experienced and environmental seasonality (van Woerden et al. 2010, 2012, 2014).

Here, we test the conjoint effects of the expensive brain and cognitive buffer hypotheses across a broad set of non-primate mammals. First, in order to assess whether we need to distinguish between environmental and experienced seasonality, we test the relationship between the actually experienced seasonality, as expressed in seasonal changes in diet composition, and the environmental seasonality, as represented by fluctuations in the habitat productivity. Next, we test predictions. The cognitive buffer hypothesis predicts a positive correlation between the degree to which experienced seasonality is buffered relative to environmental seasonality and relative brain size, whereas the expensive brain hypothesis (which is not mutually exclusive with the cognitive buffer hypothesis) predicts that species with higher degrees of experienced seasonality to show smaller relative brain sizes. Finally, we put these results into a broader perspective by additionally including the data from the previous studies of primates, including anthropoids and lemurs (data based on van Woerden et al. 2014). The data for non-primate mammals are given in a supplementary data table.

Strict carnivorans and strict herbivores are not included in this study since seasonal variation in diet composition does not represent the fluctuations in their energetic input (i.e. experienced seasonality) as their diets vary in amount ingested but not (much) in composition. We also did not include marine mammals, as the quantification of marine environmental seasonality is not possible with the available measures of environmental productivity (see Material and Methods).

Material and Methods

Seasonality Data

After an extensive literature search we compiled detailed data of seasonal diet composition on 41 non-primate mammalian species, consisting of 29 Carnivora, 11 Rodentia and 1 Artiodactyla.

The quantification of experienced and environmental seasonality as well as the amount of buffering follows van Woerden et al. (2010, 2012, 2014): The estimate of the actually experienced seasonality in terms of fluctuations in the energy input throughout the year is based on the monthly diet composition of a species compiled from the published literature (references see supplementary material). For the vast majority of species diet composition data was available for at least nine consecutive months (N=28) or is based on every second month (N=8), whereas for a few, only condensed measures of the four seasons were available (N=6). To assess robustness, all analyses were repeated excluding the species where only condensed measures of the four seasons are available. For the quantification of experienced seasonality, first, we classified the diet categories into five levels of varying nutritional value (blood/milk/egg > meat > insects/crustaceans > fruits/seeds/tubers > leaves/green fodder) according to the food classification by Langer (2002). Second, we multiplied the percentage of each level in the diet (as estimated by percentage of occurrence) with its nutritional value (80 for meat, 13 for insects/crustaceans, 5.5 for fruits/seeds/tubers and 2 for leaves /green fodder, based on crude fibre content from Langer 2002) and finally, we calculated the coefficient of variation (CV) over the year in the food category with the highest nutritional value which represents at least 10% of the mean annual proportion, best representing variation in the energetic input (CV diet) (see also van Woerden et al. 2010). However, since the current set of species largely consists of omnivorous species, the highest nutritional component might not be representative of the total energetic input. Therefore, we additionally calculated the sum of all categories per month and calculated its yearly CV, as representing the degree of seasonal variation of the total energy input (CV total diet, the corresponding analyses are shown in the supplementary material).

For environmental seasonality, we calculated the CV in the monthly plant productivity, given by the Normalized Difference Vegetation Index (NDVI) (CV NDVI). The data was extracted from the GIMMS database (Tucker et al. 2005) and was geographically matched to the study sites of the diet composition data (see also van Woerden et al. 2010). Where data on different populations or over several years were available, average CVs were calculated. For hibernating species (*M. meles*, *S. tridecemlineatus*, *U. americanus*, *U. arctos*, *U. thibetanus*) the calculation of the CV is based on the whole year with the proportion of all diet components set to zero during the inactive months, as this best represents the actual experienced seasonality.
The degree of buffering seasonality is given by the difference between the environmental and experienced seasonality (degree of buffering = CV NDVI - CV diet).

Brain and body size data

Brain size volume was measured with the glass-beads-filling method from a total of 259 adult female specimens from three American museums (American Museum of Natural History, New Work; National Museum of Natural History, Washington D.C.; Field Museum of Natural History, Chicago). If fewer than 5 specimens per species were available (N=10 species), data on female (to exclude dimorphism) brain size was complemented from the published literature (details in supplementary information). Data given in brain mass [g] was converted to brain volume based on Isler et al. 2008 (1.036 g = 1 cc).

Data on mean female body mass was also taken from the published literature (details in supplementary information). The relative brain sizes of the different species are illustrated in Fig. 4.1. Since we are interested in the effect of a potential energetic constraint, we test for relationships with relative brain size, by incorporating body mass as a covariate in all our phylogenetic regression analyses.

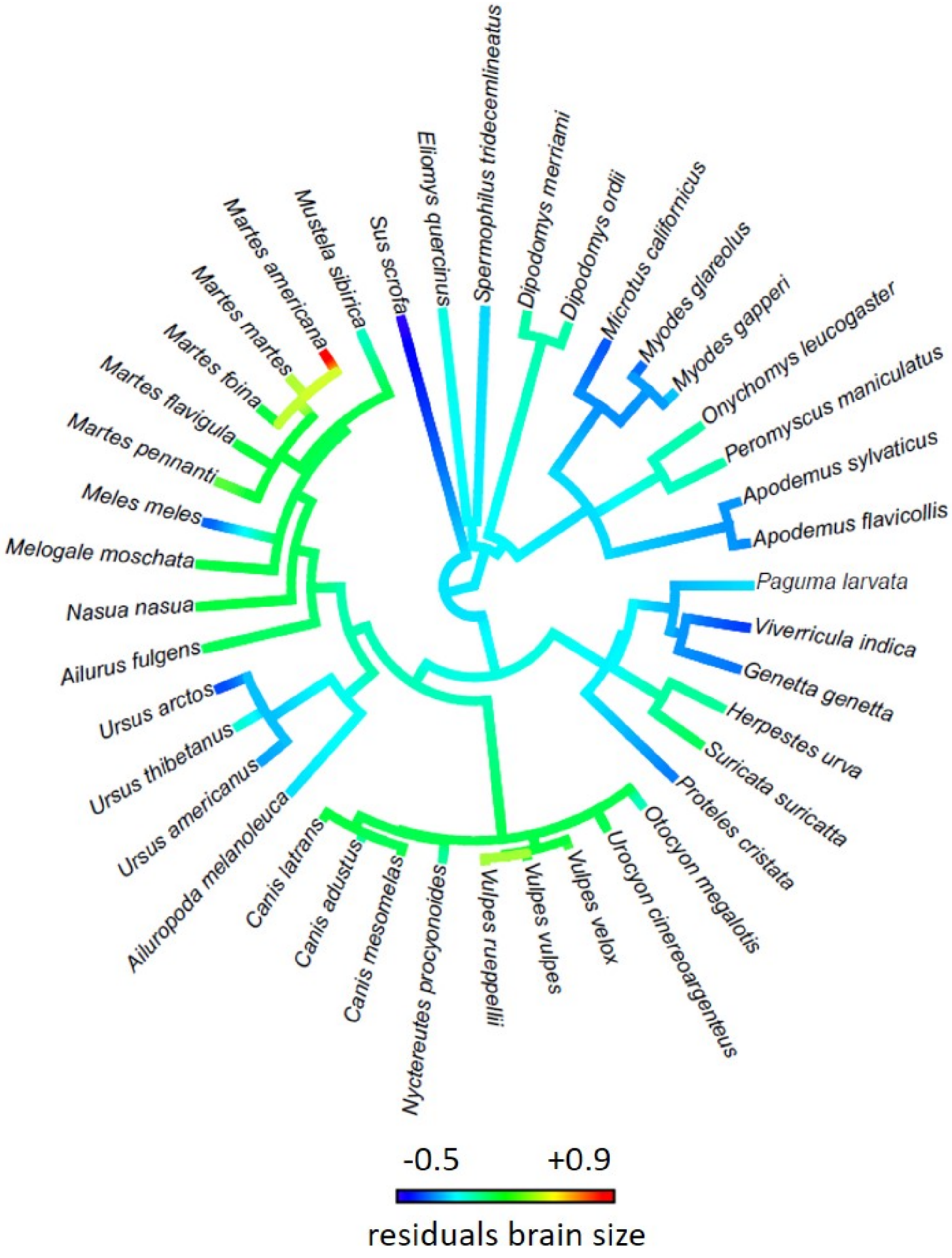

Figure 4.1: Phylogenetic Tree: Relative Brain Size Data. Phylogenetic tree of the 41 species with colors on the branches from blue to red indicating increasing brain size relative to body mass (residuals of ln brain vs. ln body).

Statistical Analysis

Due to the common evolutionary history between species, methods controlling for phylogenetic non-independence are required. We used phylogenetic least-squares regressions (PGLS, package caper, Orme 2013) and phylogenetic logistic regression (PLR, package phylolm, Ho and Ané 2014) incorpo-

rating the degree of phylogenetic inertia by estimating the phylogenetic signal lambda (Pagel 1999) and alpha (Ives and Garland 2010), respectively. The corrections for phylogenetic dependence are based on the mammalian super tree published in Fritz et al. 2009 (Fig. 4.1). To meet the model assumptions of evenly distributed residuals around zero, brain size, body mass, CV NDVI and CV diet were loge transformed prior to the PGLS analyses. From the definition of the degree of buffering, it is by necessity negatively correlated with experienced seasonality. Therefore, experienced seasonality needs to be additionally included as a covariate when testing for cognitive buffering (see also van Woerden et al. 2014).
All analyses and plots were run in the R programming language (R development core team, 2015) and the raw data is tabulated in the supplementary material in Table S4.

Results

Our results show that there is no relationship between experienced and environmental seasonality. This establishes that at least in some species the annual variability in diet (CV diet) does not follow the annual variability in habitat productivity (CV NDVI), and thus the environmental seasonality is buffered (Table 4.1A, Fig. 4.2A,B).

In accordance with the energetic constraint perspective of brain size evolution, we found that species experiencing greater fluctuations in dietary composition (i.e. higher CV diet) show smaller relative brain sizes. This effect is even stronger in the combined sample that includes the primate data (Table 4.1B; Fig. 4.2C,D).

And finally, the data reveals only weak evidence for a cognitive buffer effect when testing the effect of relative brain size on the difference between environmental seasonality and the actual fluctuations in diet (i.e. degree of buffering). For both the non-primate mammals and the combined sample we find a statistical trend (Table 4.1C; Fig. 4.2E,F). The effect is slightly stronger if hibernating species are excluded, reaching significance in the combined sample (Table S1). Notice that species showing strong cognitive buffering tend to have smaller body size, although the effect is significant in neither the non-primate nor the combined sample. Please note again that from the definition of the degree of buffering we need to additionally include experienced seasonality as a covariate when testing for cognitive buffering (see also van Woerden et al. 2014).

Very similar, but slightly weaker effects are found if the annual variability in diet is calculated in a different way in terms of total diet composition (CV total diet), or if we omitted those six species for which CV diet was determined from a condensed measure of the four seasons (Table S2, S3).

Table 4.1: Seasonality and Brain Size. PGLS regression testing (A) the relationship between experienced and environmental seasonality, (B) the expensive brain hypothesis (by examining the effect of experienced seasonality on relative brain size), and (C) the cognitive buffer hypothesis (by examining the effect of relative brain size on the degree of buffering), in the set of non-primate mammals (top) and all mammals additionally including primates (anthropoids and lemurs) (bottom). Shown are the number of species (N), coefficient of determination (R^2), strength of the phylogenetic signal (λ), and the estimate and the p-value of the predictor variables. Statistical significance (p<0.05) is indicated in bold font, and statistical trends (0.05 < p-value < 0.1) in italics.

Non - primate mammals	**N**	R^2	λ	**predictor**	**estimate**	**p-value**
A) Experienced seasonality (ln CV diet)	41	0.00	0.55	environmental seasonality (ln CV NDVI)	0.070	0.680
B) ln brain size	41	0.95	0.66	ln body	0.664	<0.001
				experienced seasonality (ln CV diet)	-0.094	**0.031**
C) Buffering seasonality (CV NDVI - CV diet)	41	0.76	0.00	ln body	-0.148	0.069
				experienced seasonality (ln CV diet)	-0.305	<0.001
				ln brain	0.190	*0.090*
All mammals						
A) Experienced seasonality (ln CV diet)	115	0.00	0.89	environmental seasonality (ln CV NDVI)	0.059	0.541
B) ln brain size	115	0.90	0.93	ln body	0.695	<0.001
				experienced seasonality (ln CV diet)	-0.087	**0.001**
C) Buffering seasonality (CV NDVI - CV diet)	115	0.48	0.81	ln body	-0.088	0.060
				experienced seasonality (ln CV diet)	-0.156	<0.001
				ln brain	0.119	*0.060*

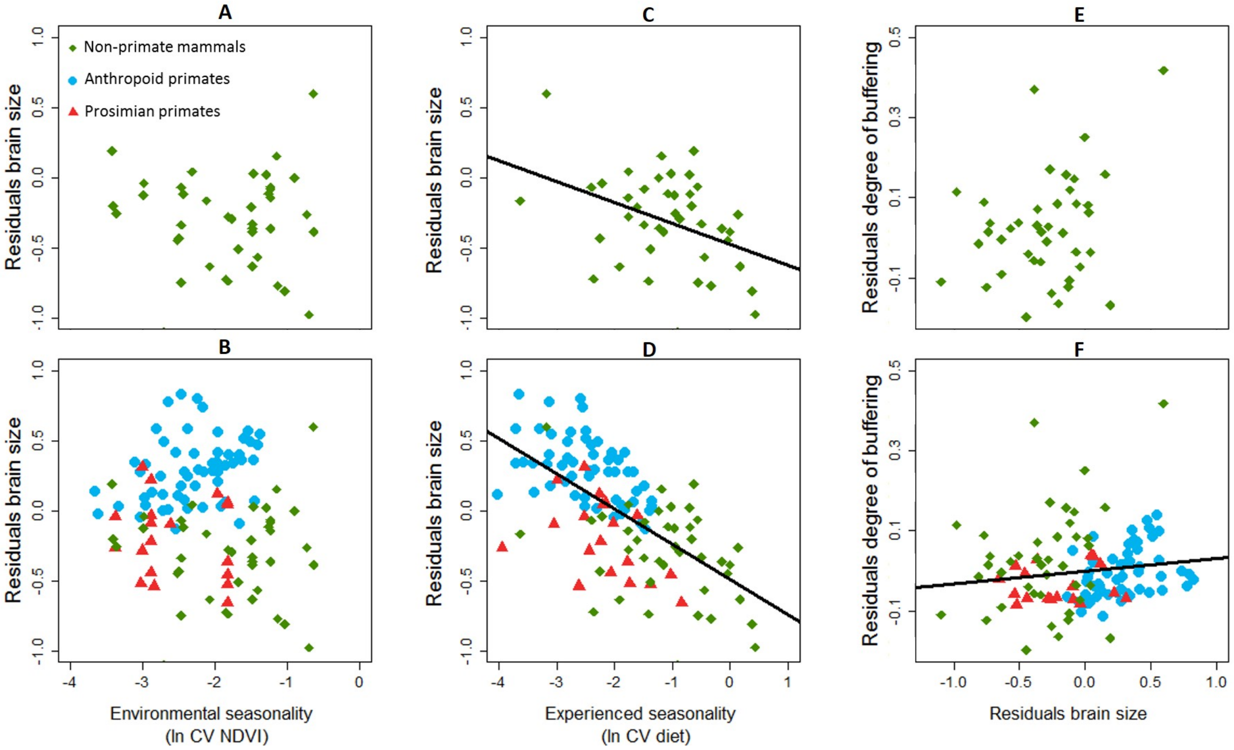

Figure 4.2: Seasonality and Brain Size. Testing the expensive brain and cognitive buffer hypothesis based on the distinction between environmental and experienced seasonality. (A, B) Relationship between environmental and experienced seasonality. (C, D) The relationship between relative brain size and experienced seasonality (expensive brain hypothesis). (E, F) Relationship between the degree of buffering (residuals of degree of buffering vs. ln CV diet) and relative brain size (residuals of ln brain size vs. ln body mass) (cognitive buffer hypothesis) for non-primate mammals (N=41, top panels A, C, and E) and the overall mammalian sample including additionally primates (anthropoids and lemurs) (N=115, bottom panels B, D, and F).

Discussion

In our sample of non-primate mammals, the degree of experienced seasonality does not follow the degree of environmental seasonality, suggesting that several species exposed to severe periods of low habitat productivity are able to keep the energetic input more constant throughout the year, i.e. buffer their environmental seasonality. This means for our data that exclusively environmental indicators and its effect on brain size do not allow us to draw conclusions about the expensive brain and cognitive buffer hypothesis and that the distinction between environmental and experienced seasonality is thus critically important. Together with the earlier work in primates (van Woerden et al. 2010, 2012, 2014), these are the first studies to distinguish between environmental and experienced seasonality and thereby to explicitly quantify the degree of buffering.

Cognitive Buffer Hypothesis

The degree to which experienced seasonality is buffered relative to environmental seasonality is only weakly associated with relative brain size among non-primate mammals. In contrast to the findings in anthropoid primates (van Woerden et al. 2012, 2014), the cognitive buffer hypothesis is thus not strongly supported as a general pattern among mammals. In fact, the ambiguous cognitive buffer effect in the current set of non-primate species is comparable to the one found in lemurs. We suggest two non-exclusive reasons to explain this discrepancy.

First, the extremely high metabolic and developmental costs of increased brain size (Striedter 2005) make cognitive buffering only feasible in species where levels of extrinsic mortality and the costs for brain growth and maintenance are relatively moderate, which particularly applies to large-bodied species with slow life histories (cf. van Woerden 2011). All non-primate species included in the current study, with a few exceptions (bear species and the wild boar), as well as lemurs, show relative small body sizes and rather fast life histories compared to anthropoids (Table 2), which drastically reduces the net cognitive benefit of a large brain. In other words, the so-called life-history filter (cf. van Schaik et al. 2012) may impede a positive effect of cognitive buffering on fitness.

Second, in some environmental conditions cognitive buffering may simply not be a feasible strategy. Extremely high degrees of environmental seasonality lead to periods of unavoidable starvation (i.e. effective food availability below maintenance level), in which cognitive buffering brings no survival benefits. With an increasing degree of environmental seasonality, and thus the chance for periods of unavoidable starvation, selection is probably likely to favor a diet composition that is less affected by environmental seasonality. Most species included in our study rely on a largely omnivorous diet, where meat as a high quality and constant food resource often represents a stable component. And our data shows, indeed, that those species living in more extreme habitats have a higher proportion of meat in their diet (PGLS: N=41, R^2=0.11, λ=0.82, response: % meat in diet, predictor: CV NDVI: estimate= 43.06, p-value=0.035). The food processing of animal prey per se, however, seems not to necessarily require enhanced cognitive abilities, as suggested by a recent study among carnivorans (Schuppli and Graber et al. 2016). In primates, on the other hand, the highest quality foods are usually fruits and invertebrates, which are highly sensitive to seasonal variation, and their spatio-temporal distribution over the year in combination with complex processing seem to depend on enhanced cognition (van Woerden et al. 2010, 2012, 2014; Melin et al. 2014; Schuppli and Graber et al. 2016). To overcome unavoidable starvation, physiological adaptations in terms of fat reserves and hibernation are probably most likely, apart from dietary adaptions, which also do not explain how non-carnivorous mammals, including lemurs, overcome lean periods in extremely seasonal habitats (Heldstab et al.

2016). Physiological buffering is indeed, mostly found among non-primate mammals, which in our sample include bears (*U. arctos*, *U. americanus*, *U. thibetanus*), badgers (*M. meles*) and squirrels (*S. tridecemlineatus*), and among primates in lemurs only. Our data confirms that with increasing habitat seasonality, hibernation is more likely (PLR: N=41, alpha= 0.027, response: hibernation, predictor: CV NDVI: estimate= 6.46, p-value=0.032). Cognitive buffering and physiological buffering strategies have been shown to be compensatory across mammals (Navarrete et al. 2011, Heldstab et al. 2016, Veitschegger 2017). The results of analyses of the current data in non-primates and the combined sample including all mammals show that if we exclude hibernating species, statistical support for a cognitive buffer effect increases, which highly supports the trade-off between cognitive and physiological buffering. Taken together, high levels of extrinsic mortality and extreme environmental conditions make cognitive buffering less feasible in non-primate mammals and lemurs and instead favor a general switch in diet towards seasonally more stable food resources and/or physiological strategies such as hibernation (Table 4.2).

Although the sample sizes in our set of species are more than sufficient to detect a cognitive buffer effect, we could not exclude some methodological artifacts and thus the conclusions remain somewhat preliminary. First, the variability in the NDVI used as a proxy for environmental seasonality might not be ideal, particularly in extreme habitats, which are largely covered by snow during low-food seasons, implying disproportionally low NDVI values. Second, many of the non-primate species rely to a considerable extent on animal prey where the NDVI might not be representative of the actual food availability (i.e. environmental seasonality). Therefore, to consolidate these conclusions for an even broader set of species, an assessment of environmental seasonality directly reflecting prey/food availability would be very useful. This would also allow us to include strict carnivorans, but for them we would also like to have direct measures of the seasonal variation in the actual energetic input (and thus in energy expenditure, i.e. in field metabolic rates). Currently, however, data on prey availability as well as on field metabolic rates have not been collected for a large enough number of species to allow interspecific comparisons.

Unlike in non-primate mammals, in birds different studies strongly suggest that cognitive buffering is an abundant phenomenon as species living in more seasonal habitats tend to have larger relative brain sizes (Schuck-Paim et al. 2008, Vincze 2016, Sayol et al. 2016). This fundamental difference may be explained the high degree of mobility in birds which enables them to easily explore and sample other habitats (cf. van Woerden et al. 2010). This way, animals can go from peak abundance to peak abundance and reach an average level of food intake that is even higher and more stable than staying in one place and buffer as much as possible. This idea can be tested by studying tropical bats. If bats are like birds, it is supported; if they are like other mammals, there may be a fundamental difference between birds and mammals.

Expensive Brain Hypothesis

Testing for the effect of experienced seasonality, we find that species experiencing higher degrees of fluctuations in the most energy-dense diet components exhibit relatively small brains, which is in concordance with the findings across primate lineages (van Woerden et al. 2010, 2012, 2014). In the combined mammalian sample including primates the effect is even more pronounced, and suggests that periods of reduced energy intake are generally not compatible with relatively large brains, as proposed by the expensive brain perspective.

It is well known that nutritional stress and malnutrition strongly affects brain development (Lukas and Campbell 2000) and also that brain maintenance requires a continuous supply of energy (Mink et al. 1981). Further, previous evidence from mainly intraspecific studies also suggest that crucial resource shortages and short growth seasons are related to a reduction in brain size, also outside of the primate clade (Köhler and Moyà-Solà 2004; Niven 2005, 2007; Taylor and van Schaik 2007; Weston and Lister 2009, Jiang et al. 2015). Together with the findings across primates (van Woerden et al. 2010, 2012, 2014) and marsupials (Weisbecker et al. 2015), the evidence from our interspecific study confirms the fundamental assumption of the expensive brain hypothesis, namely that animals with periodic troughs in energy intake, reaching its apogee in hibernating species, are unable to maintain large brains due to the inability of brains to cope with temporary reductions in energy supply. The persistent negative relationship between brain size and experienced seasonality suggests that, even though there is buffering going on (based on the absent relationship between environmental and experienced seasonality), it is apparently never strong enough to compensate for the high energetic requirements of a relatively large brain. We suggest that selection in favor of improved ecological conditions, comprising a stabilized energy intake and increased survival, is most crucial in the evolution of brain size and cognition (Graber et al. in review).

In conclusion, with this study we show that the expensive brain hypothesis applies in all examined mammalian groups so far, underscoring once again the importance of an ecological perspective on brain size evolution (van Woerden et al. 2010, 2012, 2014, Graber et al. in review). The phenomenon of cognitive buffering, however, appears to be less common in mammals in general, possibly existing as an exclusive strategy only in anthropoid primates (Table 4.2). We suggest, that only where extrinsic ecological conditions enable higher levels of cognition and behavioral flexibility to produce energetic benefits, cognitive buffering is favored as a strategy to overcome seasonally lean periods. This is in line with a recent finding among primates, showing that only where ecology paved the way for the evolution of enlarged brains, more complex eco-and socio-cognitive abilities including cognitive buffering, are possible (Graber et al. in review).

Table 4.2: Comparison of non-primate mammals vs. primates. Comparison of characteristics of non-primate mammals (current study) with lemurs and anthropoid primates (van Woerden et al. 2010, 2012, 2014).

Taxa	Expensive brain	Cognitive buffering	Life-history filter (median body mass [g] and AFR [d])	Alternative buffering
Non-primate mammals (current study)	✓	(X)	high (2250; 364)	- shift in diet -> energy rich food (meat) - fat storage and hibernation
Lemurs (van Woerden et al. 2010)	✓	(X)	medium (1908; 972)	- fat storage and torpor/hibernation (Dausmann et al. 2004, Schülke and Ostner 2007) - reduced BMR (Genoud 2002) - extreme birth seasonality (Janson and Verdolin 2005)
Anthropoid primates (van Woerden et al. 2012, 2014)	✓	✓	low (5383; 1800)	

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Supplementary Material

Tables S1-S3 present results for slight alterations of dataset in order to investigate the robustness of the results.

Table S1. Excluding hibernating species. PGLS regression testing the relationship between the degree of buffering seasonality and relative brain size in the set of non-primate mammals (top) and all mammals additionally including primates (anthropoids and lemurs) (bottom). Given are the sample size (N), coefficient of determination (R^2), phylogenetic signal (λ) as well as the estimate and the p-value of the predictor variables.

Non-primate mammals	**N**	R^2	λ	**predictor**	**estimate**	**p-value**
Buffering seasonality (CV NDVI - CV diet)	36	0.70	0.00	ln body	-0.125	0.095
				experienced seasonality (ln CV diet)	-0.240	<0.001
				ln brain	0.189	*0.065*
All mammals (inlcuding primates)						
Buffering seasonality (CV NDVI - CV diet)	108	0.50	0.45	ln body	-0.066	0.094
				experienced seasonality (ln CV diet)	-0.139	<0.001
				ln brain	0.109	**0.038**

Table S2. Experienced seasonality measured as the coefficient of variation of the dietary composition summed over all food categories (CV total diet) in non-primate mammals. PGLS regression testing (A) the relationship between experienced and environmental seasonality, (B) the expensive brain hypothesis by the effect of experienced seasonality on relative brain size, and (C) the cognitive buffer hypothesis by the effect of relative brain size on the degree of buffering. Given are the sample size (N), coefficient of determination (R^2), phylogenetic signal (λ) as well as the estimate and the p-value of the predictor variables.

Response	**N**	R^2	λ	**predictor**	**estimate**	**p-value**
A) Experienced seasonality (ln CV total diet)	41	0.00	0.62	environmental seasonality (ln CV NDVI)	0.048	0.759
B) ln brain size	41	0.94	0.70	ln body	0.665	<0.001
				experienced seasonality (ln CV total diet)	-0.092	*0.053*
C) Buffering seasonality (CV NDVI - CV total diet)	41	0.62	0.44	ln body	-0.132	0.194
				experienced seasonality (ln CV total diet)	-0.289	<0.001
				ln brain	0.193	0.186

Table S3. Excluding the six species for which CV diet was derived from condensed measures of the four seasons (non-primate mammals). PGLS regression testing (A) the relationship between experienced and environmental seasonality, (B) the expensive brain hypothesis by the effect of experienced seasonality on relative brain size, and (C) the cognitive buffer hypothesis by the effect of relative brain size on the degree of buffering. Given are the sample size (N), coefficient of determination (R^2), phylogenetic signal (λ) as well as the estimate and the p-value of the predictor variables.

Response	**N**	R^2	λ	**predictor**	**estimate**	**p-value**
A) Experienced seasonality (ln CV diet)	35	0.03	0.20	environmental seasonality (ln CV NDVI)	0.194	0.340
B) ln brain size	35	0.95	0.63	ln body	0.655	<0.001
				experienced seasonality (ln CV diet)	-0.088	*0.061*
C) Buffering seasonality (CV NDVI - CV diet)	35	0.75	0.00	ln body	-0.147	0.101
				experienced seasonality (ln CV diet)	-0.295	<0.001
				ln brain	0.183	0.140

Table S4. Supplementary Data Table. Data on environmental seasonality (CV NDVI) , experienced seasonality (CV diet), hibernation and both brain and body mass for the 41 non-primate mammalian species.

Genus species	**CV diet**	References diet composition	**CV NDVI**	**Brain size**	Reference brain size	**Hibernation**	Reference hibernation	**Body mass**	**Reference body mass**
A. melanoleuca	0.245	Wei et al. 1999	0.162	236.00	museum spec.	0	Botero et al. 2013	87500	Isler and van Schaik 2012
A. fulgens	0.173	Wei et al. 1999	0.162	42.50	museum spec.	0	Botero et al. 2013	5400	Isler and van Schaik 2012
A. flavicollis	0.292	Abt and Bock 1998	0.229	0.70	Mace et al. 1981	0	Turbill et al. 2011	31	Jenrich et al. 2010
A. sylvaticus	0.607	Abt and Bock 1998	0.229	0.58	Mace et al. 1981	0	Botero et al. 2013	23.4	Myers et al. 2006
C. adustus	0.252	Atkinson et al. 2002	0.188	48.85	museum spec.	0	Botero et al. 2013	8650	Mittermeier et al. 2013
C. latrans	0.291	Huebschman et al. 1997, Kitchen et al. 1999	0.407	89.08	museum spec.	0	Botero et al. 2013	9760	Isler and van Schaik 2012
C. mesomelas	0.201	Kaunda and Skinner 2003	0.224	53.25	museum spec.	0	Botero et al. 2013	6600	Isler and van Schaik 2012
D. merriami	0.501	Nagy and Gruchacz 1994	0.088	1.11	museum spec.	0	Botero et al. 2013	41	Isler and van Schaik 2012
D. ordii	0.171	Flake 1973	0.293	1.46	Hafner and Hafner 1984	0	Botero et al. 2013	60.2	Isler and van Schaik 2012
E. quercinus	0.516	Gil-Delgado et al. 2010	0.033	1.17	museum spec.	0	Gil-Delgado et al. 2010	49.1	Mittermeier et al. 2013
G. genetta	0.148	Amroun et al. 2013, Rosalino and Santos-Reis 2002, Carvalho and Gomes 2004	0.126	12.75	museum spec.	0	Botero et al. 2013	1820	Isler and van Schaik 2012
H. urva	0.226	Chuang and Lee 1997	0.085	20.41	museum spec.	0	Botero et al. 2013	2268	Gittleman 1986
M. americana	0.042	Zielinski et al. 1983	0.529	17.58	museum spec.	0	Botero et al. 2013	565	Mittermeier et al. 2013
M. flavigula	0.496	Zhou et al. 2011	0.275	28.00	museum spec.	0	Botero et al. 2013	2150	Mittermeier et al. 2013
M. foina	0.341	Prigioni et al. 2008	0.284	17.98	museum spec.	0	Botero et al. 2013	1450	Isler and van Schaik 2012
M. martes	0.307	Jedrzejewski et al. 1993, Caryl 2008, Prigioni et al. 2008	0.318	17.37	Gittleman 1986	0	Botero et al. 2013	982	Isler and van Schaik 2012
M. pennanti	0.173	Zielinski et al 1999	0.099	29.63	museum spec.	0	Botero et al. 2013	2250	Isler and van Schaik 2012
M. meles	0.721	Martin et al. 1995, Prigioni et al. 2008	0.323	42.43	museum spec.	1	Ruf and Geiser 2014	10100	Isler and van Schaik 2012
M. moschata	0.091	Chuang and Lee 1997	0.085	16.25	museum spec.	0	Botero et al. 2013	1200	Mittermeier et al. 2013
M. californicus	0.963	Batzli and Pitelka 1971	0.081	0.78	Mace et al. 1981	0	Botero et al. 2013	39.8	Isler and van Schaik 2012
M. sibirica	0.421	Tatara and Doi 1994	0.171	5.46	museum spec.	0	Botero et al. 2013	395	Isler and van Schaik 2012
M. gapperi	1.153	Perrin 1979	0.484	0.56	Mace et al. 1981	0	Botero et al. 2013	20.57	Myers et al. 2006
M. glareolus	1.000	Abt and Bock 1998	0.229	0.52	Mace et al. 1981	0	Botero et al. 2013	21.9	Isler and van Schaik 2012
N. nasua	0.109	Hirsch 2009	0.051	34.18	museum spec.	0	Botero et al. 2013	3000	Isler and van Schaik 2012
N. procyonoides	0.315	Sidorovich et al 2008	0.531	30.35	museum spec.	0	Sidorovich et al. 2008	4020	Isler and van Schaik 2012
O. leucogaster	0.227	Flake 1973	0.293	0.79	Mann and Towe 2003	0	Turbill et al. 2011	25.3	Isler and van Schaik 2012
O. megalotis	0.106	Bothma et al. 1984	0.082	29.29	museum spec.	0	Botero et al. 2013	4075	Isler and van Schaik 2012
P. larvata	0.640	Zhou et al. 2008	0.244	29.10	museum spec.	0	Botero et al. 2013	4800	Isler and van Schaik 2012
P. maniculatus	0.571	Flake 1973	0.293	0.57	Mace and Eisenberg 1982	0	Botero et al. 2013	16.3	Isler and van Schaik 2012
P. cristata	0.095	Bothma et al. 1984	0.158	40.05	museum spec.	0	Botero et al. 2013	8820	Isler and van Schaik 2012
S. tridecemlineatus	0.869	Flake 1973	0.293	2.34	Iwaniuk 2001	1	Botero et al. 2013	146	Isler and van Schaik 2012
S. suricatta	0.027	Doolan and MacDonald 1996	0.121	9.95	museum spec.	0	Botero et al. 2013	725	Isler and van Schaik 2012
U. cinereoargenteus	0.388	Neale and Sacks 2001	0.035	34.56	museum spec.	0	Botero et al. 2013	4010	Isler and van Schaik 2012
U. americanus	1.470	Torgersen et al. 2001	0.357	214.00	museum spec.	1	Botero et al. 2013	84700	Isler and van Schaik 2012
U. arctos	1.544	Munro et al. 2006, McLellan and Hovey 1995, Mattson et al. 1990	0.498	328.93	museum spec.	1	Botero et al. 2013	182000	Isler and van Schaik 2012
U. thibetanus	1.186	Koike 2009	0.228	261.88	museum spec.	1	Botero et al. 2013	87500	Mittermeier et al. 2013
V. indica	0.579	Chuang and Lee 1997	0.085	16.81	museum spec.	0	Botero et al. 2013	3000	Mittermeier et al. 2013
V. rueppellii	0.537	Olfermann 1996	0.033	24.43	museum spec.	0	Botero et al. 2013	1450	Mittermeier et al. 2013
V. velox	0.360	Kitchen et al. 1999, Sikes et al. 2003	0.232	30.17	museum spec.	0	Botero et al. 2013	2345	Isler and van Schaik 2012
V. vulpes	0.380	Cavallini and Volpi 1996	0.050	40.86	museum spec.	0	Turbill et al. 2011	4210	Isler and van Schaik 2012
S. scrofa	0.402	Massei et al. 1996	0.067	178.70	museum spec.	0	Botero et al. 2013	97000	Mittermeier et al. 2013

References Supplementary Material

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Chapter 5

Ecology is the Main Driver of Primate Brain Size Evolution

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Abstract

Primates evolved the largest brains relative to body size among mammals, and humans evolved the largest brains among primates. Whether these increases were driven by social or ecological selective benefits is vigorously debated. In this comparative study we offer a new conceptual approach, which systematically distinguishes between opportunities (potential selective drivers) and immediate consequences, and also include a comprehensive set of both social and ecological variables across a broad sample of primate species. The results of multivariate analyses show that selection on brain size reflects ecological rather than social opportunities, but that increased encephalization also engenders general behavioral flexibility, and therefore predicts cognitive complexity in both the ecological and social domains equally well. In conclusion, this study demonstrates that advanced social and ecological cognitive abilities in primates could only become prominent in lineages where the evolution of large brains, with their attendant energetic costs, was enabled by favorable ecological preconditions.

Introduction

The massive variation in brain size relative to body size found across animals has led to long-standing debates on its evolutionary explanation (Jerison 1973, Striedter 2005). Much of this effort has focused on primates, and especially humans, due to their unmatched degree of encephalization and concomitant cognitive abilities. The most prominent hypothesis suggests that enhanced cognition is a prerequisite for dealing with the complexities of social life (the social brain hypothesis, Dunbar 1998). Dunbar (2016) recently concluded that there "is a general consensus that the prime mover in primate brain evolution (and perhaps even that of all mammals and birds) is the evolution of more complex forms of sociality". Indeed, various features of social group living, including group size, clique size or the presence of coalitions, explain much interspecific variation in the size of primate brains or their regions (Dunbar and Shultz 2007a). However, some have proposed that solving ecological problems, such as extraction of hidden foods or general behavioural flexibility in response to environmental fluctuations, requires higher levels of cognition and ultimately drove the evolution of enlarged brains (the technical intelligence and cognitive buffer hypotheses, Allman et al. 1993, Byrne 1997, Parker and Gibson 1977). These ideas also received some comparative support (Clutton-Brock and Harvey 1980, Deaner et al. 2000, Heldstab et al. 2016, DeCasien et al. 2017). Thus, although the social brain hypothesis is widely supported and well known, it is important to reassess the relative explanatory power of these various models.

Previous comparative tests of these hypotheses had three shortcomings, all of which we address in the current study. First, although during the past two decades the social brain hypothesis has achieved the status of common knowledge, it does not explain striking differences in brain size within primates and other mammalian lineages (Holekamp 2007, Holekamp et al. 2015, van Schaik et al. 2012), and its explanatory power also has rarely been systematically compared with that of ideas postulating ecological selective benefits (Holekamp 2007, van der Bijl and Kolm 2016, but see Dunbar and Shultz 2007b; DeCasien et al. 2017), even though they are not mutually exclusive.
Second, it is becoming increasingly clear that primates show general cognitive flexibility, which across species is closely linked to brain size (Deaner et al. 2007, Reader et al. 2011). Therefore, cognitive abilities in the ecological and social domains should be equally improved by selection on larger brains, irrespective of the nature of the selective agent. Thus, we run the risk of mistaking the cognitive consequences of brain size for the selective agents that favored the evolution of larger brains. Previous studies have tended to interpret all correlates of increased brains as selective agents.
Third, previous tests of the selective agents favoring brain size evolution rarely acknowledged the fact that large brains require an energy supply that is both unusually high and non-fluctuating (Lukas and Campbell 2000, Niven and Laughlin 2008), and also require a longer period of learning and practice before being fully functional and able to produce actual fitness benefits (Schuppli and Graber et al. 2016). Consequently, increased brain size in response to any cognitive selective agent can only evolve in lineages where its positive fitness impact outweighs the negative fitness effects of the additional energetic costs and loss of time due to slower development (Isler and van Schaik 2012). The same cognitive benefit may therefore lead to an increase in relative brain size in some lineages but not in others, depending on whether it leads to a net increase in energy intake.

To remedy these shortcomings, we introduce a new conceptual approach, where we distinguish between potential selective agents (i.e. opportunities) that enabled the evolution of large brains and cognitive abilities that are a direct result of having a brain of particular size (i.e. consequences) and also include a wide range of social and ecological variables. Social and ecological variables represent opportunities

if they provide necessary but not sufficient conditions for the evolution of increased brain size. They facilitate the evolution of larger brains only in case its costs and constraints (unavoidable mortality due to predation and starvation, life-history filter, cf. van Schaik et al. 2012) can be offset. For instance, living in a large multi-male, multi-female group with tendencies towards polygynandrous mating system does not per se require a large brain, but it does represent an opportunity for the evolution of enhanced socio-cognitive abilities (and thus brain size), such as recognizing third-party dominance relations, forming intersexual social bonds or the capacity for opportunistic coalition formation.
Likewise for ecological opportunities, species with a high-energy or less seasonal diet may have more opportunities to respond to selection favoring larger brain size than those with a less energy-dense or more seasonal diet. Furthermore, a highly seasonal habitat poses the ecological challenge of how to deal with food scarcity. During the low food season, greater cognitive abilities may be beneficial for the recognition and exploitation of alternative foods resources. However, because lean seasons can also be responded to in other ways (e.g. hibernation, fat storage: Heldstab et al. 2017), seasonality is merely an opportunity variable for increased encephalization and an increase in brain size is not a necessary requirement. The same holds for other habitat characteristics such as substrate use, activity, predation risk and ranging behavior, which represent external conditions that may favor, but do not necessitate an enlarged brain.
Consequence variables are a direct result of selection on relative brain size, and a large brain is therefore a necessary precondition in order for these traits to be present. Possible examples include opportunistic coalitionary interventions among non-relatives or routine tool use. If these abilities are cognitively demanding, they could not have selectively favored their own presence.

We will test the validity of this important distinction between opportunities and consequences based on the following assumptions and predictions. First, the evolutionary paths from opportunities to brain size and from brain size to consequences should receive substantially higher statistical support than any other possible directions. Second, because the same selective agent may lead to an increase in brain size in some lineages but due to energetic constraints not in others, we predict that opportunities, be they social or ecological, show weaker relationships with relative brain size than the cognitive consequences. Third, under the general intelligence interpretation, cognitive abilities in both the social and the ecological domain are direct consequences of selection on larger brain size. Thus, we predict that social and ecological consequences not only show a strong correlation with brain size, but also show a very strong interrelationship, whereas social and ecological opportunities should not.

We used a multivariate statistical approach including over 30 ecological and social variables across a broad range of primate species (Fig. S1, Table S1). First, we defined variables as social and ecological opportunities and consequences, and then each of these four types of variables was condensed into one or two summary variables using phylogenetic principal component analysis (pPCA, Revell 2009). Next, we used a phylogenetic path analysis (von Hardenberg and Gonzalez-Voyer 2013, Gonzalez-Voyer and von Hardenberg 2014) and phylogenetic least squares regressions (PGLS, Grafen 1989) to test both the multidirectional and unidirectional relationships between the principal components (PC) and brain size.. The raw data used in this paper are tabulated as a supplementary data table.

Material and Methods

Data - Brain Size and Body Mass

Data on brain size and body mass were retrieved from Isler et al. (2008) and Isler and van Schaik (2012) which are preferentially based on female values due to sexual dimorphism. Brain size and body mass data on *Presbytis potenziani*, *Phaner furcifer* and *Brachyteles arachnoides* was supplemented based on van Woerden (2011). Because body mass shows significant effects on all the response variables (brain size, social and ecological consequence principal components), it is a necessary covariate in our models.

We tested associations with the size of the whole brain (controlled for body mass) for several reasons. The increasing body of evidence for general intelligence (Burkart et al. 2016) argues that the challenges posed by the socio-ecological environment (compound of the measures used in this study) do not have neural correlates in specific neuronal structures but most likely have impacts throughout the whole brain. In fact, it has been shown that cognitive problem solving abilities rely most likely on circuits involving multiple brain parts (Anderson 2010, Barton 2006). Along the same lines, the so-called reuse theory suggests that recombination of neural structures permits different cognitive functions (Anderson 2010), contradicting a modular brain organization. Furthermore, the sizes of particular brain areas are highly correlated with overall brain size (Barton and Harvey 2000, Finlay et al. 2001, Striedter 2005) and from the cost perspective, energetic and developmental constraints largely reflect the size of the brain in general rather than that of particular regions. Quite apart from all of this, data to date on individual brain parts are still highly limited.

Data - Social and Ecological Opportunities/Consequences

Social and ecological opportunity variables provide necessary but not sufficient conditions for the evolution of increased brain size. They indicate potential selective agents that may allow for an increase in brain size in some lineages, but not in others, depending on the strength of developmental and energetic constraints.

For social opportunities we collected species-level data on various social traits including social organization, and mating and rearing system. We included characteristics that have either been used in previous primate studies to test the social brain hypothesis or are closely related to those (reviewed in Healy and Rowe 2007). Complete data on all social opportunity variables was available for N=67 species.

For ecological opportunities, we collected data on various environmental and dietary traits that have been used in earlier studies (reviewed in Healy and Rowe 2007) or estimate additional niche characteristics that do not necessarily presuppose enhanced cognitive abilities, but may represent selective agents for them. Complete data on all ecological opportunity variables was available for N=50 species.

For the socio-and eco-cognitive consequence variables we selected measures assumed to reflect a higher degree of cognitive abilities, several of which have been shown to be related to brain size in previous studies (e.g. Reader et al. 2011). Complete data on the socio- and eco-cognitive consequences were compiled for N=60, and N=53 species, respectively. A total of 92 species, which are evenly distributed across the various primate lineages (Fig. S1), were included in the four domains (social and ecological opportunities, social and ecological consequences). The overlapping common sample includes a reduced sample size of N=29 species. Table S1 provides the descriptions and the numerical codings for all variables.

Data on the social and ecological opportunity and consequence variables are established and validated measures and were retrieved from published comparative studies as well as major mammalian encyclopedias, including the Handbook of the Mammals of the World (Mittermeier et al. 2013) and the Animal Diversity Web (Myers et al. 2006) (detailed references are given in the Supplementary Data Table). Due to a broad range of species as well as the large compilation of variables, several variables rely on multiple references. In case of multiple possible values based on within-species variation (between-population variation), we assigned the value representing the potentially highest level of complexity in a species. In concordance with our hypotheses, the highest level of complexity in opportunities presumably represents the predominating selective agent on enlarged brain size and in case of consequences, it reflects the potentially most complex consequence of enlarged brain size. For example, species which show variation in mating systems and can be either polygynous or polygynandrous were classified as polygynandrous.

For species where no data was available for limiting variables, such as visual trait dimorphism or environmental seasonality, no data for other variables were collected, even though they might be available. For others where data were not available from the main compilations, they were added based on single references, or in case of predation risk and food sharing were classified according to the original reference.

We followed the latest taxonomy according to the IUCN red list (2016) and adapted the data compilation accordingly.

Statistical Analysis

Due to the broad set of different variables we first applied phylogenetic principal component analyses (pPCA, Revell 2009; package phytools, Revell 2012) in order to get a limited number of measurements, i.e. principal components (PC). Since the main aim of the study was to test the hypothesized evolutionary relationships within the framework of relative brain size and both, ecological and social opportunities and consequences, a pPCA was applied to each of the four domains separately. For that reason, and since a pPCA is not per se able to detect biologically/evolutionarily meaningful clusters and therefore not be able to logically distinguish between opportunities and consequences, an application over all variables would not serve the purpose of this study.

Primarily, categorical variables were numerically quantified based on increasing complexity of a trait (Table S1) and the pPCAs were performed on the mode of a correlation matrix due to different scaling of the variables. For subsequent analyses the PCs explaining a major part of the variation were used (cumulative proportion $\geq 40\%$). To facilitate intuitive interpretation, signs of all factor loadings from a PC were reversed if necessary, so that its values increased with increasing complexity of the traits (note that a systematic reversal of the sign of factor loadings does simply reverse the sign of the PC, and thus does not influence the sizes but only the directions of the effects in subsequent PGLS regressions). The separate pPCAs are based on the maximum sample sizes of each of the four domains (social opportunities: N=67, ecological opportunities: N=50, social consequences: N=60, ecological consequences: N=53) so that none of the available information is lost.

In a second step, we ran a phylogenetic path analysis (von Hardenberg and Gonzalez-Voyer 2013, Gonzalez-Voyer and von Hardenberg 2014) in the package phylopath (van der Bijl 2017) in order to test for the multidirectional evolutionary paths within the conceptual framework of opportunities and consequences. We compared a total of 28 candidate models, where the main evolutionary paths point in the four possible directions (Fig. S2 - S5, indicated with A, B, C, D), with each of the basic models (Path models: A1, B1, C1, D1) including all five possible paths representing the interrelationships within the opportunities and consequences, respectively (Path models: A2-A7, B2-B7, C2-C7, D2-D7). Path models A (Fig. S2) build up on our hypothesized framework stating that opportunities facilitate the evolution of enlarged brains and the consequences are its direct results, whereas path models B

(Fig. S3) would claim the opposite evolutionary directions. Path models C (Fig. S4) would postulate that all four domains (social and ecological opportunities and consequences) act as selective agents on the evolution of brain size, suggesting that what we hypothesize as consequences also serve in the end as opportunities/drivers. For the sake of completeness, we also included path models D (Fig. S5), which propose that all variables included in this study are evolutionary consequences of enlarged brain.

Since the path analysis does not allow for cyclic, but only acyclic graphs, the interrelationships within opportunities and consequences include either the direction from the ecological to the social domain or the other way around. The best fitting models were chosen based on the corrected C statistic Information Criterion (CICc) (Gonzalez-Voyer and von Hardenberg 2014), a goodness of fit measurement based on the Akaike Information Criterion (Akaike 1974), with a ΔCICc smaller than 3. Subsequently we averaged the best fitting models weighted by the relative evidence (van der Bijl 2017). As a measurement of relative brain size within the path analysis we used the log brain size - log body mass residuals. The path analysis is based on the common sample of N=29 species.

In a third step, we tested the unidirectional associations between the PCs and relative brain size using phylogenetic least-squares (PGLS) regressions. These analyses are based on the maximum available sample sizes of the four domains (social opportunities: N=67, ecological opportunities: N=50, social consequences: N=60, ecological consequences: N=53) since the tests on the unidirectional paths are not bound to the common sample of 29 species. Thereby, none of the available information is lost and the pattern of the phylogenetic path analysis can be tested for its robustness using bigger sample sizes. The PGLS regressions were run in the package caper (Orme 2013), jointly estimating the phylogenetic signal lambda of the residuals. Based on the directions of the best-fit evolutionary path model, we tested the effect of the PCs on brain size in case of opportunities, whereas in case of consequences, we tested the effect of brain size on the PCs. Due to the strong covariance with body mass, especially with ecological variables, all PGLS regressions include body mass as a covariate in order to test the associations with relative brain size. In addition, both brain size and body mass were natural-log transformed in order to achieve evenly distributed residuals as required by the model assumptions. For the jackknife resampling analyses we calculated the mean and 95% percentile confidence intervals of the PGLS estimates. 1,000 data sets were jackknifed over tips based on sampling without replacement using a subsample size of 80% of the original sample size. To control for phylogenetic non-independence we used the primate phylogeny published by Perelman et al. (2011) (Fig. S1). All analyses and graphs were performed in the R programming language (R Core Team 2015).

Results

Phylogenetic Principal Component Analysis

The pPCAs encompassing social and ecological opportunity variables both resulted in two main principal axes explaining the largest part of the variation. In the social domain, both axes include a mixture of social structure as well as mating system characteristics (Table 5.1A, S3). PC1, explaining 22% of the variation, reflects the gradient in group size and cohesion, and the associated sexual dimorphism and (lack of) territoriality. PC2 (20%) describes the social and mating system, ranging from single male monopoly to multi-male scramble competition. The ecological traits cluster into a first principal component (26%), which reflects variation in diet composition and thus nutrient density. The second PC (18%) represents a habitat gradient, from open, seasonal terrestrial habitats with high degrees of seasonality to stable forest habitats with arboreal niches (Table 5.1B, S16). Together, they represent the gradient of ecological niche complexity.

Table 5.1: Opportunities. pPCA of A) Social opportunities and B) ecological opportunities. Given are the pPCA factor loadings for the two main principal components (cumulative prop. $\geq$ 40%) with corresponding Eigenvalues and the cumulative explained proportion. Factor loadings $\geq$ 0.5 are indicated in bold font. Detailed values for following PCs are given in Table S3 and S5, respectively.

A	Social opportunities	PC1	PC2	B	Ecological opportunities	PC1	PC2
	Eigenvalues	2.371	2.236		Eigenvalues	2.899	1.901
	Cumulative Proportion	0.216	0.419		Cumulative Proportion	0.264	0.436
	Multi-male-female group	0.049	**0.662**		Diurnality	-0.384	-0.342
	Group size	**0.509**	0.420		Wooded habitat	0.015	**-0.652**
	Gregariousness	-0.255	**0.646**		Arboreality	0.026	**-0.498**
	Fission-fusion	**0.568**	-0.123		Predation risk	0.393	0.302
	HR overlap	0.315	0.093		Mobility in ranging area	0.327	0.457
	Vocal terr. advertisement	**-0.604**	-0.458		Environmental seasonality	0.246	**0.503**
	Dispersal	-0.083	-0.423		Faunivory	**0.515**	-0.470
	Polygynandry	0.254	**0.600**		Frugivory	**0.697**	0.046
	Body size dimorphism	**0.770**	-0.246		Folivory	**-0.923**	0.065
	Visual trait dimorphism	**0.656**	**-0.586**		Extractive foraging	0.146	0.469
	Cooperative breeding	-0.405	-0.168		Diet quality	**0.896**	-0.334

Regarding the consequences, the pPCAs reduced both the socio-cognitive and eco-cognitive consequence variables to a single principal component explaining the greatest proportion of the variance (57% and 42%, respectively). In the social domain, all the factor loadings show high values (> 0.5), implying a high degree of interrelatedness among the socio-cognitive consequences (Table 5.2A, S32). In the ecological domain, all traits similarly show high loadings on this first principal component (Table 5.2B), except for the degree of buffering of environmental seasonality, which loads, also together with diet breadth, highly on the second PC (Table S39). This separation suggests that buffering habitat seasonality does not necessarily involve tool use or hunting, but rather reflects a general diet breadth expansion, which represents a separate eco-cognitive domain.

Table 5.2: Consequences. pPCA of A) Social consequences and B) Ecological consequences. Given are the pPCA factor loadings for the main principal component (cumulative prop. $\geq$ 40%) with corresponding Eigenvalues and the cumulative explained proportion. Factor loadings $\geq$ 0.5 are indicated in bold font. Detailed values for following PCs are given in Table S10 and S13, respectively.

A Socio-cognitive consequences	**PC1**	**B Eco-cognitive consequences**	**PC1**
Eigenvalues	2.281	Eigenvalues	2.111
Cumulative Proportion	0.570	Cumulative Proportion	0.422
		Buffering env. seasonality	0.113
Social learning frequency	**0.784**	Diet breadth	0.465
Coalition formation	**0.731**	Hunting	**0.769**
Social hunting	**0.856**	Tool use	**0.815**
Food sharing among adults	**0.633**	Innovation frequency	**0.791**

Multidirectional Analysis: Phylogenetic Path Analysis

Including the total of six PCs (2 each for the social and ecological opportunities and 1 each for the socio-cognitive and eco-cognitive consequences) into a phylogenetic path analysis reveals that two models show a substantial increase in the goodness of fit (delta CICc < 3) compared to the 26 other candidate models (Table S2, Fig. S6). These are the models that include the evolutionary paths from the opportunities to brain size and from brain size to consequences, as well as the two-way interrelationship between eco-cognitive and socio-cognitive consequences. The averaged standardized regression coefficients of the two best fit models show that only ecological, i.e. energetic, opportunities significantly affect the evolution of relative brain size, whereas the social opportunities show much weaker effects (Fig. 5.1, left). The path model also reveals that brain size has especially strong effects on the eco-cognitive consequences, and these, as predicted by the notion of domain-general cognitive ability, are strongly related to the socio-cognitive consequences via a positive feedback loop (Fig. 5.1, right).

These results suggest that an enlarged brain leads to complex eco- as well as socio-cognitive consequences. The weak effect from brain to the social consequences can be explained by the use of the partial regression within the path analysis to test for the effect of brain size on social consequences, while additionally controlling for ecological consequences. In fact, the weak effect most likely represents a statistical artifact, since the phylogenetic path analysis exclusively allows acyclic paths, which prevents the accurate detection of the triangular evolutionary association between relative brain size and both socio-cognitive and eco-cognitive consequences.

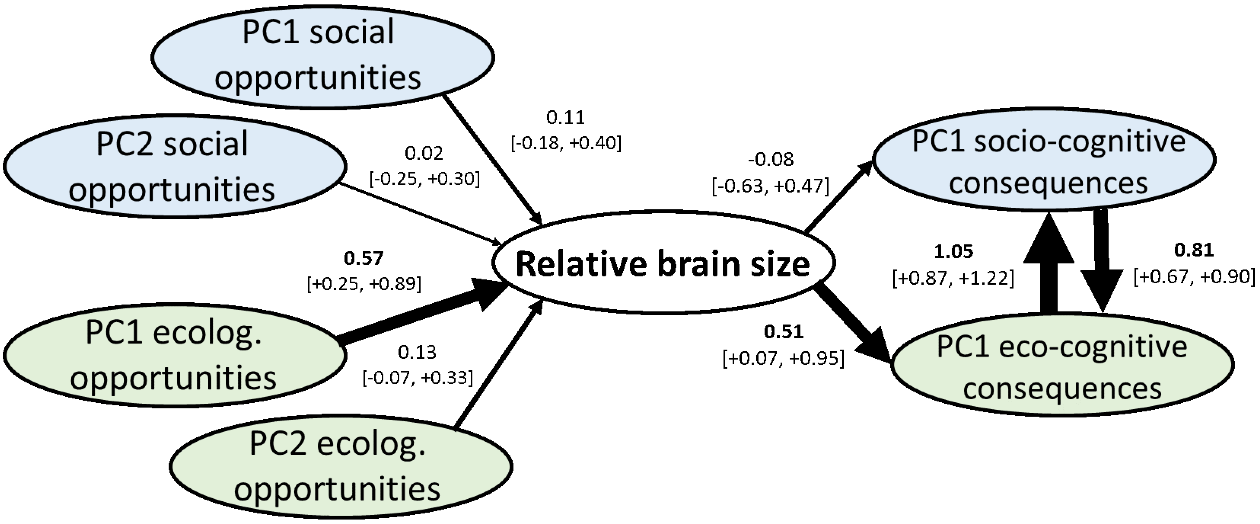

Figure 5.1: Multidirectional Analysis: Phylogenetic Path Analysis. The paths represent the average of the two models with the best goodness of fit where ΔCICc $\leq$ 3 (Models A2 and A3, Table S2, Fig. S6). Given are the average (weighted by the relative evidence) standardized regression coefficients and the corresponding confidence intervals in square brackets. Bold values indicate statistical significance, meaning the confidence interval does not include zero.

Unidirectional Analysis: Phylogenetic Least-Squares Regressions

The unidirectional PGLS regression models, which allow for bigger sample sizes, strongly support the patterns found in the phylogenetic path analysis. First, testing for the effects of the opportunity PCs on relative brain size showed that only the ecological principal components explain variation in relative brain size (PGLS: $N = 43$, $\lambda = 1.00$, $\beta_{PC1social} = 0.004$ ($p = 0.442$); $\beta_{PC2social} = -0.001$ ($p = 0.699$); $\beta_{PC1ecology} = 0.007$ ($p = 0.024$); $\beta_{PC2ecology} = 0.005$ ($p = 0.090$); Fig. 5.2A-D). This result also received high support from jackknife resampling analysis (Fig. 5.2E, F; Table S29). Further, a model selection approach using the common sample for social and ecological opportunities showed that the best-fitting model includes the two ecological PCs but none of the social PCs (Table S30).

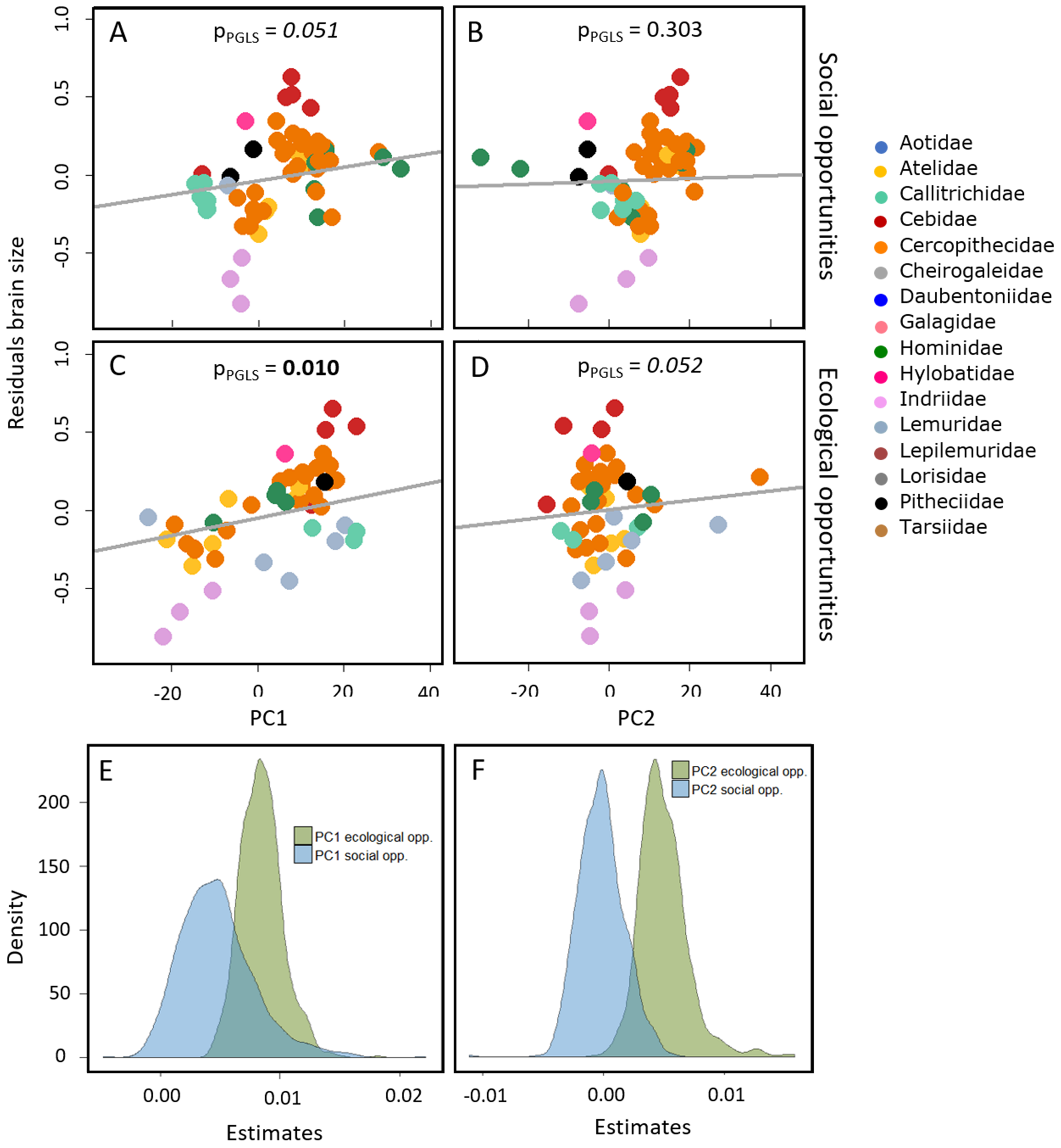

Figure 5.2: Unidirectional Analysis: PGLS on Opportunities. Bivariate relationships between relative brain size (residuals of log brain vs. log body) and the principal components of the social (A, B) and ecological (C, D) opportunities (N=43; presented are raw, non-phylogenetically corrected data; slopes of regression lines and p-values are based on the PGLS regression model). Density distributions are the result of 1,000 non-parametric jackknife resampling replicates of PGLS regression estimates (E, F; Table S29).

Second, regarding the consequences, the subsequent PGLS regressions also provided strong statistical support for a relationship between relative brain size and both the socio-cognitive PC1 (PGLS: $N = 60$, $\lambda = 0.00$, $\beta_{Brain} = 16.990$ ($p = 0.004$); Fig. 5.3A) and eco-cognitive PC1 (PGLS: $N = 53$, $\lambda = 0.81$, $\beta_{Brain} = 18.453$ ($p = 0.002$); Fig. 5.3B) (also with eco-cognitive PC2, which loads highly on the degree of buffering environmental seasonality, Table S40). Moreover, the results also show a very strong association among the socio-cognitive and eco-cognitive consequences (PGLS: response=PC1SocialConsequences, $\lambda = 0.00$, $N = 32$, $\beta_{PC1EcologicalConsequences} = 1.235$ ($p < 0.001$), Fig. 5.3C; response=PC1ecological consequences, $\lambda = 0.00$, $N = 32$, $\beta_{PC1SocialConsequences} = 0.663$ ($p < 0.001$)), even when we in additional control for relative brain size (Table S48, S49) or excluding strong outliers (Table S38, S47, S50-S53). In contrast, there were also no statistically significant relationships among the social and ecological opportunity PCs (Table S31).

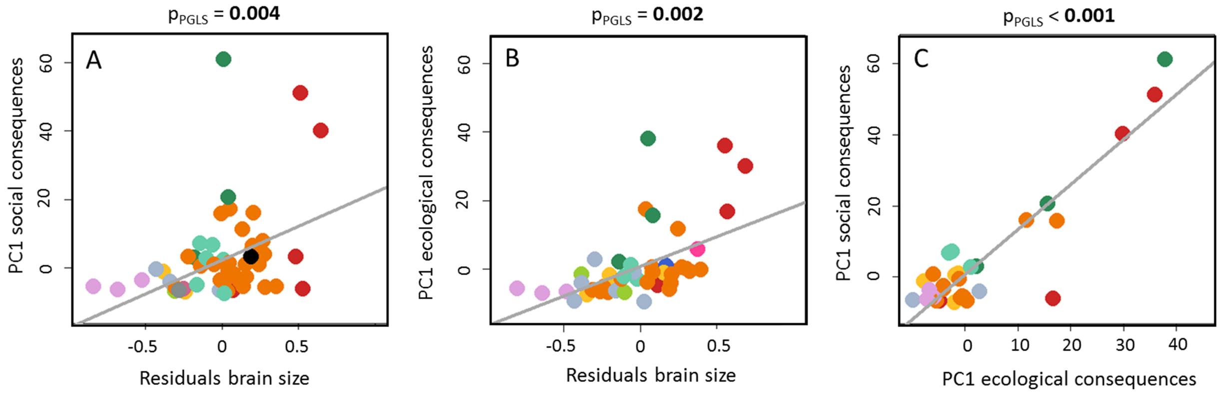

Figure 5.3: Unidirectional Analysis: PGLS on Consequences. Bivariate relationships between the first principal components of both the socio-cognitive (A) ($N_{spp.} = 60$) and eco-cognitive (B) ($N_{spp.} = 53$) consequences and relative brain size (residuals of log brain vs. log body) as well as the relationship between these two principal components (C) ($N_{spp.} = 32$) (presented are raw, non-phylogenetically corrected data; slopes of regression lines and p-values are based on PGLS). Color codes are identical to those in Fig. 5.2.

Discussion

The results were fully consistent with the presence of opportunities as potential selective agents, introduced in this study. They showed that ecological opportunities were far better predictors of relative brain size in a large sample of primates than social predictors, consistent with the predictions of the expensive brain approach. Finally, they also supported the notion of general cognitive flexibility, in that brain size in turn strongly predicted the immediate cognitive consequences, be they in the ecological or the social domain. We will discuss these main results in turn.

We used a variety of tests to validate the distinction between opportunities for selection and consequences. First, the phylogenetic path analysis revealed that the models including the paths from opportunities to brain size and from brain size to consequences as well as its interrelationships show a substantial increase in goodness of fit compared to all the other models, which strongly supports the notion of cause and effects implied by the concept of opportunities and consequences. Second, unlike for consequences, the principal axes of ecological and social opportunities were not correlated, underlining their independence. Third, they showed more modest relationships with relative brain size than the consequences, reflecting the possibility that some lineages could not (fully) respond to the opportunities they experienced. Finally, when we exchanged some variables whose assignment could be questioned, our results proved to be robust (Supplementary Information).
Given the high statistical robustness (Supplementary Results and Discussion), our results strongly suggest that selection on brain size in primates primarily reflects energetic opportunities. Since the principal components of ecological opportunities show a clear effect on relative brain size, this result suggests that highly nutritive foods linked to seasonally fluctuating environments provide species with potential access to an increased energy intake during times of scarcity, which directly supports an increase in brain size (Melin et al. 2014). The lack of statistical support for social opportunities suggests that the energetic costs of maintaining larger brains play a decisive part in enabling brain enlargement, and thus that ecological preconditions constrain brain size evolution. This pattern is consistent with previous empirical support for the role of energy in primate brain size evolution. Comparative studies have shown that the evolution of large brains is only possible in species where there is some combination of the following: the net energetic input is systematically increased (BMR: Dunbar and Shultz 2007, Isler et al. 2008; diet quality: DeCasien et al. 2017), the energetic turnover is stabilized over the year through the avoidance of starvation periods (van Woerden et al. 2010, 2012, 2014), or females receive subsidies during reproduction (Isler and van Schaik 2012).
Frugivory, if excluded from the pPCA, is the only variable to strongly reduce the effect of ecological opportunities on relative brain size (Table S28). This emphasizes the importance of net energetic input in brain size evolution and is highly consistent with the recent findings by DeCasien et al. (2017) showing that diet better predicts relative brain size in primates than sociality. However, since we also found support (even though statistically weaker) for PC2 of the ecological opportunities representing habitat cover and environmental seasonality, we would suggest that the degree of frugivory is probably not the exclusive driver. Furthermore, frugivory by itself does not explain why non-primate frugivorous species did not evolve larger brains.
Although the strong ecological perspective of brain size evolution suggests that correlations with social opportunities found in previous studies may be spurious (see also van der Bijl and Kolm 2016), a subset of the social demands posited by the social brain hypothesis may nonetheless have favored evolutionary increases in brain size, because they involve social processes that improve energy intake, such as the social learning of skills or coordination in foraging contexts.
The highly significant associations between relative brain size and both socio-cognitive and eco-

cognitive consequences, as well as the high interrelatedness among them, suggest a tight coevolution of abilities in different cognitive domains. These findings strongly support the notion of general behavioral flexibility or general intelligence, which has been postulated for mammals and birds, and is linked to relative brain size (Borrego and Gaines 2016, Burkart et al. 2016, Deaner et al. 2007, Lefebvre et al. 2004, Navarrete et al. 2016, Reader et al. 2011, Reader and Laland 2002). Furthermore, they support the inclusive concept of cultural intelligence, which states that the social acquisition of complex (ecological) skills is tightly linked to the evolution of intelligence (Whiten and van Schaik 2007, van Schaik and Burkart 2011, van Schaik et al. 2012). A larger and more complex skill repertoire, as a cognitive consequence, promote the frequencies of social learning, and vice versa, higher frequencies of social learning promote an individual‘s repertoire of ecological skills. This hypothesis therefore links ecological and social opportunities.

The absence of a clear correlation between the social and ecological opportunities strongly suggests that these two classes of opportunities arose independently. The finding that over the course of evolution ecological opportunities independently enabled the evolution of brain size explains the presence of so-called grade shifts within primates (van Schaik et al. 2012) and among taxa in different lineages (Holekamp 2007, Holekamp et al. 2015), where we find divergent relative brain sizes despite similar social opportunities.

In conclusion, these results suggest that complex cognitive abilities such as flexible tool use, understanding of third-party relationships or observational social learning could only evolve in lineages where the evolution of a large brain had been enabled by favourable ecological preconditions.

Even though our approach proposes a distinction between potential selective causes and consequences of enlarged brains, this does not exclude the fact that adaptations are often the result of evolutionary feedback loops. In other words, once a consequence has emerged, it may itself become a driver of further brain enlargement. For instance, if ecological opportunities favor simple forms of extractive foraging, selection may subsequently enhance extractive abilities by favoring manual dexterity (Heldstab et al. 2016) and tool use. Likewise, socio-cognitive abilities such as increased levels of food sharing, social learning and cooperation together may favor the exploitation of higher-quality food resources (protected plant foods, cooperative hunting for large prey) and reduced rates of mortality due to starvation and predation. This entails reduced severity of the life-history filter (cf. van Schaik et al. 2012) and thus reduced costs and thereby further releases the coevolutionary process between ecological opportunities and brain size. Nonetheless, these considerations do not refute the basic distinction because the correlation structure linking opportunities, brains and consequences should remain as envisaged here. First, not all opportunities are realized (as social opportunities did not seem to affect brain size). And second, all consequences, even if further enhanced by subsequent selection, remain consequences: enhanced extractive abilities still are an immediate reflection of brain size (Heldstab et al. 2016).

This new perspective is fully consistent with current ideas about the evolution of brain size within the hominin lineage. A substantial increase in relative brain size in *Homo ergaster* (ca 1.7 Mya) coincided with a dietary shift towards the inclusion of more nutrient dense foods (meat) in open and seasonal habitats, which was accompanied by a pronounced increase in technological (e.g. tool use) and social-ecological (e.g. extensive food sharing) complexity (Foley and Gamble 2009).

In sum, our results show that the unusually large brains of nonhuman primates did not evolve in response to the demands imposed by increasingly complex social life, but instead made ever more complex social life possible.

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Supplementary Material

Supplementary Material and Methods

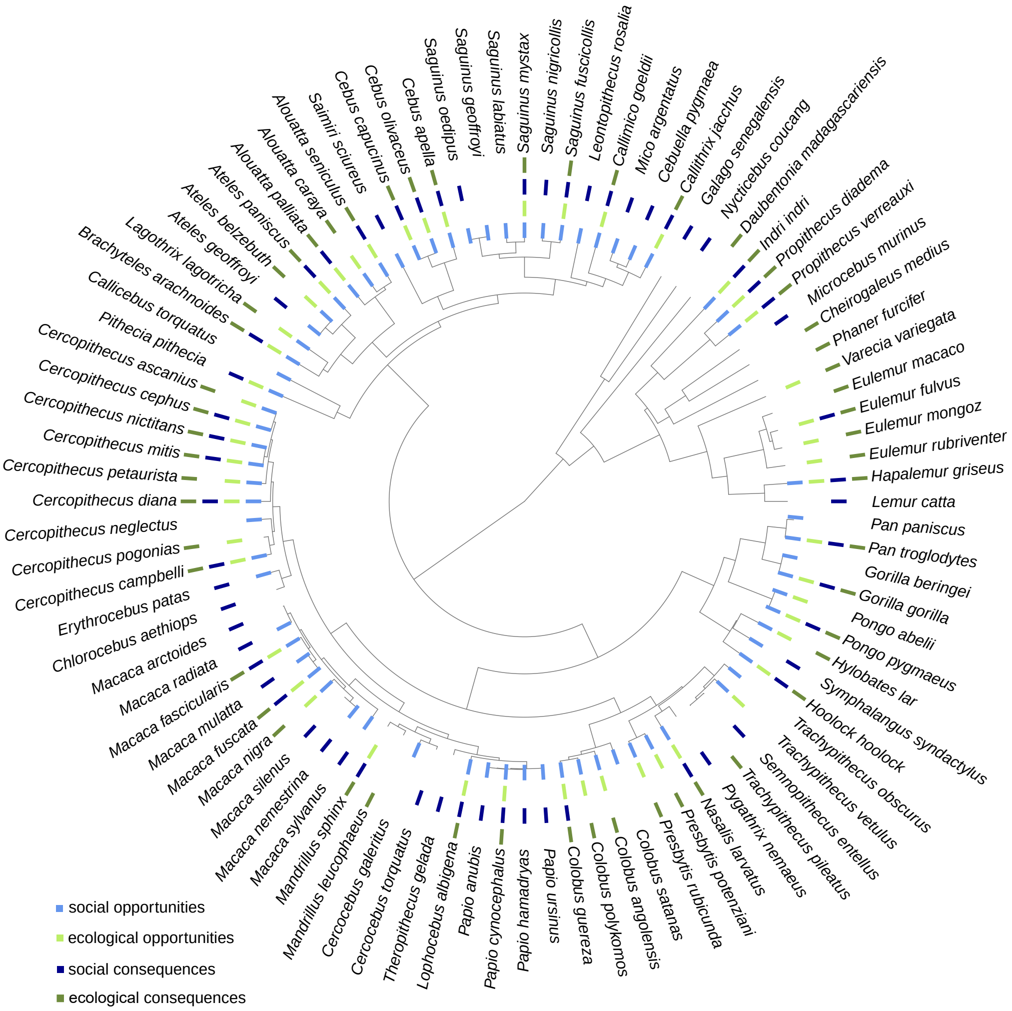

Figure S1. Phylogenetic tree of the 92 primate species showing the availability of information on the variables in the four domains including social/ecological opportunity and consequence variables.

Table S1. Measurements, numerical coding of variables and corresponding references

Variables	Measurements/Levels	References
Social Opportunities		
Social system	solitary = 0, sm-sF = 1, sM-mF/mM-sF = 2, mM-mF = 3	*41 - 43*
Home range overlap	% of the total range	*41, 42, 44*
Vocal territorial advertisement	no=0, yes=1	*41, 42*
Group size	count	*32, 41 - 43, 45*
Gregariousness	solitary=1, pairs=2, groups=3	*20, 39*
Fission-fusion	no=0, yes=1	*41 - 43, 46*
Dispersal	f/m=0, both f and m=1	*39, 45*
Mating system	monogamous=1, polygyn/polyandr.=2, polgynandrous=3	*38, 39, 47, 48*
Body size dimorphism	male / female body mass	*43, 49 - 51*
Visual trait dimorphism	sum of sex. dim. in every discernible ornament	*43*
Cooperative breeding	no=0, yes=1	*20, 41*
Ecological opportunities		
Activity period	nocturnal=0, diurnal=1	*41, 42, 52, 53*
Habitat	open=0, wooded=1	*41 - 43, 53*
Substrate	terrestrial=0, arboreal=1	*20, 41, 42, 53, 54*
Predation risk	low=1, medium=2, high=3	*53*
Mobility in ranging area	D-index=average daily path length / diameter ranging area	*41, 42, 55, 56*
Environmental seasonality	coefficient of variation (CV) in plant productivity	*57*
Faunivory	annual mean proportion of insects and meat in diet	*58 - 111*
Frugivory	annual mean proportion of fruits and seeds in diet	*58 - 111*
Folivory	annual mean proportion of leaves in diet	*58 - 111*
Extractive foraging	no=0, yes=1	*16, 19, 112*
Diet quality	sum of annual mean proportion of each diet category times its quality value	quality value from *113*
Socio-cognitive consequences		
Social learning frequency	orth. residuals log-log with zool. record article count	*16*
Coalition formation	no=0, mm/ff=1, mm and ff=2	*112, 114, 115*
Social hunting	no=0, yes=1	*19, 46, 52, 116, 117*
Food sharing among adults	no=0, yes=1	*112*
Eco-cognitive consequences		
Buffering env. seasonality	CV in plant productivity - CV in diet composition	*57*
Diet breadth	number of diet categories >=10%	*52*
Hunting	no=0, yes=1	*19, 46, 52, 116*
Tool use	no=0, only captive=1, wild=2	*118*
Innovation frequency	orth. residuals log-log with zool. record article count	*16*

Supplementary Tables and Figures: Phylogenetic Path Analysis

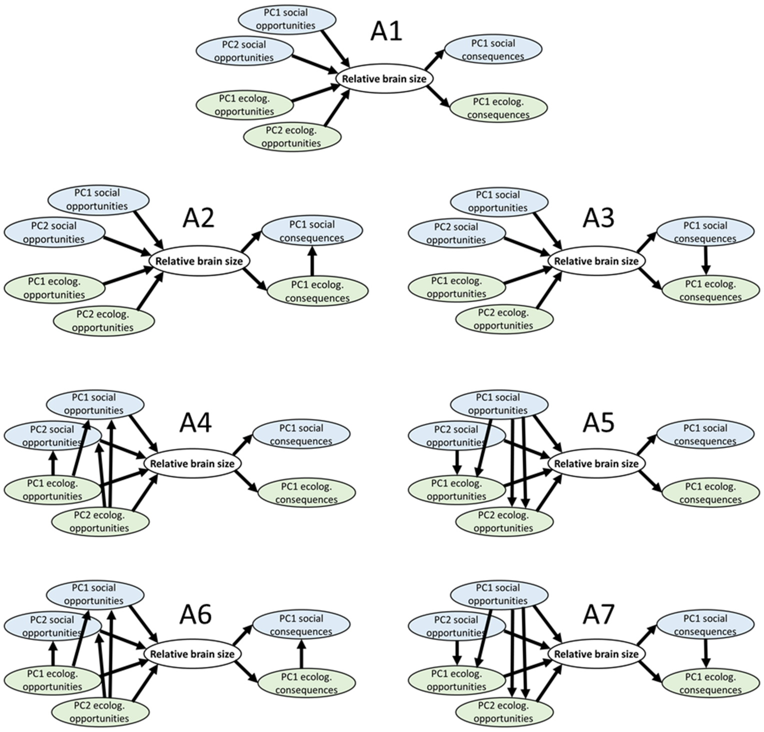

Figure S2. Phylogenetic Path Analysis. Candidate models A: Opportunities → brain size → consequences.

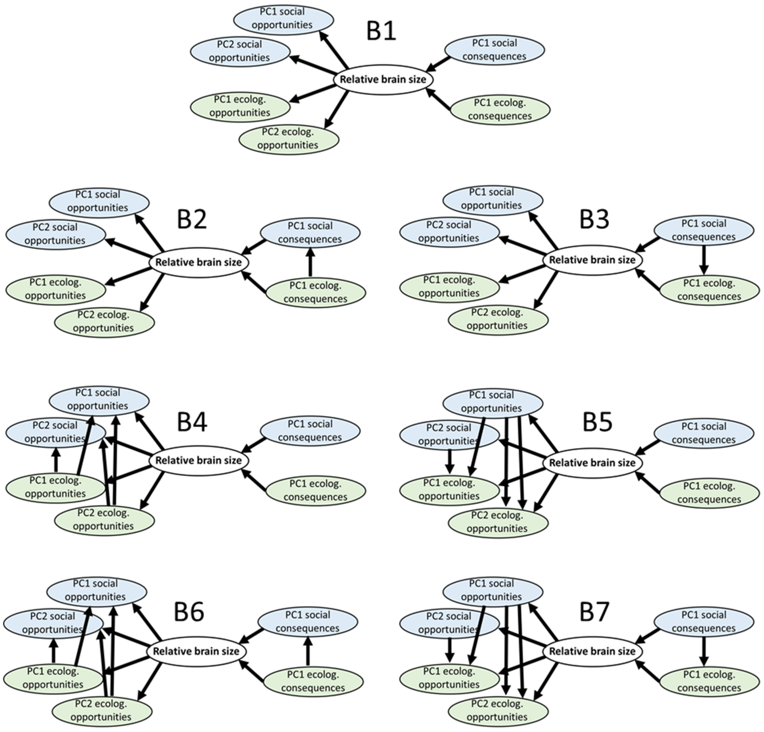

Figure S3. Phylogenetic Path Analysis. Candidate models B: Opportunities ← brain size ← consequences.

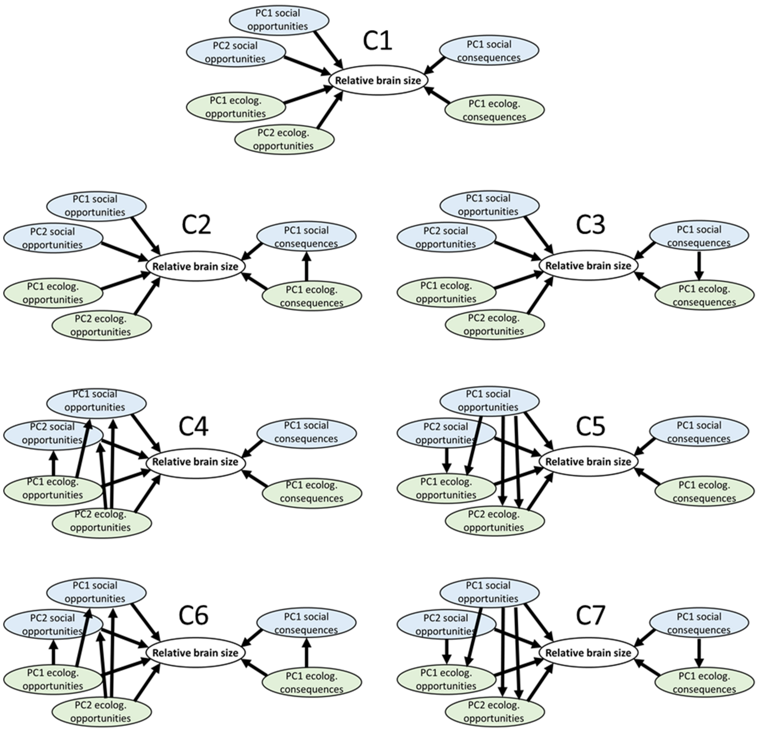

Figure S4. Phylogenetic Path Analysis. Candidate models C: Opportunities → brain size ← consequences.

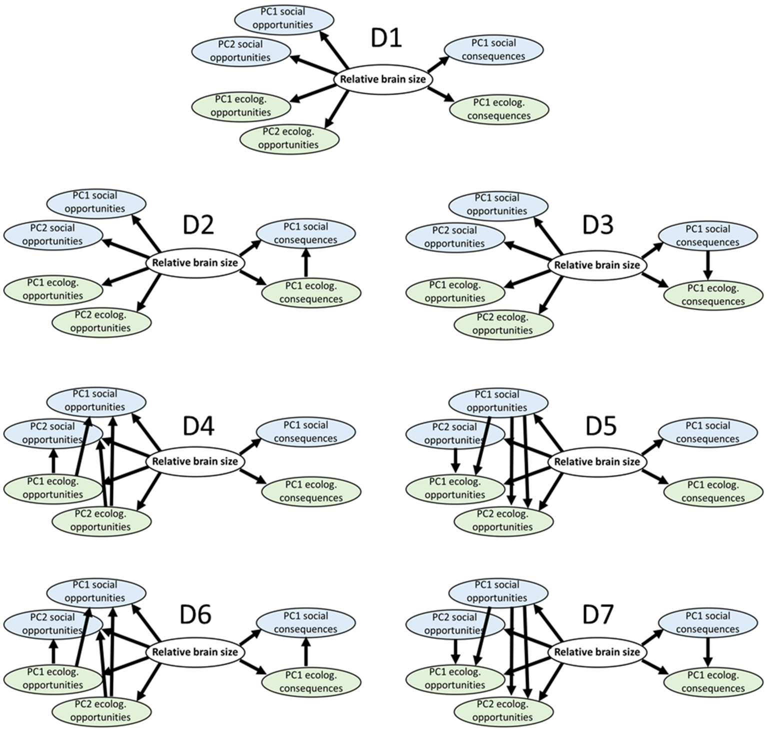

Figure S5. Phylogenetic Path Analysis. Candidate models D: Opportunities ← brain size → consequences.

Table S2. Phylogenetic path analysis. N = 29. Given are the number of conditional independencies (= number of d-separation statements) (k), C statistic (C), p-value (p), corrected C statistic information criterion (CICc) and the difference in the CICc (delta CICc) for each of the 28 candidate path models. Models A2 and A3 show the best goodness of fit (delta CICc < 3).

model	k	C	p	CICc	delta_CICc
A2	14	24.08	0.68	82.08	0.00
A3	14	26.65	0.54	84.65	2.56
D2	14	29.01	0.41	87.01	4.93
B2	14	29.59	0.38	87.59	5.51
B3	14	31.57	0.29	89.57	7.49
D3	14	31.57	0.29	89.57	7.49
C2	14	34.12	0.20	92.12	10.04
C3	14	42.83	0.04	100.83	18.74
A7	10	17.54	0.62	121.94	39.86
A6	10	17.72	0.61	122.12	40.03
B7	10	21.03	0.40	125.43	43.35
D7	10	21.03	0.40	125.43	43.35
A1	15	75.75	0.00	126.02	43.94
D6	10	21.84	0.35	126.24	44.16
B6	10	22.42	0.32	126.82	44.74
D1	15	80.68	0.00	130.95	48.86
B1	15	80.85	0.00	131.12	49.03
C6	10	29.03	0.09	133.43	51.34
C7	10	34.82	0.02	139.22	57.14
C1	15	89.47	0.00	139.74	57.65
A4	11	67.92	0.00	157.56	75.47
A5	11	69.05	0.00	158.69	76.60
D4	11	71.94	0.00	161.58	79.50
B4	11	72.11	0.00	161.75	79.66
D5	11	72.54	0.00	162.18	80.09
B5	11	72.71	0.00	162.34	80.26
C5	11	79.13	0.00	168.77	86.68
C4	11	80.66	0.00	170.30	88.21

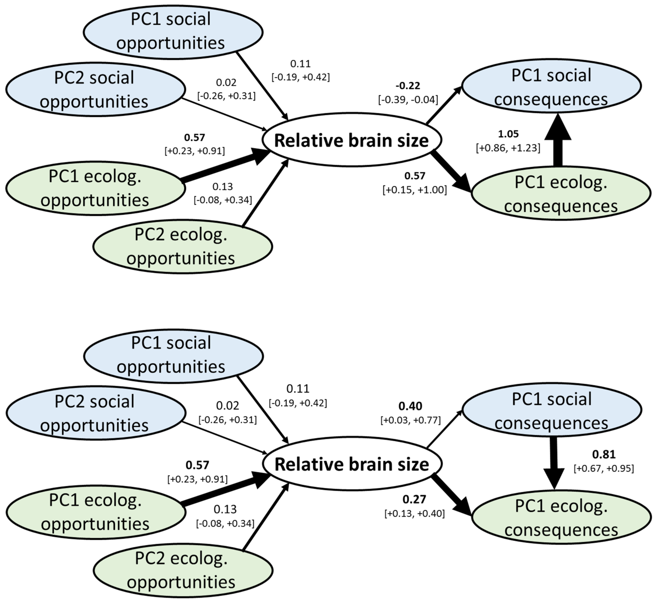

Figure S6. Phylogenetic Path Analysis: Best fit models A2 (top) and A3 (bottom). Given are the standardized regression coefficients and the corresponding confidence intervals (CI). Significant coefficients ($0 \notin$ CI) are indicated in bold.

Supplementary Tables and Analyses of Robustness: Phylogenetic Least-Squares Regressions

We tested the robustness of our conclusions in several different ways.
First, we systematically excluded each of the variables from the pPCAs (new loadings given in Tables S4 - S14, S17 - S27, S33 - S36, S41 - S45), and reran the subsequent PGLS regressions with the corresponding PCs to exclude the possibility that the relationships might actually be driven by a single variable. For the social opportunities, excluding single variables from the pPCA resulted in the majority of the cases in non-significant effects of the resulting two PCs on relative brain size (Table S15). For the ecological opportunity variables, the effects of the PCs on relative brain size remained basically similar (and significant for PC1), independent of which variable was excluded from the pPCA (Table S28). These findings imply that the statistical trend of PC1 of the social opportunities in the original analysis is not robust and thus reinforces ecology as the main driver of primate brain size evolution. The analogous analyses regarding consequence variables did not change our main findings (Tables S37, S46). Only the exclusion of hunting from the pPCA encompassing the ecological consequences yielded a non-significant result of PC1 with relative brain size, but that was because the factor loadings of the pPCA redistributed and loaded also highly on the second PC (Table S43), which therefore showed a highly significant association with relative brain size (Table S46). Additionally, we can exclude that the few large-brained hunting species are driving the association between relative brain size and ecological consequences, since excluding *Cebus appella*, *Cebus capucinus* and *Pan troglodytes* still yield a highly significant result (Table S47).
Second, we reclassified variables for which the assignment to opportunities could be questioned (fission-fusion and extractive foraging). Living in a *fission-fusion* society might not necessarily require a large brain, and is therefore classified as an opportunity variable. However, it has also been argued to require enhanced cognition in terms of long-term memory and recognition, in which case it should be classified as a consequence. *Extractive foraging*, on the one hand can be classified as an opportunity, since it simply represents a foraging technique used for specific types of foods (e.g. roots, tubers, specific insects), in special cases with morphological adaptations (e.g. *Daubentonia madagascariensis*), which does not necessarily require enhanced cognition. On the other hand, extracting foods from embedding matrices, closely linked to tool use, can be argued to be intrinsically cognitively demanding, in which case it must be classified as a consequence variable. This reclassification from opportunities to consequences made our results even stronger (see below).
Finally, we excluded striking outliers (*Cebus capucinus*, *Cebus apella*, *Pan troglodytes*) (S38, S47, S50 - S53), conducted a jackknife resampling technique without replacement (shown only for the combined model of opportunities, Table S29) and used common limited samples (where data were available on both social and ecological opportunity variables as well as the consequence variables, not shown), but also none of this changed our results.

Social Opportunities

Table S3. Phylogenetic PCA of social opportunity variables. N=67; lambda=0.95. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding factors.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Eigenvalues	2.3709	2.2358	1.3607	1.1637	0.8673	0.7445	0.7012	0.5851	0.5366	0.2335	0.2008
Cumulative Proportion	0.2155	0.4188	0.5425	0.6483	0.7271	0.7948	0.8585	0.9117	0.9605	0.9817	1.0000
Home range overlap	0.3147	0.0928	-0.4359	0.6620	-0.1648	-0.0653	-0.3717	0.1963	0.2122	0.0137	-0.1036
Vocal territorial advertisement	-0.6039	-0.4583	0.1831	-0.0401	-0.1851	0.1844	-0.4118	-0.0494	-0.3312	0.1167	-0.1630
Group size	0.5091	0.4197	0.4096	-0.1523	-0.2198	0.1424	-0.2075	0.4457	-0.2039	-0.0454	0.1407
Gregariousness	-0.2551	0.6456	0.4197	0.2832	0.3027	-0.0904	0.2311	0.1872	-0.0997	-0.0134	-0.2518
Fission fusion	0.5680	-0.1229	0.4491	-0.4173	0.0675	-0.3062	-0.2355	-0.0653	0.3012	0.1449	-0.1289
Body size dimorphism	0.7696	-0.2462	-0.0445	0.2968	-0.0067	-0.0209	0.2764	-0.0663	-0.3041	0.2882	0.0117
Visual trait dimorphism	0.6557	-0.5859	0.2002	0.1324	-0.0353	-0.0005	0.0286	-0.1462	-0.1473	-0.3316	-0.1188
Cooperative breeding	-0.4050	-0.1683	0.3663	0.2350	-0.6222	-0.4228	0.2141	0.0160	0.0601	-0.0026	0.0511
Dispersal	-0.0832	-0.4229	0.5577	0.3698	0.0943	0.4922	0.0746	0.0151	0.3185	0.0547	0.0710
Social system - multi M/F	0.0493	0.6619	0.3058	0.3287	0.0800	-0.0812	-0.2916	-0.4823	-0.0967	-0.0169	0.1327
Mating system - Polygynandry	0.2541	0.6000	-0.1031	-0.2016	-0.5076	0.3948	0.1669	-0.2175	0.1053	0.0138	-0.1555

Table S4. Phylogenetic PCA of social opportunity variables excluding Home range overlap. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.32	2.19
Cumulative Proportion	0.23	0.45
Vocal territorial advertisement	0.34	-0.65
Group size	-0.34	0.60
Gregariousness	0.45	0.49
Fission fusion	-0.64	0.14
Body size dimorphism	-0.78	0.07
Visual trait dimorphism	-0.85	-0.27
Cooperative breeding	0.29	-0.32
Dispersal	-0.15	-0.40
Social system - multi M/F	0.21	0.61
Mating system - Polygynandry	0.03	0.66

Table S5. Phylogenetic PCA of social opportunity variables excluding Vocal territorial advertisement. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.30	1.86
Cumulative Proportion	0.23	0.42
Home range overlap	-0.13	0.22
Group size	-0.12	0.78
Gregariousness	0.60	0.31
Fission fusion	-0.53	0.35
Body size dimorphism	-0.72	0.31
Visual trait dimorphism	-0.89	0.07
Cooperative breeding	0.16	-0.34
Dispersal	-0.27	-0.25
Social system - multi M/F	0.40	0.60
Mating system - Polygynandry	0.25	0.61

Table S6. Phylogenetic PCA of social opportunity variables excluding Group size. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.31	1.99
Cumulative Proportion	0.23	0.43
Home range overlap	-0.17	0.38
Vocal territorial advertisement	0.16	-0.80
Gregariousness	0.60	0.24
Fission fusion	-0.52	0.13
Body size dimorphism	-0.75	0.34
Visual trait dimorphism	-0.88	-0.05
Cooperative breeding	0.20	-0.46
Dispersal	-0.23	-0.45
Social system - multi M/F	0.38	0.49
Mating system - Polygynandry	0.22	0.59

Table S7. Phylogenetic PCA of social opportunity variables excluding Gregariousness. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.40	1.92
Cumulative Proportion	0.24	0.43
Home range overlap	0.34	0.00
Vocal territorial advertisement	-0.73	0.21
Group size	0.61	-0.18
Fission fusion	0.50	0.29
Body size dimorphism	0.65	0.52
Visual trait dimorphism	0.43	0.80
Cooperative breeding	-0.44	0.11
Dispersal	-0.25	0.53
Social system - multi M/F	0.26	-0.50
Mating system - Polygynandry	0.45	-0.56

Table S8. Phylogenetic PCA of social opportunity variables excluding Fission fusion. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.25	2.15
Cumulative Proportion	0.23	0.44
Home range overlap	0.27	0.36
Vocal territorial advertisement	-0.70	-0.32
Group size	0.59	0.16
Gregariousness	0.44	-0.56
Body size dimorphism	0.17	0.84
Visual trait dimorphism	-0.21	0.82
Cooperative breeding	-0.35	-0.31
Dispersal	-0.42	0.09
Social system - multi M/F	0.60	-0.30
Mating system - Polygynandry	0.65	-0.04

Table S9. Phylogenetic PCA of social opportunity variables excluding Body size dimorphism. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.22	1.86
Cumulative Proportion	0.22	0.41
Home range overlap	-0.21	-0.11
Vocal territorial advertisement	0.64	0.35
Group size	-0.55	-0.43
Gregariousness	-0.51	0.47
Fission fusion	-0.06	-0.75
Visual trait dimorphism	0.33	-0.77
Cooperative breeding	0.30	0.35
Dispersal	0.43	-0.10
Social system - multi M/F	-0.63	0.19
Mating system - Polygynandry	-0.66	-0.04

Table S10. Phylogenetic PCA of social opportunity variables excluding Visual trait dimorphism. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.28	1.69
Cumulative Proportion	0.23	0.40
Home range overlap	0.30	-0.21
Vocal territorial advertisement	-0.76	0.13
Group size	0.65	0.07
Gregariousness	0.24	0.78
Fission fusion	0.33	-0.37
Body size dimorphism	0.40	-0.61
Cooperative breeding	-0.42	0.31
Dispersal	-0.35	-0.03
Social system - multi M/F	0.47	0.61
Mating system - Polygynandry	0.59	0.22

Table S11. Phylogenetic PCA of social opportunity variables excluding Cooperative breeding. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.41	2.29
Cumulative Proportion	0.24	0.47
Home range overlap	-0.36	-0.17
Vocal territorial advertisement	0.76	-0.09
Group size	-0.67	0.22
Gregariousness	-0.08	0.76
Fission fusion	-0.49	-0.27
Body size dimorphism	-0.58	-0.58
Visual trait dimorphism	-0.32	-0.81
Dispersal	0.36	-0.23
Social system - multi M/F	-0.38	0.61
Mating system - Polygynandry	-0.56	0.35

Table S12. Phylogenetic PCA of social opportunity variables excluding Dispersal. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.35	2.11
Cumulative Proportion	0.24	0.45
Home range overlap	-0.27	0.14
Vocal territorial advertisement	0.51	-0.52
Group size	-0.46	0.51
Gregariousness	0.33	0.67
Fission fusion	-0.60	-0.03
Body size dimorphism	-0.80	-0.12
Visual trait dimorphism	-0.74	-0.43
Cooperative breeding	0.37	-0.18
Social system - multi M/F	0.05	0.71
Mating system - Polygynandry	-0.14	0.62

Table S13. Phylogenetic PCA of social opportunity variables excluding Social system - multi M/F. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.35	1.95
Cumulative Proportion	0.24	0.43
Home range overlap	-0.28	0.15
Vocal territorial advertisement	0.53	-0.58
Group size	-0.47	0.41
Gregariousness	0.31	0.46
Fission fusion	-0.60	-0.14
Body size dimorphism	-0.79	-0.16
Visual trait dimorphism	-0.73	-0.55
Cooperative breeding	0.37	-0.30
Dispersal	-0.01	-0.57
Mating system - Polygynandry	-0.16	0.67

Table S14. Phylogenetic PCA of social opportunity variables excluding Mating system - Polygynandry. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.35	1.94
Cumulative Proportion	0.24	0.43
Home range overlap	-0.24	0.23
Vocal territorial advertisement	0.42	-0.62
Group size	-0.37	0.52
Gregariousness	0.41	0.63
Fission fusion	-0.60	0.07
Body size dimorphism	-0.81	0.02
Visual trait dimorphism	-0.81	-0.33
Cooperative breeding	0.32	-0.30
Dispersal	-0.09	-0.39
Social system - multi M/F	0.14	0.69

Table S15. Estimates and p-values of the effects of PCs of social opportunities on relative brain size (mulitple PGLS regression). In the first row the result of the original analysis is given, in the subsequent rows, the results are based on PCs from pPCAs where systematically each of the variable is left out. All analyses are based on the maximum sample size used for the original analysis N=67. ∗Numerical optimization problem using PGLS in the package caper, alternatively applied bayesian phylogenetic mixed model in the package `MCMCglmm`, yielding equivalent results.

	PC1		PC2	
	estimate	p-value	estimate	p-value
all variables - original analysis	0.0056	0.0506	0.0030	0.3025
excluding Home range overlap	0.0039	0.1326	0.0056	0.0919
excluding Vocal territorial advertisement *	0.0017	0.5393	0.0036	0.3474
excluding Group size	0.0039	0.1334	0.0100	0.0042
excluding Gregariousness	0.0066	0.0306	0.0020	0.4214
excluding Fission fusion	0.0050	0.1144	0.0041	0.1567
excluding Body size dimorphism	0.0048	0.1435	0.0039	0.1811
excluding Visual trait dimorphism	0.0076	0.0181	-0.0074	0.0278
excluding Cooperative breeding *	0.0045	0.1444	-0.0005	0.8548
excluding Dispersal	0.0041	0.1305	0.0018	0.5761
excluding Social system - multi M/F	0.0064	0.0276	0.0063	0.0424
excluding Mating system - Polygynandry	0.0040	0.1266	0.0052	0.1451

Ecological opportunities

Table S16. Phylogenetic PCA of ecological opportunity variables. N=50; lambda=0.66. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding factors.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11
Eigenvalues	2.8990	1.9007	1.6252	1.3576	1.1027	0.6716	0.5531	0.4233	0.3088	0.1018	0.0561
Cumulative Proportion	0.2635	0.4363	0.5841	0.7075	0.8078	0.8688	0.9191	0.9576	0.9856	0.9949	1.0000
Predation risk	0.3930	0.3017	-0.2521	-0.0913	0.7377	0.0261	0.0334	-0.3135	0.1959	-0.0021	-0.0057
Mobility in ranging area	0.3274	0.4570	-0.3084	-0.5449	-0.1412	-0.3824	0.1583	0.2690	0.1532	-0.0684	0.0102
Environmental seasonality	0.2464	0.5027	0.6376	-0.0159	0.2464	-0.2322	0.2391	-0.0282	-0.3256	0.0334	-0.0072
Faunivory	0.5154	-0.4699	-0.4966	0.3352	0.2012	0.0042	0.2184	0.0964	-0.1865	-0.1096	0.1011
Frugivory	0.6970	0.0458	0.5676	-0.0288	-0.2742	0.0697	-0.1796	-0.1765	0.0697	-0.1999	0.0309
Folivory	-0.9231	0.0646	-0.1793	-0.1205	0.1324	0.0441	0.0942	-0.0589	-0.1184	-0.2024	-0.1013
Extractive foraging	0.1457	0.4687	-0.6264	0.1405	-0.3082	-0.2256	-0.3142	-0.2456	-0.2042	0.0180	-0.0014
Diet quality	0.8963	-0.3339	-0.0975	0.1741	-0.0079	-0.0377	-0.0035	0.0952	-0.0205	0.0116	-0.1850
Substrate - arboreality	0.0256	-0.4981	0.0816	-0.6019	0.3834	-0.1174	-0.4319	0.1077	-0.1523	-0.0011	0.0164
Activity - diurnality	-0.3843	-0.3422	0.2211	0.5187	0.1251	-0.6095	-0.0809	-0.0366	0.1466	-0.0269	0.0022
Habitat - wooded	0.0152	-0.6517	-0.0400	-0.4929	-0.2950	-0.1621	0.2985	-0.3545	-0.0223	0.0437	-0.0017

Table S17. Phylogenetic PCA of ecological opportunity variables excluding Predation risk. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	3.08	1.79
Cumulative Proportion	0.31	0.49
Mobility in ranging area	-0.35	0.12
Environmental seasonality	-0.31	-0.67
Faunivory	-0.63	0.50
Frugivory	-0.68	-0.31
Folivory	0.95	-0.03
Extractive foraging	-0.42	-0.09
Diet quality	-0.92	0.30
Substrate - arboreality	0.20	0.64
Activity - diurnality	0.12	-0.01
Habitat - wooded	0.11	0.68

Table S18. Phylogenetic PCA of ecological opportunity variables excluding Mobility in ranging area. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.78	1.84
Cumulative Proportion	0.28	0.46
Predation risk	-0.28	-0.33
Environmental seasonality	-0.20	-0.68
Faunivory	-0.53	0.46
Frugivory	-0.73	-0.26
Folivory	0.93	0.10
Extractive foraging	0.01	-0.27
Diet quality	-0.93	0.23
Substrate - arboreality	-0.09	0.51
Activity - diurnality	0.30	0.22
Habitat - wooded	-0.10	0.73

Table S19. Phylogenetic PCA of ecological opportunity variables excluding Environmental seasonality. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.78	1.88
Cumulative Proportion	0.28	0.47
Predation risk	0.28	0.43
Mobility in ranging area	0.24	0.61
Faunivory	0.56	-0.18
Frugivory	0.69	-0.12
Folivory	-0.92	0.03
Extractive foraging	0.06	0.72
Diet quality	0.93	-0.17
Substrate - arboreality	0.10	-0.45
Activity - diurnality	-0.36	-0.50
Habitat - wooded	0.13	-0.54

Table S20. Phylogenetic PCA of ecological opportunity variables excluding Faunivory. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2

	PC1	PC2
Eigenvalues	2.70	1.85
Cumulative Proportion	0.27	0.45
Predation risk	0.35	0.40
Mobility in ranging area	0.36	0.48
Environmental seasonality	0.38	0.18
Frugivory	0.80	-0.27
Folivory	-0.92	0.18
Extractive foraging	0.10	0.68
Diet quality	0.79	-0.29
Substrate - arboreality	0.02	-0.52
Activity - diurnality	-0.43	-0.34
Habitat - wooded	-0.03	-0.62

Table S21. Phylogenetic PCA of ecological opportunity variables excluding Frugivory. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.61	1.88
Cumulative Proportion	0.26	0.45
Predation risk	-0.51	0.29
Mobility in ranging area	-0.40	0.45
Environmental seasonality	-0.10	0.48
Faunivory	-0.67	-0.44
Folivory	0.83	0.07
Extractive foraging	-0.28	0.49
Diet quality	-0.89	-0.32
Substrate - arboreality	-0.02	-0.52
Activity - diurnality	0.40	-0.34
Habitat - wooded	0.00	-0.66

Table S22. Phylogenetic PCA of ecological opportunity variables excluding Folivory. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.22	1.86
Cumulative Proportion	0.22	0.41
Predation risk	-0.59	0.13
Mobility in ranging area	-0.51	0.31
Environmental seasonality	-0.22	0.54
Faunivory	-0.54	-0.60
Frugivory	-0.49	0.06
Extractive foraging	-0.36	0.34
Diet quality	-0.78	-0.45
Substrate - arboreality	0.03	-0.53
Activity - diurnality	0.53	-0.21
Habitat - wooded	0.08	-0.66

Table S23. Phylogenetic PCA of ecological opportunity variables excluding Extractive foraging. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.90	1.83
Cumulative Proportion	0.29	0.47
Predation risk	-0.39	-0.21
Mobility in ranging area	-0.31	-0.31
Environmental seasonality	-0.26	-0.73
Faunivory	-0.52	0.61
Frugivory	-0.71	-0.26
Folivory	0.93	0.02
Diet quality	-0.90	0.33
Substrate - arboreality	-0.05	0.40
Activity - diurnality	0.37	0.25
Habitat - wooded	-0.03	0.61

Table S24. Phylogenetic PCA of ecological opportunity variables excluding Diet quality. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.29	1.71
Cumulative Proportion	0.23	0.40
Predation risk	-0.48	-0.20
Mobility in ranging area	-0.52	-0.30
Environmental seasonality	-0.51	0.05
Faunivory	-0.14	0.18
Frugivory	-0.68	0.52
Folivory	0.77	-0.42
Extractive foraging	-0.28	-0.67
Substrate - arboreality	0.15	0.54
Activity - diurnality	0.54	0.13
Habitat - wooded	0.24	0.58

Table S25. Phylogenetic PCA of ecological opportunity variables excluding Substrate - arboreality. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2

	PC1	PC2
Eigenvalues	2.88	1.81
Cumulative Proportion	0.29	0.47
Predation risk	-0.38	0.38
Mobility in ranging area	-0.32	0.55
Environmental seasonality	-0.25	0.55
Faunivory	-0.51	-0.56
Frugivory	-0.70	0.07
Folivory	0.93	0.09
Extractive foraging	-0.13	0.35
Diet quality	-0.90	-0.37
Activity - diurnality	0.38	-0.43
Habitat - wooded	-0.02	-0.53

Table S26. Phylogenetic PCA of ecological opportunity variables excluding Activity - diurnality. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.80	1.84
Cumulative Proportion	0.28	0.46
Predation risk	0.35	0.28
Mobility in ranging area	0.24	0.34
Environmental seasonality	0.24	0.62
Faunivory	0.56	-0.45
Frugivory	0.70	0.17
Folivory	-0.94	-0.05
Extractive foraging	0.09	0.39
Diet quality	0.93	-0.25
Substrate - arboreality	0.04	-0.55
Habitat - wooded	0.04	-0.72

Table S27. Phylogenetic PCA of ecological opportunity variables excluding Habitat - wooded. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.78	1.79
Cumulative Proportion	0.28	0.46
Predation risk	0.30	0.37
Mobility in ranging area	0.24	0.74
Environmental seasonality	0.23	0.35
Faunivory	0.48	-0.45
Frugivory	0.73	0.00
Folivory	-0.93	0.08
Extractive foraging	0.03	0.53
Diet quality	0.90	-0.31
Substrate - arboreality	0.08	-0.26
Activity - diurnality	-0.36	-0.57

Table S28. Estimates and p-values of the effects of the PCs of ecological opportunities on relative brain size (multiple PGLS regression). In the first row the result of the original analysis is given, in the subsequent rows, the results are based on PCs from pPCAs where systematically each of the variable is left out. All analyses are based on the maximum sample size used for the original analysis N=50.

	PC1		PC2	
	estimate	p-value	estimate	p-value
all variables - original analysis	0.0061	0.0102	0.0034	0.0516
excluding Predation risk	0.0043	0.0295	0.0027	0.0591
excluding Mobility in ranging area	0.0058	0.0137	0.0054	0.0079
excluding Environmental seasonality	0.0055	0.0320	0.0033	0.1119
excluding Faunivory	0.0072	0.0031	0.0021	0.2470
excluding Frugivory	0.0042	0.0972	0.0028	0.1008
excluding Folivory	0.0061	0.0170	0.0020	0.2488
excluding Extractive foraging	0.0057	0.0121	0.0040	0.0224
excluding Diet quality	0.0077	0.0012	0.0011	0.5344
excluding Substrate - arboreality	0.0061	0.0099	0.0038	0.0339
excluding Activity - diurnality	0.0060	0.0122	0.0043	0.0201
excluding Habitat - wooded	0.0064	0.0128	0.0040	0.0684

Social and Ecological Opportunities - models based on common sample

Table S29. Jackknife resampling (over tips) of PGLS regression model including all four opportunity PCs: N_{iter} =1000, subsample size =34 (80% of N=43). Given are the original estimates and corresponding p-values from the original PGLS regression as well as the mean estimates and 95% confidence intervals (CI) of the jackknifed sample.

	True estimate	p-value	Jackknife mean estimate	Jackknife 95% CI
(Intercept)	-1.675	0.002	-1.794	[-2.4899, -1.2383]
log(Body.Mass)	0.671	0.000	0.685	[0.619, 0.7582]
PC1.Social.Opportunity	0.004	0.442	0.005	[-3e-04, 0.0122]
PC2.Social.Opportunity	-0.001	0.699	-0.000	[-0.0034, 0.0037]
PC1.Ecological.Opportunity	0.007	0.024	0.008	[0.0053, 0.0123]
PC2.Ecological.Opportunity	0.005	0.090	0.005	[0.0016, 0.0097]

Table S30. Model selection based on Akaike Information Criterion (AIC). PGLS models with log brain size as the response and the social and ecological opportunity PCs as predictor variables. Models are based on the common sample of social and ecological opportunities ($N = 43$) and include log body mass as a covariate. Given are the estimates and corresponding p-values in brackets.

	AIC	PC1 social opp.	PC2 social opp.	PC1 ecological opp.	PC2 ecological opp.
model 1	-26.51	0.006 (0.231)	0.001 (0.761)	-	-
model 2	-33.49	-	-	0.008 (**0.010**)	0.004 (0.109)
model 3	-31.07	0.003 (0.514)	-	0.007 (**0.037**)	-
model 4	-26.10	-	0.001 (0.841)	-	0.003 (0.335)
model 5	-28.28	0.006 (0.158)	-	-	0.004 (0.199)
model 6	-30.66	-	<0.001 (0.920)	0.007 (**0.022**)	-
model 7	-30.31	0.004 (0.442)	-0.001 (0.699)	0.007 (**0.024**)	0.005 (*0.090*)

Relationships between Social and Ecological Opportunities

Table S31. Relationships between social and ecological opportunity PCs. PGLS models are based on the common sample of social and ecological opportunity variables ($N = 43$). Given are the estimates and corresponding p-values.

Response variable	Predictor variable	estimate	p-value
PC1 social opp.	PC1 ecological opp.	0.072	0.549
PC1 social opp.	PC2 ecological opp.	-0.028	0.804
PC2 social opp.	PC1 ecological opp.	0.076	0.527
PC2 social opp.	PC2 ecological opp.	0.154	0.173
PC1 ecological opp.	PC1 social opp.	0.122	0.549
PC1 ecological opp.	PC2 social opp.	0.128	0.523
PC2 ecological opp.	PC1 social opp.	0.160	0.204
PC2 ecological opp.	PC2 social opp.	0.186	0.142

Social Consequences

Table S32. Phylogenetic PCA of social consequence variables. N=60; lambda=0.24. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding factors.

	PC1	PC2	PC3	PC4
Eigenvalues	2.2814	0.8267	0.5271	0.3647
Cumulative Proportion	0.5704	0.7770	0.9088	1.0000
Social learning frequency	0.7839	0.0346	0.6200	0.0008
Coalition formation	0.7306	0.5515	-0.2336	0.3278
Social hunting	0.8559	0.0310	-0.2503	-0.4515
Food sharing among adults	0.6330	-0.7214	-0.1597	0.2312

Table S33. Phylogenetic PCA of social consequence variables excluding Social learning frequency. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	1.81	0.83
Cumulative Proportion	0.60	0.88
Coalition formation	-0.75	0.58
Social hunting	-0.89	0.04
Food sharing among adults	-0.67	-0.70

Table S34. Phylogenetic PCA of social consequence variables excluding Coalition formation. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	1.90	0.63
Cumulative Proportion	0.63	0.84
Social learning frequency	-0.79	-0.46
Social hunting	-0.84	-0.13
Food sharing among adults	-0.75	0.63

Table S35. Phylogenetic PCA of social consequence variables excluding Social hunting. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	1.68	0.82
Cumulative Proportion	0.56	0.83
Social learning frequency	-0.84	-0.06
Coalition formation	-0.73	-0.57
Food sharing among adults	-0.66	0.71

Table S36. Phylogenetic PCA of social consequence variables excluding Food sharing among adults. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.01	0.56
Cumulative Proportion	0.67	0.86
Social learning frequency	-0.79	0.59
Coalition formation	-0.81	-0.46
Social hunting	-0.85	-0.11

Table S37. Estimates and p-values of the effects of relative brain size on PC1 and PC2 of the social consequences (mulitple PGLS regression). In the first row the result of the original analysis is given, in the subsequent rows, the results are based on PCs from pPCAs where systematically each of the variable is left out. All analyses are based on the maximum sample size used for the original analysis N=60.

	PC1		PC2	
	estimate	p-value	estimate	p-value
all variables - original analysis	16.9897	0.0039	8.2686	0.0819
excluding Social learning frequency	17.1027	0.0019	8.9190	0.0681
excluding Coalition formation	13.5149	0.0383	-0.9076	0.7696
excluding Social hunting	13.2897	0.0075	-8.3163	0.0795
excluding Food sharing among adults	15.5943	0.0019	-5.0924	0.0641

Excluding outliers - *Cebus capucinus, Cebus apella, Pan troglodytes*

Table S38. PGLS. Response: PC1.Social.consequences; N=57; R^2=0.14; λ=0; AIC=376.18

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	4.164	9.678	0.430	0.669
log(Body.Mass)	-3.468	2.654	-1.307	0.197
log(Brain.Size)	6.120	3.267	1.873	0.066

Ecological Consequences

Table S39. Phylogenetic PCA of ecological consequence variables. N=53; lambda=0.77. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding factors.

	PC1	PC2	PC3	PC4	PC5
Eigenvalues	2.1107	1.4236	0.6438	0.4845	0.3374
Cumulative Proportion	0.4221	0.7069	0.8356	0.9325	1.0000
Degree of buffering env. seasonality	0.1128	0.8661	0.2546	0.4003	0.1094
Diet breadth	0.4652	0.6695	-0.4735	-0.3253	0.0736
Hunting	0.7692	0.1049	0.5206	-0.3040	-0.1838
Tool use	0.8151	-0.1926	-0.2876	0.3476	-0.3080
Innovation frequency	0.7908	-0.4209	0.0322	0.0716	0.4374

Table S40. PGLS. Response: PC2.Ecological.consequences; N=53; R^2=0.19; λ=1; AIC=361.35

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	45.791	16.592	2.760	0.008
log(Body.Mass)	-14.473	4.266	-3.392	0.001
log(Brain.Size)	19.063	5.705	3.341	0.002

Table S41. Phylogenetic PCA of ecological consequence variables excluding Degree of buffering env. seasonality. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.09	0.95
Cumulative Proportion	0.52	0.76
Diet breadth	-0.42	0.88
Hunting	-0.75	0.07
Tool use	-0.82	-0.13
Innovation frequency	-0.81	-0.39

Table S42. Phylogenetic PCA of ecological consequence variables excluding Diet breadth. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	2.22	1.04
Cumulative Proportion	0.56	0.81
Degree of buffering env. seasonality	-0.14	0.98
Hunting	-0.83	0.12
Tool use	-0.87	-0.02
Innovation frequency	-0.87	-0.25

Table S43. Phylogenetic PCA of ecological consequence variables excluding Hunting. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	1.67	1.39
Cumulative Proportion	0.42	0.77
Degree of buffering env. seasonality	0.27	0.81
Diet breadth	-0.20	0.84
Tool use	-0.88	0.15
Innovation frequency	-0.89	-0.09

Table S44. Phylogenetic PCA of ecological consequence variables excluding Tool use. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	1.64	1.35
Cumulative Proportion	0.41	0.75
Degree of buffering env. seasonality	-0.47	0.74
Diet breadth	-0.68	0.43
Hunting	-0.81	-0.30
Innovation frequency	-0.54	-0.72

Table S45. Phylogenetic PCA of ecological consequence variables excluding Innovation frequency. Given are the factor loadings as well as the Eigenvalues and the cumulative proportion of the corresponding PC1 and PC2.

	PC1	PC2
Eigenvalues	1.75	1.13
Cumulative Proportion	0.44	0.72
Degree of buffering env. seasonality	-0.52	0.74
Diet breadth	-0.75	0.33
Hunting	-0.73	-0.33
Tool use	-0.63	-0.61

Table S46. Estimates and p-values of the effects of relative brain size on PC1 and PC2 of the ecological consequences (mulitple PGLS regression). In the first row the result of the original analysis is given, in the subsequent rows, the results are based on PCs from pPCAs where systematically each of the variable is left out. All analyses are based on the maximum sample size used for the original analysis N=53. ∗Numerical optimization problem using PGLS in the package `caper`, alternatively applied bayesian phylogenetic mixed model in the package `MCMCglmm`, yielding equivalent results.

	PC1		PC2	
	estimate	p-value	estimate	p-value
all variables - original analysis	18.4526	0.0024	15.8780	0.0010
excluding Degree of buffering env. seasonality	16.3623	0.0059	12.0691	0.0047
excluding Diet breadth	21.2454	0.0116	13.8787	0.0012
excluding Hunting	7.4136	0.1108	17.6009	0.0000
excluding Tool use	19.6248	0.0000	9.6581	0.0568
excluding Innovation frequency *	24.4871	0.0004	5.0702	0.2681

Excluding outliers - *Cebus capucinus*, *Cebus apella*, *Pan troglodytes*

Table S47. PGLS. Response: PC1.Ecological.consequences; N=50; R^2=0.29; λ=0; AIC=309.09

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	18.665	8.729	2.138	0.038
log(Body.Mass)	-7.560	2.202	-3.433	0.001
log(Brain.Size)	10.810	2.655	4.071	0.000

Relationship between social and ecological consequences

Table S48. PGLS. Response: PC1.Social.consequences; N=32; R^2=0.84; λ=0; AIC=221.43

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-16.238	13.487	-1.204	0.239
PC1.Ecological.consequences	1.365	0.130	10.489	0.000
log(Body.Mass)	6.063	3.702	1.638	0.113
log(Brain.Size)	-8.421	4.861	-1.732	0.094

Table S49. PGLS. Response: PC1.Ecological.consequences; N=32; R^2=0.87; λ=0; AIC=194.27

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	16.380	8.503	1.927	0.064
PC1.Social.consequences	0.584	0.056	10.489	0.000
log(Body.Mass)	-6.391	2.229	-2.868	0.008
log(Brain.Size)	9.228	2.856	3.232	0.003

Excluding outliers: *Cebus capucinus*, *Cebus apella*, *Pan troglodytes*

Table S50. PGLS. Response: PC1.Social.consequences; N=29; R^2=0.41; λ=0; AIC=186.95

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.426	1.094	-0.389	0.700
PC1.Ecological.consequences	0.669	0.155	4.319	0.000

Table S51. PGLS. Response: PC1.Social.consequences; N=29; R^2=0.44; λ=0; AIC=189.5

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-11.117	12.168	-0.914	0.370
PC1.Ecological.consequences	0.765	0.182	4.198	0.000
log(Body.Mass)	3.583	3.283	1.091	0.286
log(Brain.Size)	-4.783	4.225	-1.132	0.268

Table S52. PGLS. Response: PC1.Ecological.consequences; N=29; R^2=0.41; λ=0; AIC=184.32

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.031	1.048	-0.029	0.977
PC1.Social.consequences	0.611	0.141	4.319	0.000

Table S53. PGLS. Response: PC1.Ecological.consequences; N=29; R^2=0.57; λ=0; AIC=179.41

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	15.058	9.947	1.514	0.143
PC1.Social.consequences	0.540	0.129	4.198	0.000
log(Body.Mass)	-6.122	2.545	-2.406	0.024
log(Brain.Size)	8.978	3.166	2.835	0.009

Reclassification of opportunities to consequences: fission-fusion and extractive foraging

Reclassifiying fission-fusion and extractive foraging as consequence variables made the original results even stronger. The factor loadings of pPCA on the opportunity variables are equivalent to the original analysis (Table S54), and the subsequent PGLS regressions show even stronger evidence for ecological rather than social factors driving brain size evolution. In fact, whereas the social opportunity PCs show no effect on brain size (PGLS: $N = 67$, $\lambda = 0.99$, $\beta_{PC1social} = 0.005$ ($p = 0.114$); $\beta_{PC2social} = 0.004$ ($p = 0.157$)), both PCs of the ecological domain show significant effects (PGLS: $N = 50$, $\lambda = 1.00$, $\beta_{PC1ecology} = 0.006$ ($p = 0.012$); $\beta_{PC2ecology} = 0.004$ ($p = 0.022$)). These results hold when combining the four PCs into a single regression model (PGLS: $N = 43$, $\lambda = 1.00$, $\beta_{PC1social} = 0.002$ ($p = 0.655$); $\beta_{PC2social} = 0.004$ ($p = 0.358$), $\beta_{PC1ecology} = 0.006$ ($p = 0.030$); $\beta_{PC2ecology} = 0.005$ ($p = 0.045$)).

Table S54. Phylogenetic PCA of opportunity variables.

A **Social opportunities**	**PC1**	**PC2**	**B** **Ecological opportunities**	**PC1**	**PC2**
Eigenvalues	2.252	2.150	Eigenvalues	2.900	1.826
Cumulative Proportion	0.225	0.440	Cumulative Proportion	0.290	0.473
Social system - Multi M/F group	**0.597**	-0.304	Diurnality	-0.369	-0.255
Group size	**0.590**	0.156	Wooded habitat	0.031	**-0.612**
Gregariousness	0.439	**-0.556**	Arboreality	0.048	-0.400
HR overlap	0.268	0.363	Predation risk	0.392	0.207
Vocal terr. advertisement	**-0.696**	-0.324	Mobility in ranging area	0.307	0.306
Dispersal	-0.420	0.093	Environmental seasonality	0.258	**0.728**
Mating system - Polygynandry	**0.654**	-0.045	Faunivory	**0.519**	**-0.615**
Body size dimorphism	0.168	**0.838**	Frugivory	**0.709**	0.265
Visual trait dimorphism	-0.207	**0.824**	Folivory	**-0.928**	-0.015
Cooperative breeding	-0.352	-0.308	Diet quality	**0.903**	-0.334

Also in case of the consequences, the pPCA as well as the subsequent PGLS regressions result in equivalent patterns as the original analysis. For the ecological and social domain, all variables load highly on the first PC (Table S55), and relative brain size shows strong effects on both, the social and ecological consequence PC (socio-cognitive PC1 PGLS: $N = 55$, $\lambda = 0.00$, $\beta_{Brain} = 16.393$ ($p = 0.007$); eco-cognitive PC1 PGLS: $N = 53$, $\lambda = 0.91$, $\beta_{Brain} = 20.033$ ($p = 0.015$); eco-cognitive PC2 PGLS: $N = 53$, $\lambda = 0.00$, $\beta_{Brain} = 17.910$ ($p < 0.001$)). Also the relationsip between the social and ecological consequence PCs is highly significant (PGLS: $N = 31$, $\lambda = 0.00$, $\beta_{PC1EcologicalCons.} = 0.889$ ($p < 0.001$)), whereas there is no relationship between the opportunity PCs (results not shown).

Table S55. Phylogenetic PCA of consequence variables.

A Socio-cognitive consequences	**PC1**	**B Eco-cognitive consequences**	**PC1**
Eigenvalues	2.367	Eigenvalues	2.510
Cumulative Proportion	0.474	Cumulative Proportion	0.418
		Extractive foraging	**0.652**
Fission-fusion	0.359	Buffering env. seasonality	0.020
Social learning frequency	**0.776**	Diet breadth	0.426
Coalition formation	**0.732**	Hunting	**0.738**
Social hunting	**0.835**	Tool use	**0.807**
Food sharing among adults	**0.634**	Innovation frequency	**0.841**

Chapter 6

General Discussion

General Implications and Future Research

This dissertation aimed to explain parts of the large variation in relative brain size among vertebrate lineages in relation to social and ecological factors, as well as to the interplay between those factors. Using a phylogenetic comparative approach, I tested specific hypotheses and integrated a broad range of factors from the social and ecological domain into a comprehensive framework which differentiates between potential drivers and cognitive consequences of enlarged brains.

Niche Complexity and Cultural Intelligence

The first part of this thesis investigated how extended periods of development and nutritional dependence, representing extended opportunities for acquiring skills, are linked to the evolution of relative brain size and cognition in primates, carnivorans (chapter 2) and birds (chapter 3). The cultural intelligence hypothesis proposes that more opportunities for socially mediated learning (time or number of tolerant role models) is closely linked to the size and complexity of skill repertoires and ultimately to increased relative brain size.

In chapter 2, we found evidence for two different basic life history pathways which allow for extended periods of learning: elongating the duration of post-weaning provisioning and decelerating the pace of development. Both serve as buffers against energetic deficits reducing the risk of brain starvation and concomitantly offer more time to practice or (socially) acquire skills. Different mammalian orders were shown to use either one or the other of these life history pathways. Whereas in carnivorans foraging niche complexity increases with prolonged periods of post-weaning provisioning, primates living in complex foraging niches rather exhibit a slowed-down pace of development. The discrepant findings in the life-history pathways between primates and carnivorans are most likely explained by fundamental differences in their feeding biology. Primates largely rely on small and easily accessible (albeit not necessarily easily processed) food items including leaves, insects and fruits, which are difficult to monopolise but do not necessitate active provisioning of the young. Many carnivorans, on the other hand, actively hunt large prey, often even cooperatively. This may explain why in carnivorans young individuals strongly depend on active provisioning during the period of skill acquisition, whereas in primates this in not the case.

Furthermore, we showed that in primates, but not in carnivorans, the degree of foraging niche complexity is positively related to relative brain size. In primates this supports the notion of the cultural intelligence hypothesis suggesting an evolutionary feedback loop between extended opportunities for skill acquisition, complex foraging niches and an increase in brain size. In carnivorans, on the other

hand, the lack of such a correlation suggests that the interaction with a complex foraging niche, as defined in chapter 2, does not necessarily require enhanced cognitive abilities, and these skills are simply practiced until full competence is reached.
Linked to these discrepant findings, the two mammalian groups show general differences in foraging behavior and relative brain size. Primates live on average in more complex foraging niches (e.g. extractive foraging and tool use are more common), show a larger behavioral repertoire (Changizi 2003) as well as increased levels of behavioral flexibility (Holekamp 2007) compared to carnivorans. Additionally, primates show a general grade-shift in relative brain size, being relatively larger brained compared to carnivorans (Boddy et al. 2012, cf. Holekamp et al. 2013).

One potential explanation for these discrepancies may be the morphological differences between the two lineages that are based on different feeding biologies.
First, primate species have hands, while most carnivorans have paws. This may ultimately shape the evolution of cognition differently in the two lineages. Hands in contrast to paws allow for high levels of manipulative complexity, which are closely linked to complex food processing techniques including extractive foraging and tool use (Heldstab et al. 2016). These more complex techniques, which occur mostly in primates and much less often in carnivorans, are learned late during ontogeny and are proposed to be the cognitively demanding elements of a foraging niche (Gunst et al. 2010, Meulman et al. 2013, Melin et al. 2014, Heldstab et al. 2016, Heldstab et al. in prep.). Similarly, the actual degree of manipulation complexity is correlated with relative brain size in primates (Heldstab et al. 2016), but not in carnivorans (Iwaniuk et al. 1999). In addition, Holekamp et al. (2013) suggested that the difference between hands and paws may have implications for opportunities for social learning during ontogeny. Grasping hands allow young to cling onto the parents' fur and therefore primates have the chance to observe and learn the interactions with the ecological (and social) environment from early on. In carnivorans, on the other hand, offspring are often left behind while parents go out and hunt. Put in a larger context, more opportunities for social learning in primates compared to carnivorans might promote the effect of cultural intelligence and thus also the evolution of brain size.
Second, the discrepancy in relative brain size and its relation with foraging niche complexity between the two lineages might be based on craniofacial constraints due to diet. The morphology of the carnivoran skull may be subject to a stronger trade-off between the extremely pronounced feeding apparatus required for feeding on prey and the brain case, and thus brain size (Holekamp et al. 2013). Therefore, brain size evolution in carnivorans in general might be more constrained compared to primates, entailing lower variation upon which selection can act on (Holekamp et al. 2013).

Besides morphological adaptations, higher levels of unavoidable mortality (e.g. infectious diseases) may further constrain brain size evolution in carnivorans. Thus, the life-history filter, which prevents the evolution of larger brains if their benefit for survival is limited by factors that cannot be influenced by increased cognitive abilities, may be more severe in carnivorans than in primates. In other words, if the costs of developing bigger brains are too high, the coevolutionary process between social learning, complex foraging niches and enhanced cognition is also less likely to be favored by evolution (Burkart and van Schaik 2010).

Taken together, the discrepancy in life history characteristics, niche complexity and brain size between primates and carnivorans might be the result of differences in feeding biology and the related morphological constraints (limbs and skull) as well as a more severe life-history filter. Even though both lineages are presumably subject to similar selective pressures, adaptations in ancestral forms together high levels of extrinsic mortality may have prevented evolutionary responses, i.e. increase in brain size, in one lineage (carnivorans) but not the other (primates) (Holekamp et al. 2013).

Although we found no correlation between foraging niche complexity and brain size in carnivoran species, it is premature to reject the cultural intelligence hypothesis for carnivorans. It might not be the cumulative sum of foraging niche complexity, but rather specific elements which are linked to the evolution of cognition. Indeed, social hunting does not only need prolonged periods of learning (Schuppli et al. 2012), but we also found that it is associated with enlarged brains in carnivorans, unlike extractive foraging or diet breadth. In agreement with this speculation, earlier work has suggested that primarily carnivorous carnivorans show increased relative brain sizes due to more complex foraging techniques and processing involved in hunting prey (Gittleman 1986, Swanson et al. 2012). Besides that, the time to nutritional independence, which is correlated with increased foraging niche complexity, represents only one dimension of opportunities for social learning in carnivorans. Many carnivoran species show extremely high levels of sociality and cooperation, entailing increased levels of social tolerance (Smith et al. 2012, Burkart et al. 2014). In order to further investigate the links between opportunities for social learning, foraging complexity and the evolution of cognition, more targeted studies are required where the foraging strategies should be characterised in more detail (e.g. individual hunting vs. social hunting, small prey vs. big prey, immobile prey vs. mobile prey) and further dimensions of opportunities for social learning (e.g. number of tolerant role models, degree of cooperation and thus social tolerance) should be taken into account.

In birds, the results of chapter 3 showed that extended opportunities for socially mediated skill transmission coevolved with increased relative brain size. We further found that the time in association with tolerant role models is related to relative brain size even after we additionally control for the effect of long-term pair bonding. A derived version of the social brain hypothesis proposes that high levels of cooperation and negotiation in long-lasting pair bonds are the driving forces in the evolution of enhanced cognitive abilities (Shultz and Dunbar 2010). Based on our results, however, we suggest that intensive cooperation in species with strong pair bonding entail high levels of social tolerance that in turn facilitate social learning. In other words, we suggest that the effect of long-term pair bonding on brain size, found by Shultz and Dunbar (2010), represents family living in terms increased opportunities for social learning, rather than the dynamics of pair-bonding.

Furthermore, we found striking differences between the two major lineages of birds. Passerine species clearly show the pattern described above, whereas no effect was found for non-passerine species. We suggest that fundamental differences in metabolism and vulnerability to starvation may lead to differences in the need to socially acquire complex skills, which allow passerines access to highly nutritive food sources. These differences, however, have yet to be tested empirically by looking at links with foraging niche complexity and habitat seasonality.

It should be noted that the high degree of mobility in birds makes niche complexity much more flexible than in mammals, entailing high levels of intraspecific variation in the former. Furthermore, the skill repertoire of a bird includes more than only foraging skills, as there is a large variety within the foraging dimension of a niche regarding habitat selection, search methods/patterns, food recognition and selection, prey capture and handling techniques (reviewed in Wunderle 1991). Finally, in birds, particular morphological adaptations enable them to explore specific niches (e.g. hummingsbirds showing co-evolution with ornithophilous flowers), which means that although the niche may appear complex to us, an individual bird does not necessarily have to learn or understand much. Therefore, capturing the dimensions of what makes a niche more or less complex in birds is hard to quantify on a species level and a rough classification into mobile prey, extractive foraging and tool use as applied in mammals (chapter 2) is not appropriate. To further consolidate the predictions of the cultural intelligence hypothesis in birds, future studies are therefore necessary to develop appropriate measures of niche complexity. Furthermore, including measures of seasonal variation in diet composition and energy intake similarly to the methodology used in chapter 4 could be helpful to investigate the discrepancy between passerines and non-passerines. This may yield further insights into whether passerine species do indeed rely on more complex foraging techniques to buffer lean periods than non-passerines.

In sum, both the findings from chapter 2 and 3 confirm the predictions of the cultural intelligence hypothesis, particularly in primates and birds and suggest that the evolution of enlarged brains is only feasible in species in which an enlarged and more complex skill repertoire can be acquired and socially learned over prolonged time periods. Therefore, the interplay between social factors in terms of socially mediated learning and ecological factors in terms of complex skills and foraging niches is indispensable for understanding the evolution of relative brain size. In carnivorans, future studies should be more targeted in characterizing the complexity of a foraging niche to test whether the cultural intelligence hypothesis holds across all major mammalian lineages. And in birds, the link between opportunities for social learning and brain size should be set in context with the size of skill repertoires and niche complexity.

Seasonality and the Evolution of Brain Size

In chapter 4 we integrated the cost and benefit perspective of ecological factors by investigating how the evolution of brain size is affected by seasonality. We tested the concomitant effects of two non-exclusive hypotheses in a sample of non-primate mammals: (i) the cognitive buffer hypothesis, which suggests large-brained species are better at coping with seasonally lean periods, and (ii) the expensive brain hypothesis, which proposes that seasonal fluctuations in food availability impose energetic constraints on the evolution of enlarged brains. Previous studies in anthropoid primates found evidence for both hypotheses (van Woerden et al. 2012, 2014). In lemurs, however, evidence for the expensive brain hypothesis but only weak support for the cognitive buffer hypothesis was found (van Woerden et al. 2010). Building up on these studies, we also used independent measures for environmental seasonality (i.e. fluctuations environmental productivity) and actually experienced seasonality (i.e. fluctuations in energy-rich diet composites). The expensive brain hypothesis was consolidated as a ubiquitous pattern among all so far investigated mammalian species. However, comparable to the findings in lemurs, we found only weak support for the cognitive buffer hypothesis in non-primate mammals. Thus, a cognitive buffer effect does not seem to be a ubiquitous pattern in mammals.

We suggest that extremely high metabolic and developmental costs of increased brain size as well as periods of unavoidable starvation in extreme seasonal habitats may make cognitive buffering a less feasible strategy in lemurs and non-primate mammals. Instead, selection seems to favor shifts in diet towards high quality foods (e.g. meat) and physiological buffering including hibernation and adipose depots.

This absence of a clear cognitive effect outside of anthropoid primates falls in line with the findings from chapter 2 that provide evidence for an association between niche complexity and relative brain size only among primates, but not among carnivorans (including also omnivorous carnivorans). Again, as discussed in the previous section, this fundamental difference between primate and carnivoran brain size evolution might be based on ancestral adaptations in morphology (limbs and skull) as well as different degrees of severity of the life-history filter.

In our study on seasonality, we did not include strict carnivorans and strict herbivores because there is no seasonal variation in diet composition or in the relative proportion of the diet component with the highest nutrient density. To proxy the experienced fluctuations in the energetic intake over the year in such species, a more direct measure of actual intake such as prey capture rate or time spent feeding would be needed.

We expect that also within those two groups a higher annual variation in energy intake constrains the evolution of brain size. However, for strict carnivorans, relying primarily on meat, we would predict that they experience relatively lower fluctuations in the caloric intake compared to other mammalian groups. The availability of animal prey (excluding invertebrates) as a high quality food resource is much less sensitive to fluctuations in environmental seasonality and thus enables a predator or scavenger to meet the minimum energetic requirements throughout the year, even in extremely seasonal habitats. Together with the overall improved diet quality, this may therefore explain why primarily carnivorous carnivorans have relatively larger brains than omnivorous and insectivorous carnivorans (Gittleman 1986, Swanson et al. 2012). Also, efficient and successful hunting techniques (e.g. cooperative hunting) seem not only to require elongated periods of learning (Schuppli et al. 2012), but also enhanced cognitive abilities, in carnivorans (chapter 2: Table S4) and also primates (chapter 5: relative brain size vs. socio-cognitive consequences including social hunting). However, whether these sophisticated hunting techniques and the potential link to cognition represents cognitive buffering needs to be tested in more detail.

In strict herbivores relying exclusively on leaves, shrubs and herbs, one might predict that the processing does not require higher cognitive capacity (cf. van Woerden 2011). Furthermore, on average the predation risk may be higher in herbivores compared to carnivorans (increased severity of life-history filter), which would make cognitive buffering a less feasible strategy.

However, more detailed characterization of dietary habits and an assessment of experienced seasonality through more direct measures of the seasonal variation in the actual energetic input (or expenditure, i.e. field metabolic rate) are required. Currently this data has not been compiled for a large and broad enough sample of species, and would require targeted studies.

What is cognitive buffering?

In both primates and non-primate mammals, the degree of buffering is measured by the difference between fluctuations in dietary composition relative to the fluctuations in environmental productivity. This quantification implies that in both groups buffering comprises some sort of dietary flexibility. Brain size is, however, only clearly associated with the degree of buffering in anthropoids, but not in lemurs and non-primate mammals. This suggests therefore that only in higher primates the stabilized energy intake goes together with enhanced cognition. To further understand the evolution of cognition, it is important to understand what are the cognitively demanding dietary adaptations used to buffer seasonality in higher primates, or in other words, what cognitive buffering actually comprises.

Primates rely mostly on hard-to-access resources as fallback foods such as roots or embedded invertebrates (Kaplan et al. 2000, Johnson and Bock 2004, Marshall and Wrangham 2007, Melin et al. 2014), which often require extractive foraging and tool use and have been suggested to be the cognitively demanding elements of a foraging niche (Melin et al. 2014, van Woerden et al. 2012). One might therefore expect skills used for cognitively buffering environmental seasonality to also be part of more complex foraging niches, particularly more complex knowledge niches (including extractive foraging and tool use). Posterior analyses using a common sample of primates with data of the knowledge niche complexity score from chapter 2 and the measurements of the degree of buffering from van Woerden et al. (2014), however, show no significant association between the two in anthropoid primates (PGLS: $N = 34$, $\lambda = 0.94$, response = knowledge niche complexity, predictor = degree of buffering, estimate = -2.65, $p = 0.10$, $R^2 = 0.08$). Furthermore, the PCA of the ecological consequences in chapter 5 sep-

arates extractive foraging and tool use from the degree of buffering, which also suggests that cognitive buffering is not necessarily linked to sophisticated foraging techniques. Similarly, one could predict that increasing levels of manipulative complexity used for sophisticated foraging techniques (Heldstab et al. 2016) reflect the cognitively demanding aspects of exploiting alternative food resources, i.e. buffering in higher primates. However, a systematic score measuring the degree of manipulation complexity, which is closely linked to brain size (Heldstab et al. 2016, unpublished data S. Heldstab), also yields no significant correlation with the degree of buffering in anthropoid primates (PGLS: N = 20, $\lambda = 1.00$, response = manipulation complexity, predictor = degree of buffering, estimate = -3.20, p = 0.10, $R^2 = 0.14$).
Overall, this would suggest that cognitive buffering of seasonally lean periods, as found across anthropoid primates, is not necessarily related to sophisticated technology involving high degrees of manipulative complexity. In orangutans it is known that complex foraging techniques (extractive foraging and tool use) are not necessarily used during the lean season, but mainly during the season when fruits and seeds are abundant (Koops et al. 2014; Schuppli, van Schaik and van Noordwijk unpublished data). Furthermore, a comparative study including chimpanzees, orangutans and capuchin monkeys showed that the evolution of complex technology, e.g. tool use, is related to environmental opportunities (resource density and amount of terrestriality), rather than to the necessity to compensate for seasonal lack of preferred foods (Koops et al. 2014). This suggests that complex foraging technologies and high manipulative complexity, which requires a relatively large brain (Heldstab et al. 2016), have not evolved primarily to compensate for seasonally lean periods, but rather enhance continuous access to high quality food resources, increasing the general total energy intake throughout the year.

In chapter 5 our results showed that the degree of buffering environmental seasonality shares high proportions of variation with dietary breadth in primates (PC2). Further posterior analyses reveal that diet breadth explains quite a bit of variation in the degree of buffering (PGLS: N = 42, $\lambda = 0.70$, response = degree of buffering, predictor = diet breadth, estimate = 0.05, p = 0.004, $R^2 = 0.19$). Therefore, cognitive buffering may mainly allow for a broad, general diet and the required knowledge for the spatio-temporal distribution of resources, i.e. when and where to find what. One way to empirically test this hypothesis would be to look at the ranging behavior of various species. If a species has a clear mental representation of its physical environment and its foraging niche, individuals are expected to move in a more goal-directed fashion from food patch to food patch. Otherwise, individuals are expected to show rather random ranging patterns. In any case, yet more targeted studies, which systematically test for factors best explaining the fluctuations in direct measures of energetic input are needed.

The Concept of Opportunities and Consequences

The aim of chapter 5 was to combine social and ecological hypotheses and their correlates of brain size evolution by integrating a wide range of factors. We suggested a conceptual approach distinguishing between potential selective pressures, referred to as opportunities, and eco- and socio-cognitive abilities which are enabled once a large brain has evolved, referred to as consequences. The aim of this study was twofold: first, to solve the long-lasting debate on whether ecological or social factors are the main drivers of increased brain size in primates; and second, to emphasize that understanding the evolution of cognition is not only about finding the main potential drivers which enable brains to become bigger. It is also about using the variation in brain size itself to explain why certain species show specific eco- and socio-cognitive behaviors whereas others do not. In other words, statistically speaking, relative brain size should be used as both dependent and independent (explanatory) variable. Thereby, this conceptual framework helps to understand the evolution of cognition from a much broader and more comprehensive perspective.

Regarding evolutionary opportunities, our analyses showed stronger statistical support for potential ecological rather than social selection pressures, suggesting that selection on brain size in primates reflects ecological more than social preconditions. Since both of the two principal components of ecological opportunities, diet and habitat stability, showed a significant effect or a strong trend with relative brain size, this result is not uniquely attributable to either of the two characteristics, but rather means that an ecological niche in its entirety enables increased encephalization. More challenging ecological niches do not only pose selective pressures but also provide a species access to an increased energy intake, which directly supports an increase in brain size. This finding is consistent with the expensive brain framework (Isler and van Schaik 2009) and the corresponding findings in chapter 4. We showed that an increase in brain size is possible only where ecological conditions favor a net increase in energy through either a generally improved diet quality (PC1 of ecological opportunities) or greater habitat stability and thus a more constant energy input (PC2 of ecological opportunities). This conclusion is further consistent with a recent study across a broad comparative sample in primates, showing diet rather than measures of social complexity to be a main correlate of increasing brain size (DeCasien et al. 2017).

Regarding the consequences of a relatively large brain, the highly significant associations with both the social and ecological consequences as well as the interrelationship between them shows that large-brained primates are competent in a broad range of complex cognitive abilities. This supports the idea of general behavioral flexibility as a close associate of enhanced cognition (Reader and Laland 2002, Deaner et al. 2006, Reader et al. 2011, Navarrete et al. 2016). Further, these results are in line with the findings in chapter 2, where we showed that large-brained primates are the ones with a more complex foraging niche including a broader diet, tool use and cooperative hunting, all elements representing ecological as well as social consequences. The positive feedback loop between ecological and social consequences also supports the inclusive cultural intelligence framework, for which we found evidence not only in primates (chapter 2), but also in birds (chapter 3). This feedback loop entails that more complex ecological skills and foraging niches are promoted by higher frequencies of social learning and vice versa. Ultimately this allows for access to more nutritive resources and thus more energy, which again boosts an increase in brain size.

Even though the concept proposes a distinction between potential causes and consequences of enlarged brains, it does not exclude the fact that adaptations are often the result of evolutionary feedback loops. In other words, once a consequence has emerged, it may itself boost the effect of the ecological drivers on enlarged brains. As consequences facilitate new opportunities, both opportunities and consequences are meaningful for brain size evolution. For example, if social complexity (e.g. social learning ability) can be used to coordinate ecological problems it may as well facilitate the effect of ecological opportunities on the evolution of enlarged brains by reducing the life-history filter (see also *Implications for Human Evolution*, p.162; Fig. 6.2).

Future work should test the concept of opportunities and consequences also in other lineages. Considering the results in chapter 2 and 4, where no cognitive link with more complex foraging niches and no clear cognitive buffer effect was found across non-primate mammals, enhanced cognition might entail different eco- and socio-cognitive consequences of enlarged brains in these lineages.

General Conclusions

This thesis investigated the coevolutionary patterns between relative brain size and three main elements encompassing social as well as ecological factors: (1) opportunities for socially mediated skill acquisition, (2) foraging niche complexity and (3) a stabilized energetic intake (Fig. 6.1).

First, we showed that more opportunities for social learning in terms of prolonged learning periods and more tolerant role models enable the evolution of enlarged brains, in birds (chapter 3), and indirectly in primates (chapter 2). Vice versa, chapter 5 provided evidence that large-brained primate species show higher frequencies of social learning as part of the socio-cognitive consequences.

Second, we showed that the evolution of complex foraging niches or specific elements thereof show correlated evolution with increased brain size. In primates, larger-brained species show higher levels of food processing (chapter 2) and make use of a broader diet and sophisticated foraging techniques including tools and hunting (chapter 2 and chapter 5). In carnivorans, on the other hand, we suggest that the evolution of enhanced cognition is linked to more complex foraging niches, such as sophisticated hunting techniques (e.g. cooperative hunting) (chapter 2). Yet, this remains to be investigated in more detail. Additionally, our results in chapter 2 show that extended periods of (social) learning also allow for the evolution into more complex foraging niches in primates as well as carnivorans. Together, these findings suggest an evolutionary feedback loop between opportunities for skill learning, complex foraging niches and relative brain size.

Third, we found evidence across all mammals that low degrees of experienced seasonality and thus a stable consumption of energy-rich foods is crucial for brain size to increase (chapter 4). However, our findings suggest that larger brains did not necessarily evolve to compensate for the lack of preferred foods during the lean season. In fact, there is no clear evidence for the claim that larger-brained non-primate mammalian species buffer seasonality more than smaller-brained species, in contrast to previous findings in anthropoid primates (van Woerden et al. 2012, 2014).

Finally, the last chapter of this thesis integrated all three elements together with other social and ecological factors in primates, and provides clear evidence that ecological more than social preconditions are the main drivers in the evolution of increased brain size. Further, the findings showed that once a large brain has evolved, the evolution of a variety of more complex socio- and eco-cognitive abilities is possible. Potential differences between lineages (e.g. between primates and carnivorans) have yet to be studied systematically by testing the conceptual framework of opportunities and consequences also in non-primate mammals.

Future research should test systematically how opportunities for social learning and specific aspects of foraging niche complexity are related to higher cognition in carnivorans. Furthermore, it should investigate the role of complex foraging niches in relation to opportunities for social learning and brain size, as well as how seasonality is related to the evolution of cognition across birds.

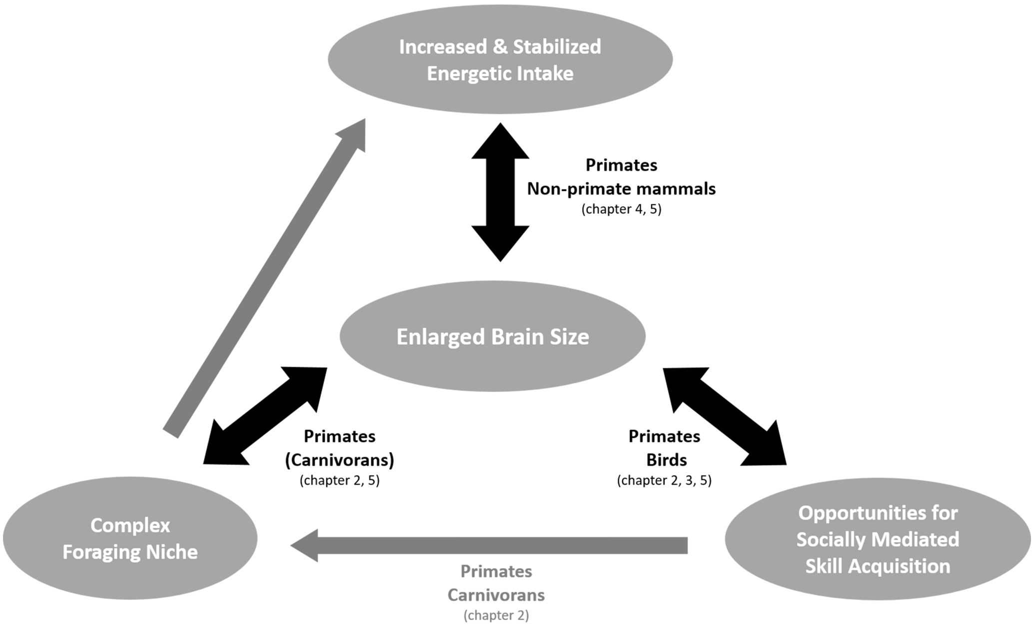

Figure 6.1: The evolutionary pathways between relative brain size, opportunities for socially mediated skill acquisition, foraging niche complexity and the energetic intake investigated in this thesis.

Implications for Human Evolution

The findings of this thesis ultimately help to understand the evolutionary history of our own lineage, and helps to explain why humans stand out among all animals with a unique combination of the features investigated in this thesis (Fig. 6.1): (1) complex foraging niches, (2) settling in all the world's habitats despite being exposed to various degrees of seasonality, (3) high levels of cumulative culture and (4) an extremely large brain and its associated highly developed intelligence.

We humans inherited a slow developmental pace from our great ape ancestor and combined that with high degrees of provisioning and resource sharing with infants, juveniles and even adults (Kaplan and Gurven 2005). This allows for extended periods of practice and learning, ultimately enabling the evolution into more complex foraging niches. In chapter 2, we showed that in primates a slow life history and in carnivorans elongated periods of provisioning provide more time to learn skills and thus allow to evolve into more complex foraging niches.
Around 2 Million years ago, genus *Homo* adopted persistent carnivory which lead to an overall increase in diet quality implying a stable and substantial increase in the energetic supply (Ferraro et al. 2013). This foraging adaptation towards a carnivorous and more nutrient dense diet co-occured with the emergence of big-game hunting, more complex foraging technologies relying on tool use and a substantial increase in relative brain size in *Homo ergaster* (Kaplan et al. 2000, Foley and Gamble 2009). We showed that a shift in diet towards higher proportions of meat allow non-primate mammals to live in more seasonal habitats. Together with preceding studies in higher primates providing evidence for cognitive buffering (van Woerden et al. 2012, 2014), this would suggest that in humans the combination of a carnivorous foraging niche and high levels of cognitive buffering enabled for a high and constant energetic input.
High quality and large, monopolizable foods are suggested to have further favored the evolution food sharing and high levels of cooperation in the history of hominin evolution (Kaplan et al. 2000). The eventual change in social system with the emergence of cooperative breeding with allomaternal care

did not only allow females to buffer seasonality (Helstab et al. 2017), but also led to an increase in social tolerance and thus more opportunities for social learning (Burkart et al. 2009). Thus, an increase in brain size was further promoted through the effect of cultural intelligence (van Schaik et al. 2012), for which we have shown comparative evidence in non-human primates as well as birds.

Furthermore, the positive feedback loop shaping the evolutionary history of the hominin lineage proposed by Kaplan et al. (2000) is fully consistent with the concept of opportunities and consequences (Fig. 6.2). Changing ecological conditions during the Pleistocene (1.7 MYA) led to the emergence of the African Savanna, where energy-rich and difficult to process foods including animal and protected plant foods (roots, tubers) became available. Besides that, the adoption of bipedality allowed for efficient locomotion and thus wide-ranging foraging habits. Together these changes offered high degrees of ecological opportunities driving the evolution of enlarged brains. Larger brains then entailed, on the one hand, more complex eco-cognitive abilities in terms of enhanced skills and on the other hand, socio-cognitive consequences such as high levels of food sharing and cooperation as well as social learning. Together, these consequences led again to food resources of even higher quality, reduced rates of mortality due to starvation and predation (i.e. a reduced severity of the life-history filter, cf. van Schaik et al. 2012). In turn, this facilitates the coevolutionary processes in which ecological opportunities favor the evolution of enlarged brains even more. In sum, the relatively large brain and unmatched degree of intelligence in humans is the result of a positive feedback loop between an increasing foraging niche complexity with high quality and stable foods, slow conservative development and extended opportunities for social learning. This thesis shows that such a scenario is supported by general patterns of correlated evolution that can also be found across other animals.

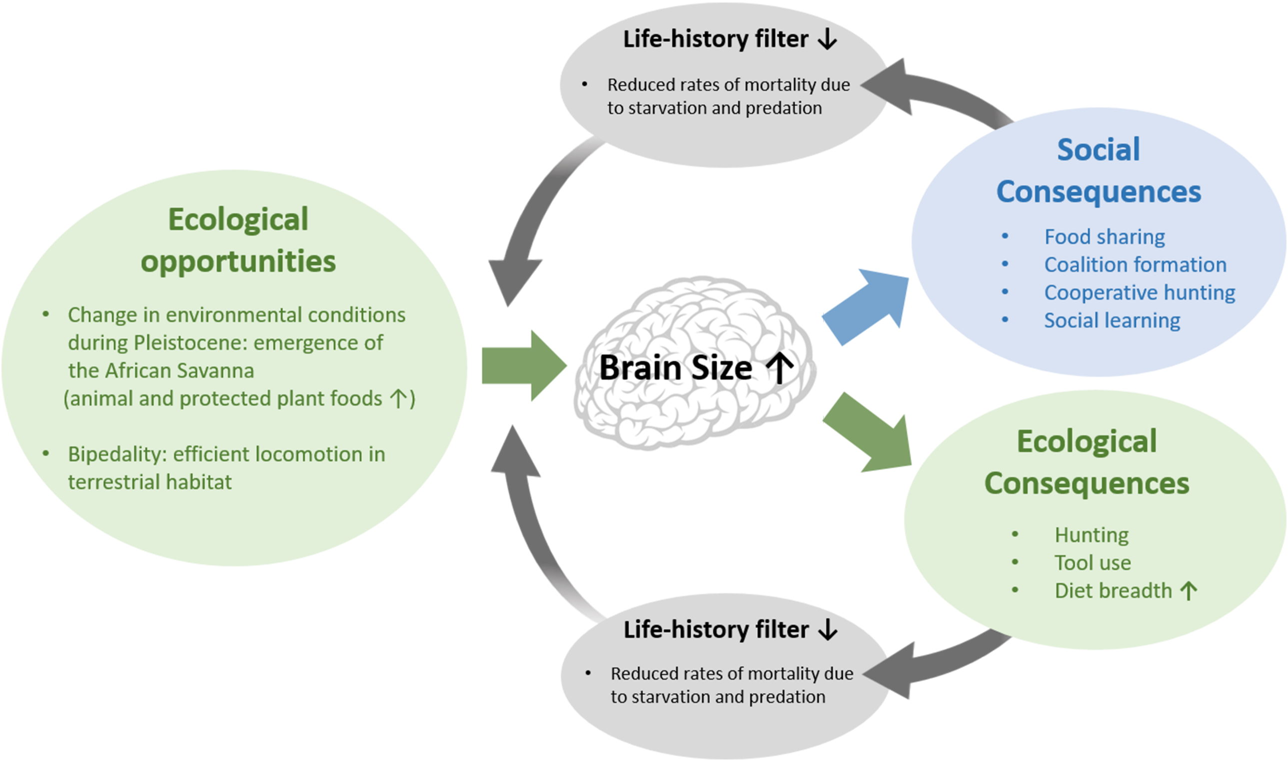

Figure 6.2: The history of hominin brain size evolution in terms of ecological opportunities and social and ecological consequences.

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