THE ROLE OF SKILL LEARNING IN COGNITIVE EVOLUTION:

FROM NICHE COMPLEXITY TO CULTURAL INTELLIGENCE

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To my Grandmother,

In memory, with love

Contents

Contents

Contents

Zusammenfassung

Mit zahlreichen Theorien ist versucht worden, die Evolution der unvergleichlich hohen menschlichen Intelligenz zu erklären. Kognitive Fähigkeiten für sich alleine sind unzureichend, um die energetisch kostspielige Vergrösserung des Gehirns, die mit gesteigerten kognitiven Fähigkeiten untrennbar einher geht, plausibel zu machen, es sei denn diese ermöglichen den Erwerb von Fertigkeiten mit bedeutenden Fitnessvorteilen: Obschon kognitive Fähigkeiten (und somit das Potential für die Entwicklung von Fertigkeiten) und nicht die Fertigkeiten selbst genetisch vererbt werden, sind es einzig die Fertigkeiten, die für die Natürliche Selektion fassbar sind. Das Hauptthema dieser Dissertation ist der Erwerb dieser Fertigkeiten, sprich Lernen als Teil des Entwicklungsprozesses. Der erste Fokus gilt den Bedingungen, die es einer Art erlauben, den Zeitraum auszuweiten, in dem Fertigkeiten erlernt werden, sowie in welchem Masse diese Bedingungen mit der Komplexität der Nahrungsnische einer Art zusammenhängen. Der zweite Fokus liegt auf der Hypothese der Kulturellen Intelligenz (Cultural intelligence hypothesis: CIH), welche einen Versuch darstellt, die kognitive Evolution durch die Möglichkeiten zu sozialem Lernen zu erklären. Die CIH besagt, dass auf der proximaten Ebene die Anzahl Möglichkeiten zu sozialem Lernen während der Entwicklung die Anzahl Fertigkeiten bestimmt, die ein Individuum erwerben wird, und sich dies aufgrund eines Erfahrungseffektes dann auch positiv auf die gegenwärtige Lernfähigkeit auswirkt. Des Weiteren können gemäss dieser Hypothese diese Unterschiede im Laufe der Evolution genetisch fixiert werden, woraus sich ergibt, dass die Möglichkeiten zu sozialem Lernen letztendlich ultimativ auch die angeborene Lernfähigkeit positiv beeinflussen.

Im Vergleich zu den meisten anderen Säugetieren erreichen auf ursprüngliche Weise in Jäger- und Sammler-Gesellschaften lebende Menschen ihre volle (adulte) Fertigkeitskompetenz in der Nahrungsbeschaffung (dem Aufsuchen und Verzehr von Nahrung) sehr spät in ihrer Entwicklung, lange nach dem Beginn der eigenen Reproduktionsphase. Das Ziel des zweiten Kapitels war es, die Faktoren zu untersuchen, welche die Länge der Lernperiode bestimmen, in der diese Fertigkeiten erworben werden können. Meine Analyse von Daten aus veröffentlichter Literatur zu 57 Säuger- und Vogel Arten hat gezeigt, dass die meisten Säuger ihre Fertigkeiten zur Nahrungssuche lange vor der Geschlechtsreife erlangen, wogegen die meisten Vögel adult ähnliche Fähigkeiten erst um den Zeitpunkt der eigenen Fortpflanzung herum erreichen. Innerhalb der Säuger verschiebt sich das Alter, bei dem die volle Fertigkeitskompetenz erreicht wird, mit zunehmender Komplexität der

Nahrungsnische nach hinten in der Entwicklung. Ein hohes Mass an Soziabilität, eine langsame und konservative Entwicklung sowie die systematische Versorgung der Jungtiere nach der Entwöhnung sind die Faktoren, die es gewissen Säuger Arten ermöglichen, ihre volle Fertigkeitskompetenz später in der Entwicklung zu erreichen. Arten, die ein systematisches und intensives Teilen von Ressourcen zeigen, wie zum Beispiel kooperative Jäger, erlangen ihre volle Fertigkeitskompetenz in der Nahrungssuche oft erst nach Beginn der eigenen Fortpflanzung. Ich zog daher den Schluss, dass das Menschliche Muster des späten Erwerbs der Nahrungsbeschaffungskompetenz nur dadurch evolvieren konnte weil bei unseren Vorfahren eine extensive und systematische Versorgung der Jungtiere und anderer Gruppenmitglieder sowie die kooperative Grosswildjagd mit einer für Menschenaffen typischen, langsamen Entwicklung zeitlich zusammentraf.

Im dritten Kapitel ging es darum, die Faktoren in der Lebensgeschichte zu bestimmen, die es einer Art ermöglichen, in eine komplexe Nische zu evolvieren. Hierfür habe ich die Korrelation zwischen der Komplexität der Nahrungsnische, verschiedenen Faktoren der Lebensgeschichte und der Hirngrösse von 78 Primaten- und 65 Karnivoren Arten untersucht. Die Resultate haben gezeigt, dass bei Primaten eine langsame und konservative Entwicklung mit der Komplexität der Nahrungsnische zusammenhängt und bei Karnivoren die Länge des Zeitraumes, über den Jungtiere versorgt werden. Bei Primaten, nicht jedoch Karnivoren, habe ich eine positive Korrelation zwischen Hirngrösse und der Komplexität der Nahrungsnische gefunden. Dies weist darauf hin, dass die Natürliche Selektion nur bei jenen Arten die Evolution in eine komplexe Nahrungsnische fördern kann, die sich entweder langsam entwickeln oder ihre Jungtiere über einen längeren Zeitraum versorgen. Beide Faktoren (eine langsame Entwicklung und eine verlängerte Jungtierversorgung) können verminderte Nahrungserträge während der Lernperiode (die durch die Inkompetenz des lernenden jungen Individuums für dieses entstehen) ausgleichen und so ist zu vermuten, dass sie limitierend auf die Evolution in komplexe Nischen wirken. Die Erkenntnisse dieser Studie deuten darauf hin, dass es der Mensch geschafft hat, in die komplexeste Nahrungsnische von allen Säugern zu evolvieren, in dem er eine langsame Entwicklung (wie bei allen Primaten) mit einer systematischen Versorgung von Jungtieren und anderen Gruppenmittgliedern (wie bei vielen Karnivoren) kombiniert hat. Des Weiteren unterstreichen die Resultate dieser Studie auch die Bedeutung von ökologischen Faktoren während der Kognitiven Evolution.

Das Ziel des zweiten Teils dieser Dissertation war es, die Voraussagen der CIH in Bezug auf Orang-Utans (*Pongo spp.*), einem unserer nächsten Verwandten, zu testen. Verschiedene Orang-Utan Populationen zeigen ein grosses Mass an Variation in ihrer Soziabilität, was mit grossen Unterschieden in den

Möglichkeiten zu sozialem Lernen einhergeht. Orang-Utans stellen daher ein natürliches Experiment dar, um den Effekt von variierenden Möglichkeiten zu sozialem Lernen auf den Fertigkeitserwerb und die Lernfähigkeit zu testen. Im Rahmen dieser Dissertation verglich ich eine Population von Sumatra Orang-Utans in Suaq Balimbing, Süd Aceh, die ein aussergewöhnlich hohes Mass an Soziabilität zeigt, mit einer weniger soziablen Population von Borneo Orang-Utans in Tuanan, Zentral Kalimantan, Indonesien. Ich habe hierfür die Entwicklung von 20 Jungtieren untersucht, wobei ihre Mütter als adulte Referenzpunkte dienten. Verhaltensdaten wurden nach einem standardisierten Protokoll durch Focal Scan Sampling mit Intervallen von zwei Minuten gesammelt. Für die meisten Tiere meiner Studie wurden diese Daten schon über mehrere Jahre vor dem Beginn meiner Studie auf eben diese Art erhoben. Zusätzlich, speziell im Rahmen dieser Studie, wurden all-occurrence Daten zu den im Fokus dieser Dissertation stehenden Verhaltensweisen erhoben, sprich zu allen Indikatoren für Soziales und Individuelles Lernen.

Damit die Voraussagen der CIH getestet werden können, muss der Modellorganismus bestimmte Voraussetzungen erfüllen. Die erste Voraussetzung hierbei ist der Besitz von Fertigkeiten, die im Laufe der Entwicklung erlernt wurden und nicht intrinsisch festgelegt sind. Im zweiten Kapitel habe ich daher den Erwerb der Nahrungsbeschaffungsfertigkeiten bei Jungtieren beider Populationen untersucht. Die Nahrungsbeschaffungsfertigkeiten wurden dabei in Nahrungserkennungs-, Nahrungsverarbeitungs- und Nahrungslokalisierungskompetenz unterteilt. Um diese Fertigkeiten zu messen, habe ich Daten zu Nahrungszusammensetzung, Verzehrgeschwindigkeit und Räumlichem Verhalten gesammelt. Die Auswertung meiner Daten hat gezeigt, dass die Jungtiere beider Populationen mehrere Jahre für den Erwerb ihrer Nahrungsbeschaffungsfertigkeiten benötigen. Volle Kompetenz in Nahrungserkennung und Nahrungslokalisierung werden um den Zeitpunkt der Entwöhnung herum, im Alter von 6.5 - 9 Jahren, erreicht. Nahrungsverarbeitungskompetenz hingegen wird kurz nach der Entwöhnung erreicht. Im Allgemeinen wird die Kompetenz in komplexeren Fertigkeiten (Z.B. bei Fresstechniken, die aus mehreren Schritten zusammengesetzt sind) später erreicht als in weniger komplexen. Die komplexesten Techniken wie zum Beispiel Werkzeuggebrauch werden zuletzt erlangt, wobei volle Kompetenz hier zum Teil auch erst nach dem Beginn der eigenen Fortpflanzung erreicht wird. Beide Erkenntnisse legen nahe, dass Orang-Utans ihre Nahrungsbeschaffungsfertigkeiten erst durch einen Lernprozess erwerben und diese Fertigkeiten nicht genetisch festgelegt sind.

Die zweite Voraussetzung, um die CIH testen zu können ist, dass die Fertigkeiten des Modellorganismus zumindest teilweise durch soziales Lernen erworben werden. Um zu testen, ob dies bei den Orang-Utans der Fall ist, habe ich die Häufigkeit und den Kontext des Peering Verhaltens

(aufmerksames Beobachten der Aktivität eines anderen Tieres aus nächster Nähe) der Jungtiere beider Populationen untersucht. Wie sich herausstellte, kommt Peering am häufigsten in Kontexten vor, die erlernte Fertigkeiten voraussetzen, nämlich Nahrungsbeschaffung und Nestbau. Es zeigte sich auch, dass die Häufigkeit von Peering im Nahrungskontext positiv mit der Komplexität sowie der Seltenheit des Futters korreliert ist. Unmittelbar nach dem Peering stieg die Häufigkeit von explorativem Verhalten mit demselben Nahrungsgegenstand signifikant an, sowie auch die Wahrscheinlichkeit, dass das Jungtier denselben Nahrungsgegenstand zu fressen beginnt wie jenes Tier, welches es gerade zuvor beobachtet hat. Des Weiteren ist den Daten zu entnehmen, dass Jungtiere unmittelbar nachdem sie ihre Mutter beim Nestbau dabei beobachtet hatten, dies signifikant häufiger selber üben. Ebenso stellte sich heraus, dass das Interesse an anderen Tieren mit zunehmenden Alter ansteigt, währendem die jüngeren Jungtiere ausschliesslich auf ihre Mutter konzentriert sind (d.h. alles Peering ist auf die Mutter gerichtet). All diese Ergebnisse sprechen dafür, dass Orang-Utan Jungtiere ihre Fertigkeiten zumindest teilweise sozial erlernen.

Ziel des fünften Kapitels war es, die ontogenetischen Voraussagen der CIH zu testen, nämlich dass Individuen, die in Populationen mit mehr Möglichkeiten zu sozialem Lernen aufwachsen, eine erhöhte gegenwärtige Lernfähigkeit entwickeln. Hierfür verglich ich die Häufigkeit von Peering und explorativem Verhalten der Tiere beider Populationen. Es stellte sich heraus, dass Tiere aus der soziableren Population in Suaq signifikant häufiger peeren als Tiere aus Tuanan. Dieser Unterschied blieb auch bestehen nachdem die Ergebnisse für unterschiedliche Peering-Möglichkeiten (verursacht durch Unterschiede in der Zeit die die Tiere zusammen mit anderen verbringen) korrigiert wurden. Zudem zeigen Jungtiere aus Suaq im Vergleich mit gleichaltrigen Tiere aus Tuanan signifikant häufigeres exploratives Verhalten. In beiden Population nimmt die Häufigkeit von explorativem Verhalten zu, sobald die Tiere im Verband mit anderen Tieren sind, verglichen damit wenn sie alleine unterwegs sind. Die Unterschiede in der Häufigkeit von explorativem Verhalten zwischen den Populationen bleiben auch dann bestehen, wenn man die Ergebnisse um den Zeitfaktor korrigiert, mit welchem dem Umstand Rechnung getragen wird, dass sich die Populationen ungleich lange im Verband mit anderen Tieren aufhielten. Innerhalb einer Population ist der Soziabilitätsgrad der Mutter positiv mit ihrer eigenen Explorativität sowie der ihres Kindes korreliert. All diese Erkenntnisse sprechen deutlich dafür, dass sich eine während der Entwicklung erhöhte Soziabilität langzeitig positiv auf die individuelle Explorativität auswirkt, und unterstützen somit die ontogenetische Vorhersage der CIH.

Abstract

Numerous theories have been developed to explain the evolution of the unmatched human cognition. Cognitive abilities per se are insufficient to explain the costly expansion of the brain that goes hand in hand with enhanced cognition, unless they translate into skills with significant fitness benefits: Even though it is the potential for the development of cognitive abilities that is genetically inherited, only the actual skills this produces are visible to selection. Thus, the main topic of this dissertation is the link between skill acquisition and cognitive evolution. The first focus is on the conditions which allow species to acquire skills over extended periods of time and how these are connected to the complexity of the foraging niche. The second focus is on the cultural intelligence hypothesis (CIH), an attempt to explain the evolution of cognition through a focus on social skill acquisition. The CIH states that opportunities for social learning during development positively affect the number of skills an individual will have acquired as an adult and, through an experience effect, also its current learning ability. Over evolutionary time, these developmental differences can become genetically fixed and ultimately, opportunities for social learning are a precondition if a species is to attain a high innate learning ability.

Humans stand out amongst most other mammals by reaching adult-level foraging skills very late in their development, well after the onset of reproduction. The aim of chapter 2 was to investigate which factors determine the length of a species' skill acquisition period. Data from the published literature on 57 mammal and bird species showed that most mammals reach adult-level foraging skills well before the developmental period is completed, whereas most birds reach adult-level foraging skills around the time of sexual maturity. However, among mammals, with increasing niche complexity, the age of adult-level skill competence moves closer to the age at first reproduction whereby gregariousness, slow conservative development, and post-weaning provisioning allow mammals to reach their skills later. Finally, in species with intense sharing of resources (such as cooperative hunters) competence in foraging skills may even reach peak values after the age of first reproduction. I concluded that the human pattern of skill acquisition could evolve because our hominin ancestors added extensive provisioning and big game hunting to the slow development typical of great apes with increasingly complex niches.

In chapter 3 I asked which life history features allow species to evolve into more complex niches. We therefore looked at the correlation between niche complexity, different life history parameters, and brain size in a sample of 78 primate and 65 carnivoran species. I found that in primates slow, conservative development and in carnivorans the length of provisioning of offspring are positively correlated with niche complexity. Only in primates, but not in carnivorans, complex foraging niches in the cognitive domain are correlated with brain size. These patterns show that selection favors evolution into complex niches in species that either develop more slowly or provision their young for an extended period of time. Both slow development and provisioning can buffer low energy yields during periods of learning and therefore may be limiting the evolution of complex niches. These findings help 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.

In the second part of this dissertation I aimed to test the predictions of the CIH on one of our closest relatives: the orangutan (*Pongo spp.*). Different orangutan populations vary substantially in their degree of sociability and thus in their opportunities for social learning. Accordingly, they represent a natural experiment on the effects of varying opportunities for social learning on skill development and cognition. I compared a highly sociable population of Sumatran orangutans at Suaq Balimbing, South Aceh, Indonesia, with a less sociable population of Bornean orangutans at Tuanan, Central Kalimantan, Indonesia. I looked at the development of 20 immatures over multiple years, as well their mothers as adult reference points. For data collection I followed a standardized protocol with scan sampling at two minute intervals. At both research sites, this kind of data had already been collected on many of our focal animals for multiple years before the onset of this study. In addition, all-occurrence data on the focus behaviors of this dissertation, namely all indicators for social- and independent learning were collected during the course of this study.

To be able to test the CIH, the study system must meet two preconditions. The first is that skills must be learned rather than be intrinsic. In chapter 4 I thus looked at the acquisition of foraging skills in the immatures at both populations. I divided foraging skills into food detection competence, food processing competence, and food locating competence. To assess these skills we collected data on diet competition, feeding rates, and ranging competence. I found that in both populations it takes immatures multiple years to acquire their foraging skills: food detection- and food locating competence are reached by the age of weaning, which is around the age of 6.5 - 9 years. For food processing competence, adult levels are reached shortly thereafter. More complex skills (e.g.

processing techniques that require multiple steps) take longer to reach adult-like levels than simpler ones. The most complex skills, such as tool use, are reached last, sometimes even after the onset of reproduction. Both findings strongly suggest that in orangutans foraging skills are learned during development rather than genetically canalized.

The second precondition of the CIH is that skills must be at least partially acquired through social learning. To test for social learning, in chapter 5 I looked at the frequencies and contexts of peering (attentive and sustained close range watching of the activities of conspecifics) in immatures. I found that most peering happens in skill-intense contexts where learning is likely to occur, namely feeding and nest building. Within the feeding context, we found that peering rates increase with increasing rarity and complexity of the food item. Also, food peering events are followed by an increased probability of the immature to feed on or explore the same food item. For nest building we found that the age in which immatures show increased nest peering rates coincides with the age at which they show the highest frequencies of nest practice behavior. Nest peering is directly followed by increased rates of nest practicing behavior. I also found that whereas younger immatures are solely focused on their mothers, as they grow older they shown an increasing preference for role models other than the mother. All these findings imply that immature orangutans rely on social learning for skill acquisition.

To test the developmental prediction of the CIH, namely that individuals in a population with more opportunities for social learning show an increased current learning ability, in chapter 6 I compared rates of peering and explorative behavior in the two study populations. I found that individuals in the more sociable population at Suaq show significantly higher rates of peering than individuals at Tuanan, even when corrected for differences in opportunities to peer. Also, immatures and adults at Suaq showed significantly higher rates of exploration than their peers at Tuanan. In both populations, exploration rates increase when in association with another individual, suggesting direct effects of associations on exploration rates. However, the difference in exploration rates remained significant when controlled for differences in association time between the populations. Furthermore, the level of sociability of the mother is correlated with her own exploratory tendency as well as with her offspring's. These findings are in line with lasting developmental effects of increased association frequencies on exploratory tendency and are in full support of the developmental version of the CIH.

Chapter 1: General Introduction

Humans show a level of cognition that is significantly higher than that of any other species. However, there is growing evidence that general intelligence is not a uniquely human phenomenon but can be found in a variety of species, suggesting some degree of evolutionary continuity [1-3]. Thus, to understand the evolution of human cognition, we have to look at related taxa. Enhanced cognition requires larger brains [4]. In absolute size, the human brain is indeed more than three times bigger than the one of our closest living relative, the chimpanzee (*Pan troglodytes*) as well as the one of our last common ancestor. When looking across species, human brain size is significantly greater than the expected value in relation to body size. But what drives the evolution of enhanced cognition?

Most theories on cognitive evolution have focused on a set of either social- or ecological factors that favored an increase in brain size through fitness benefits of enhanced cognition. The most prominent hypothesis from the social domain is the social brain hypothesis [5, 6]. It states that cognitive abilities are determined by the size of the social group in which a species lives and the social challenges this implies. Subsequent versions have stressed specific elements of group living, such as social bonds [7] to be the main driver of the evolution of enhanced cognition. Ecological factors that have been proposed to promote the evolution of cognition include the spatio-temporal distribution of food sources, which may favor enhanced memory and ability to plan[8] or the size of the home range, with large home ranges requiring better mental maps and thus enhanced cognition[9]. Foods that require complex and coordinated processing techniques (e.g. extractive foraging) have also been suggested to have selected for increased cognitive capacities [10, 11]. Since extracted foods are often rich in nutrients and available all year around, they also deliver the necessary energy for brain expansion. The final ecological hypothesis suggested that the ability to move around in the arboreal three-dimensional space was put forward to have favored the evolution of increased cognitive abilities (arboreal clambering [12]).

All of the above described theories on the evolution of brain size have focused on the cognitive challenges that drove brain size evolution. However, brain tissue is energetically among the most expensive tissues to maintain and grow [13, 14]: in humans, about 20% of all energy at resting state is devoted to brain maintenance [15]. These energetic costs are likely to constrain cognitive evolution and have to be taken into account in order to understand under which conditions positive selection pressures on brain size have the capacity to act in the first place. Not all species have equal potential to offset the costs of brain size expansion [16]. In general, the costs of a relatively large brain can be met in two ways (or by a combination of both): by an increased total energy turnover or reduced energy allocation to other expensive functions [17]. The first pathway means that the cognitive benefits of larger brains directly lead to a higher energy intake, for example through an improved diet quality or reduced experienced seasonality in the diet. The second pathway entails that less energy is used for other functions, either maintenance (e.g. digestion and locomotion) or production (growth and reproduction). Whether selection favors this tradeoff depends on the effects of the cognitive skills produced by the increased allocation to brains (the so-called life-history filter) on survival (and thus ultimately on life history).

An important factor for the evolution of the large human brain was, doubtlessly, the adoption of a cooperative breeding system with extensive allomaternal care [18-20]. This system enabled humans to offset the costs of large brained offspring and drastically shorten their inter-birth intervals. Cooperative breeding thus gave humans the demographic advantage to respond to cognitive pressures with increased brain size [21]. About 2 Mya years ago, humans started to include meat of large mammals in their diet on a regular basis [22, 23], which must have gone along with systematic food sharing [24-26]. These changes led to a higher, more stable mean energy intake that could sustain an increase in brain size [27]. Paleontological evidence suggests that both a cooperative breeding system and a meat-based diet, were in place by the time of the emergence of *Homo erectus*, whose relative brain size was significantly greater than the ones of great apes [22, 28]. Becoming top carnivores and less vulnerable to predation, both likely connected to an enhanced complexity in their stone technology[24, 29, 30] enabled *Homo erectus* to drastically increase adult longevity [25, 31]. An increased adult life span should have further allowed fitness benefits through increased cognitive performance to act.

So far, most research on cognitive evolution has either focused on the selection pressures that drove it or on the mechanisms that make it possible to offset its costs. However, what is often forgotten when studying the evolution of cognition is probably the greatest twist in the story: that which is inherited is the capacity to learn skills, whereas that which enhances fitness, and thus can be targeted by natural selection, is the set of learned skills produced by this ability. Without understanding the developmental link between capacity and skillset one cannot fully understand cognitive evolution. Developmental approaches are also the next step to complement the story of the evolution of human intelligence [32]. Our cognitive capacity translates into a vast repertoire of highly complex skills that enable us to exploit a variety of resources. Finding out which factors have allowed humans to reach this unmatched level of skill complexity will shed light on the evolution of human cognition as well as cognitive evolution across taxa in general. In terms of skill acquisition, humans stand out from other mammals in two ways. First they show uniquely long periods of skill acquisition, allowing for multiyear practice and fine-tuning of skills. Second, humans acquire virtually all their skills through social learning. Social learning allows for skills to be passed on to future generations, in other words social learning makes skills heritable.

The main topic of this dissertation is thus the link between developmental skill acquisition and cognitive evolution. We hypothesize that the length of the skill acquisition period as well as social skill acquisition both play a crucial role in the evolution of cognition across taxa and especially in the extreme case of human cognitive evolution. The first focus will be on the conditions that allow species in general to acquire more complex skills and evolve into more complex niches as well as how this is linked to cognition. The second focus will be on the role of social learning in the evolution of cognition.

Part 1- Skill acquisition, niche complexity and the evolution of cognition

Animal species that live in complex foraging niches have improved access to energy-rich and seasonally stable food sources which is needed to sustain expanded brains (relative to the ancestral state [25, 33-35]). Humans have evolved as hunter-gatherers or foragers into the most complex foraging niche: relying on highly complex forms of extractive foraging and hunting, they manage exploit a great variety of resources and live in large number of different environments. Complex niches include skill intense foraging strategies and are thus likely to go in hand with extended periods of learning as well as enhanced cognition. Human hunter-gatherers indeed stand out in terms of the length of their period of skill acquisition: it takes more than two decades to reach proficiency in several of their everyday foraging skills [26, 36, 37]. This means that peak values are only reached well after the onset of reproduction. Reaching skill competence even after the onset of reproduction goes against the general notion that in order to sustain the costs of reproduction, full efficiency is needed [38]. It is also in great contrast to what we see in most other mammals, including most primate species, where adult level skills are reached around or shortly after weaning [39]. Thus, in general, expanding the developmental period provides a species with more time to learn skills but at the cost of reproduction. In general, the overall length of the developmental period is highly correlated with brain size whereby larger brained species show longer developmental periods in relation to body size. Several theories have been proposed to explain this correlation. They come in two classes.

The *needing to learn hypothesis* states that larger-brained animals mature slowly because they need to acquire skills and knowledge essential for successful adult survival and reproduction[40]. Accordingly, the time to acquire the skills needed for successful adult performance in the foraging or social domains is the main limiting factor on the age of sexual maturity. The length of the developmental time is thus constrained by the number and complexity of skills a species has to acquire. The *embodied capital hypothesis* is in line with this hypothesis but focuses on the evolution of the derived slow human life history [25, 36, 37, 41]. It sees the shift to cognitively more demanding foraging strategies that gave access to high quality, difficult to acquire food sources as a cause for the extension of the life history parameters [25, 41, 42]. The transition to more learning-intense feeding strategies caused a prolonged period of immaturity with low productivity, which is then paid off by higher adult performance. However, such an immature period with low own productivity was only made possible through systematic provisioning of the younger generation. The investment in developing a large brain is compensated by decreased mortality and thus longer reproductive periods, which ultimately result in greater reproductive outcome.

The e*xpensive brain framework* focuses on the effects of the high energy costs of large brains on somatic development rather than skill acquisition [43, 44]. Brain tissue is energetically among the most expensive tissues to maintain [13] and requires even more energy to grow and develop[14]. Especially developing brains are highly susceptible to temporary energy shortages [45]. Thus, brain development can only happen at a rate where it can be constantly sustained with the requisite amount of energy. Because brain growth is completed before somatic growth [46-48], high energetic investment of larger-brained species into brain development results in a later physical development of the body. Consequently, in large brained species, the onset of the reproductive period is delayed [43, 49, 50]. The *expensive brain framework* is in line with the correlation of large brains with delayed maturation found across species. Within species, it predicts that body growth is only completed just before the age of fist reproduction, particularly in females.

The aim of this first part of this thesis is find out how humans have managed to become such good skill learners and how this ability has allowed our ancestors to evolve into a foraging niche of unmatched complexity. Assuming a concept of evolutionary continuity, we will look across species and test which life history features allow for an extension of skill learning periods and how they are connected to complex niches as well as brain size (figure 1.1). For this we will use a comparative approach, looking at data on a variety of mammal and bird species from the published literature.

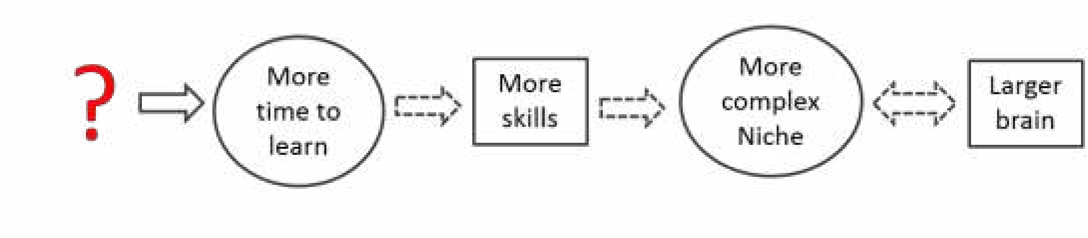

Figure 1.1. Hypothesized connection between skill acquisition, niche complexity and brain size: Factors that enable an extension of the skill acquisition period will ultimately allow for the acquisition of more skills and the evolution into more complex niches, which is likely to be connected with cognition and thus brain size.

Part 2 - Social learning and the evolution of cognition

Uniquely vast and complex skill sets have allowed ancestral humans to gain access to different resources in an unmatched variety of habitats and ultimately, successfully colonize this planet. The most striking point, however, is that no individual human being would be able to acquire the skills necessary to survive in any of those habitats on his own [51]. Humans are utterly dependent on the social acquisition of skills, in other words on social learning (learning that is influenced by the interaction with another individual or its products [52]: In all cultures, humans rely heavily on social learning and do so with uniquely high fidelity [53, 54]. Thus, the ability to learn from others was doubtlessly a mile-stone in human evolution. It has even been argued that the difference in cognition between us and our closest relatives, the great apes, is not nearly big enough to explain the difference in the success of the two species, but that the key must lie in the ability to learn from each other and transfer and accumulated skills and knowledge across generations [51].

The focus of most theories on the evolution of cognition was the independent learning ability. However, independent learning in itself is costly, whereas social learning is hypothesized to be more efficient [32]: social learning increases the signal to noise ratio of information, allows for skill acquisition without risky innovation and enables the accumulation of knowledge and skills. Thus, social learning should enable a faster acquisition of more complex skills. Indeed, experiments have shown that individuals acquire skills faster when exposed to role models as opposed to when they have to rely on independent learning [55, 56]. Also, individuals with more opportunities for social learning show a faster acquisition of more complex skills [57, 58]. Furthermore, even though only skills are visible to selection, it is still the underlying ability that is genetically inherited. Only social transmission of the actual skills to future generations will make skills heritable. Consequently, the net benefit per unit brain tissue is higher in lineages with social learning and it should be easier for selection to favor the evolution of increased learning ability in species that rely on social learning.

The intraspecific correlation between asocial and social learning abilities also suggests that asocial and social learning ability depend on the same basic cognitive mechanisms [52]. Social learning most likely includes an element of individual evaluation[59] and may indeed largely rely on existing asocial-learning mechanisms [60, 61]. Also, a growing body of evidence suggests that even observational forms of social learning mostly entail a phase of independent practice of the observed behavior [62-64]. The exception to this is probably blind copying as it has been shown in humans (e.g. over-imitation [53, 54, 65]). Selection on social learning will therefore automatically also favor the evolution of an improved independent-learning ability. As a result, social and asocial learning abilities will coevolve. Based on these inferences, the *cultural intelligence hypothesis* proposes that opportunities for social learning and independent learning ability and the size of skill repertoires are positively correlated, at both the proximate and ultimate levels [32, 66].

For humans it has been known for a long time that social inputs during childhood have a determining impact on the development of the cognitive skill set. In 1978, Voygotsky described cultural effects on the cognitive development in humans. Since then, numerous studies confirmed that skills of human children are shaped by their interaction with others [67]. Studies on institutionalized children have shown that children raised with limited social inputs will develop disadvantages in a variety of domains including language, social-emotional development and intelligence [67, 68]. These differences are also evident on the physiological and anatomical level, expressed in structural and functional changes of the brain[69, 70]. Growing evidence suggests that these effects are not uniquely human but that similar processes are at work in a variety of species [71-73]: Whereas social deprivation during development diminishes adult skill sets and reduces learning abilities [74-76], enculturation leads to larger adult skill sets as well as increased learning ability [77, 78].

The *cultural intelligence hypothesis* [32, 79] builds directly up on Vygotsky’s work[80] but proposes developmental effects of social inputs not just in humans but systematically across species. At its core, the *cultural intelligence hypothesis* states that increased opportunities for social learning lead to larger adult skill sets. Social learning allows for the acquisition of skills that could not be acquired by individual learning. However, since social learning is most likely based on the same mechanisms as involved in individual learning, experiences and abilities gained through social learning are hypothesized to be transferred to new situations and thus increase overall cognitive performance [32, 81]. Thus, social learning not just positively influences the size of skill sets but may also result in a higher current (realized) asocial learning ability. Going one step further, the *cultural intelligence hypothesis* also predicts that increased learning abilities go hand in hand with higher exploratory tendencies and thus result in an increased likelihood of innovation. Thus, populations offering more opportunities for social learning should exhibit overall larger and more complex repertoires of learned skills.

In sum, the *cultural intelligence hypothesis* predicts effects of opportunities for social learning on two levels [32]. First, on the developmental (proximate) level it states that individuals with more opportunities for social learning during their development will acquire larger sets of learned skills and an increased current asocial learning ability (figure 2). An increased asocial learning ability increases the probability of innovations and thus eventually the skill pool of the population, creating a positive feedback loop. As a result, the total set of learned skills by an individual will depend on its asocial learning ability and even more so on opportunities for social learning as well as the size of a population's skill pool. Second, on an evolutionary (ultimate) level, the cultural intelligence hypothesis predicts that species with more opportunities for social learning will be selected to evolve an increased innate learning ability (figure 1.2). Cultural intelligence can explain the evolution of the unusual human intelligence: a chimpanzee-level intelligence was combined with pedagogy, shared intentionality due to a shift in the social system as well as technology which ensured that cognitive skills are translated into improved fitness [66].

The aim of the second part of this dissertation is to test the predictions of the *cultural intelligence hypothesis*. We will use two populations of wild orangutans as a model system. Orangutans are a particularly interesting species for exploring the developmental link between skill acquisition and cognition for reasons explained in the following subsection.

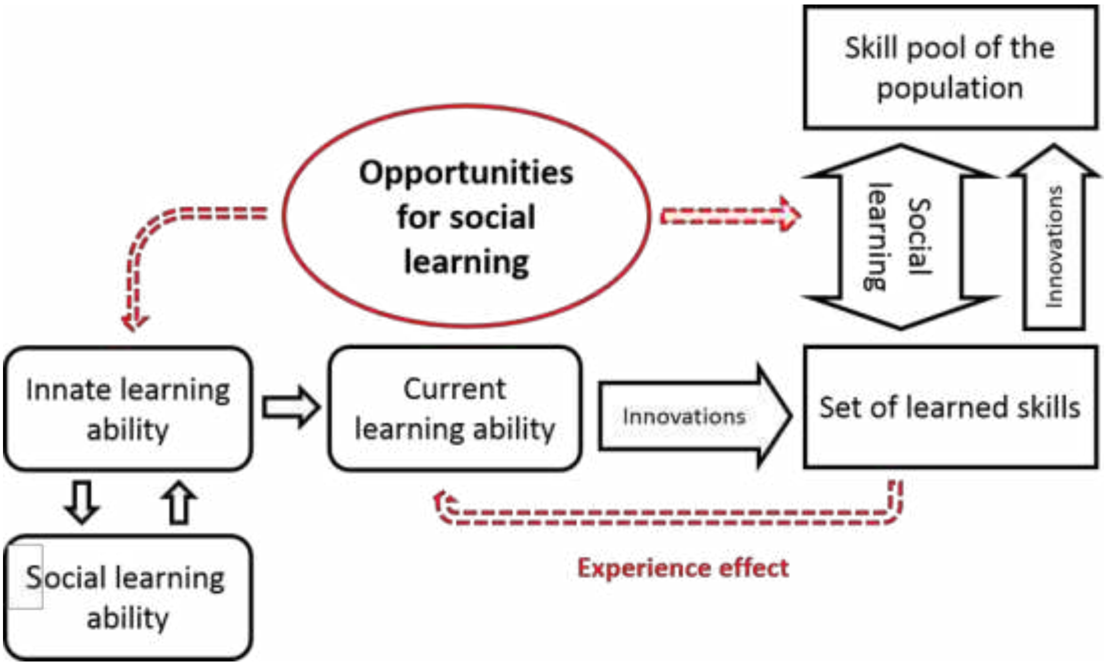

Figure 1.2. The cultural intelligence hypothesis: Opportunities for social learning proximately influence skill sets as well as current learning ability and ultimately a species innate learning ability.

Orangutans as a model system

Belonging to the great apes, orangutans (*Pongo spp.*) are one of humans' closest relatives. Our last common ancestor lived approximately 9-13 million years ago [82, 83]. There are two species of orangutans: the Sumatran orangutan (*Pongo abelii*) and the Bornean Orangutan (*Pongo pygmaeus*), whereby the latter is subdivided into three subspecies [84] (figure 1.3). Like all other great apes, orangutans are relatively large-brained, with Sumatran orangutans showing slightly larger brains and smaller body sizes than Borneans [85, 86]. Of all great ape species, orangutans show the greatest flexibility in their social system across different populations: Sociability levels range from semi-solitary to low-level fission-fusion, with Sumatran orangutans generally spending more time in associations than Bornean orangutans [86-89]. Depending on the specific population, orangutan mother offspring pairs spend 10-50% of their time in association with at least one other individual [90].

Orangutans show the latest age at first reproduction of any nonhuman- and the latest age of weaning of any primate species [91, 92], with substantial variation in these life-history parameters between the different orangutan species and populations. Their entire infancy, orangutans spend in permanent and very close association with their mothers [90], which provides them with plenty of opportunities for social learning. Immature Sumatran orangutans are weaned at the age of 7.5-9 years, 1-2 years later than their Bornean peers [90, 92, 93]. Weaning is followed by a multiyear juvenile period during which individuals start to range more and more independently: Depending on species and population, fully independent immatures spend 30-90% of their time on their own whereas the remaining time they mainly associate in small peer groups [90, 93, 94]. Thus, unlike all the other great apes, already from a juvenile age on, orangutans cannot systematically rely on social information but have to be able to rely on their own knowledge. Whereas Bornean orangutan females have their first offspring at the age of 12-14 years, their Sumatran peers start reproducing around the age of 15-16y [92, 95].

Orangutans live in a complex foraging niche: food availability in orangutan habitats fluctuates without following any clear seasonal pattern [96]. Orangutans also show broad diets and rely on a variety of difficult to process food items including some that require tool use at some populations [97, 98]. Also, orangutans build daily nests to sleep in: multi-layered constructions in a tree or combination of trees and made of bent branches to which additional components such as pillows or are added [99-101]. There is evidence that immature orangutans rely on social information to acquire some of their skills [62, 102]. Also, across different populations there is variation in several behaviors that cannot be explained by genetic or environmental differences and is correlated with geographic distance [86, 103, 104]. This clearly speaks for cultural differences, with skills being socially transmitted between generations. Controversially, despite showing broad repertoires of learned skills, wild orangutans show very low exploration rates and are highly novelty averse [66, 105] . This raises the question how the large innovation repertoires of orangutans could evolve in the first place. Interestingly, top-end complexity skills such as tool use are only found on a habitual level in some populations of Sumatran orangutans.

Due the substantial variation in their level of sociability, orangutans offer the ideal natural experiment to test predictions on the effects of varying opportunities for social learning on skill acquisition and cognitive performance. Looking at orangutan skill acquisition and investigating how it is connected to their derived life history niche might elucidate the evolution of our own species into the most complex foraging niche. Comparing repertoires of innovations as well as exploratory tendencies in different orangutan populations might help us to understand the evolution of the unmatched innovative tendency in humans.

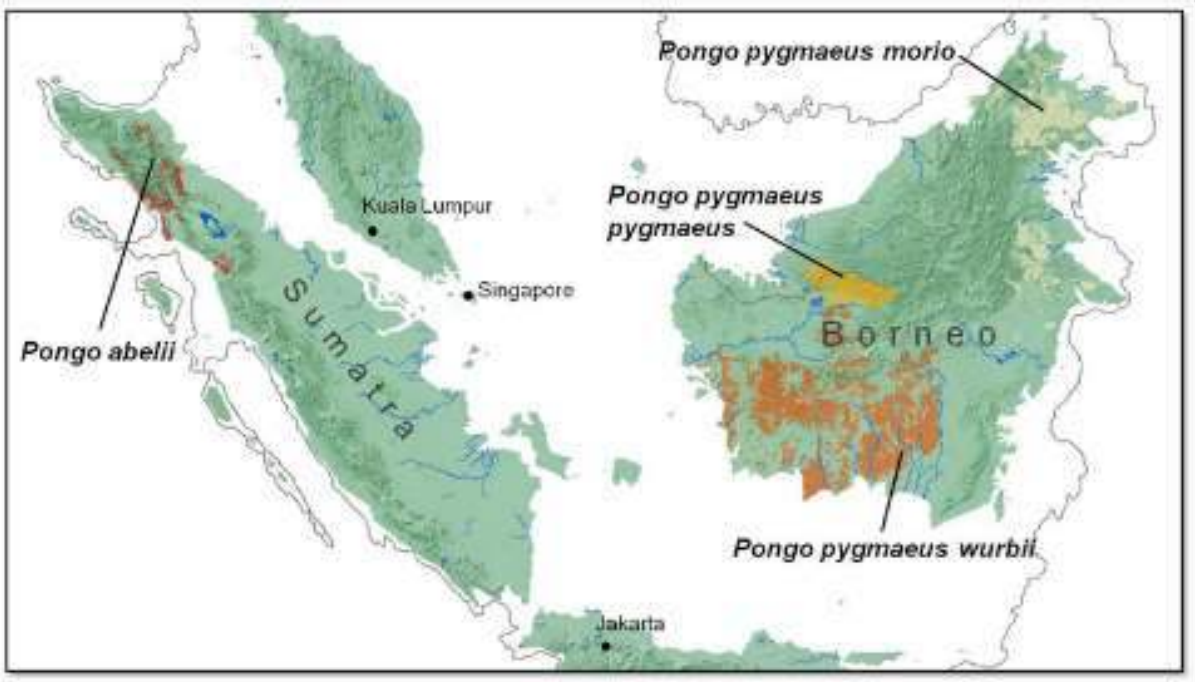

Figure 1.3. Map of Sumatra and Borneo: The distribution of the different orangutan species (Map by E. Willems).

Content and aims of this dissertation

This dissertation in divided into two parts. The first part (chapter 2 & 3) focuses on the connection between skill acquisition, niche complexity and cognition. The second part (chapters 4-6) focuses on the cultural intelligence hypothesis (CIH).

Part 1: Skill acquisition, niche complexity and the evolution of cognition

The vast number of highly complex skills have allowed humans exploit a unique variety of resources and evolve into the most complex foraging niche. Being able to exploit a complex niche might have provided humans with the necessary energy for brain size expansion. The vast skill repertoires seem to be connected to an extended skills acquisition period: Human hunter gatherers reach peak values in their foraging skills exceptionally late in development. To understand the evolution of the human skill complexity and evolution of their foraging niche we will look at how species can expand their skill acquisition periods and evolve into complex niches and lastly, how this is connected to cognition.

Chapter 2: How to explain the unusually late age at skill competence among humans?

The aim of chapter 2 is to investigate which factors determine the length of a species skill acquisition period. Using a comparative approach, we will look at the relation between age at skill competence and age at first reproduction, as well as other life history parameters and investigate how these factors are correlated with the overall complexity of the foraging niche a species lives in. We will use data retrieved from the published literature for 57 mammal and bird species.

Chapter 3: Life history, cognition and the evolution of complex foraging niches

In chapter 3, I ask which life history factors allow a species to evolve into a complex foraging niche, and also how niche complexity is related to relative brain size as a measure of cognition. I will hereby divide niche complexity into a knowledge- and a motor dimension. Using a comparative approach, we look at the correlation between niche complexity, different live history parameters and brain size in a sample of 78 primate and 65 carnivore species.

Part 2: Social learning and the evolution of cognition

The developmental version of the CIH states that opportunities for social learning during development affect the number and complexity of the skills an individual will have acquired as an adult and its current learning ability. In order to be able to test these predictions, the study system needs to meet two preconditions. First, skills have to be acquired though learning as opposed to being genetically fixed. Second, skills need to be at least partly acquired through some form of social learning. To test the preconditions and predictions of the CIH, I will compare two populations of wild orangutans that differ substantially in their degree of sociability: the one at Suaq Balimbing as the most sociable of all known orangutan populations versus the one at Tuanan with a significantly lower sociability level[106, 107].

Chapter 4: Development of foraging skills in two orangutan populations: needing to learn or needing to grow?

In chapter 4, I test whether the foraging skills of orangutans are learned rather than intrinsic, by looking at immature skill acquisition. If skills are learned, I expect them to be attained late in development and skill complexity to be positively correlated with the age at skill competence. I will also compare skill trajectories between the two study populations in relation to somatic growth and life history parameters. I will assess foraging skill by collecting data on diet competition, feeding rates and ranging competence. To estimate growth, we will use non-invasive laser photogrammetry.

Chapter 5: Observational social learning and socially induced practice of routine skills in wild immature orangutans

To investigate if immature orangutans learn through observational social learning, in chapter 5, I look at the role of peering (attentive close range watching of a conspecifics activity) in the skill acquisition process. I expect that peering will be more frequent in learning-intense contexts, namely feeding and nest building, and be followed by selective practice of the observed behavior. In the feeding context I expect peering rates to be dependent on complexity and rarity and in all contexts. With increasing age, I expect a growing interest in role models other than the mother with potentially new skills.

Chapter 6: Developmental effects of sociability on exploration rate in wild orangutans

To test the developmental predictions of the CIH, in chapter 6, I will compare peering rates and exploratory tendency, of the two study populations. Differences in peering rates will show if the increased level of sociability at Suaq indeed leads to more frequent opportunities for social learning. I aim to disentangle proximate effects of increased association on exploration rates from developmental effects by comparing exploration rates in the solitary context and by testing the effects of the sociability level of the mother on her offspring's exploratory tendency.

Chapter 2: How to explain the unusually late age at skill competence among humans

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Abstract

Humans stand out among primates and other mammals in reaching adult-level foraging skills very late in development, well after the onset of reproduction. The aim of this paper is to place this unusual human skill development into a broader comparative context. Among birds and mammals in general, duration of immaturity, indexed by age at first reproduction (AFR), and adult brain size have undergone correlated evolution. This pattern is consistent with two causal processes: AFR is either limited by the time needed to learn adult-level skills (*needing to learn*) or by the energy needed to grow brain and body to full size (*energetic constraints*). We tested predictions arising from these two hypotheses with data retrieved from the published literature for 57 mammal and bird species. First, most mammals reach adult-level foraging skills well before the developmental period is completed, implying that energy constraints determine the age at first reproduction, whereas most birds reach adult-level foraging skills around the time of maturity, suggesting time needed for skill acquisition determines the onset of reproduction. Second, within mammals we found that with increasing niche complexity, the age of adult-level skill competence creeps up toward the age at first reproduction. Third, when looking at how adult-level skills can be reached later, we found that gregariousness, slow conservative development and post-weaning provisioning allow mammals to reach their skills later. Finally, in species with intense sharing of resources (such as cooperative hunters) competence in foraging skills may even reach peak values after age of first reproduction. We conclude that the human pattern of skill acquisition could arise because our hominin ancestors added cooperative hunting and resource pooling to the slow development they had as great apes with increasingly complex niches. This result provides a broad biological foundation for the embodied capital model.

Introduction

Human children take many years to learn how to forage efficiently. Among human foragers, women reach peak foraging efficiency in their mid-20s, i.e. well after the age at first reproduction of around 19 for women, whereas men reach theirs even later, in their 30s or 40s [26, 36, 37]. Some components, for instance strength and athleticism (e.g. ability to hit a target [108]), reach their peak values soon after AFR, but human foraging, especially hunting, requires experience-based knowledge of detailed processing techniques and prey behavior. Moreover, there is no reason to assume that hunters and gatherers do not maximize their returns during foraging trips, supporting the interpretation that the experience required for successful gathering, and hunting in particular, takes years to accumulate. The *embodied capital hypothesis* [25, 36, 37] argues that the late acquisition of peak foraging efficiency in humans reflects the coevolution of our complex foraging niche and our unique provisioning system. Thus, the exceptionally late acquisition of efficient skills can be linked to the skill intensity of the foraging niche, and is made possible by massive intergenerational transfers of food from adults to immatures.

Humans are therefore unusual in two distinct ways [36]. First, we reach adult-level skill competence well after weaning, whereas most mammals do so around or soon after weaning (see also [39]). This raises the general question in which conditions selection favors or allows an increase in the age at which adult-level skills are reached relative to the timing of weaning. Second, we reach skill competence not just late, but well beyond the age at first reproduction. This is unexpected, because animals that are less efficient than reproducing adults are not expected to be able to sustain the additional effort of reproduction. Almost certainly, therefore, skill acquisition after the onset of reproduction requires extensive food sharing or net provisioning, which raises the broader question about the role of provisioning in the evolution of highly complex foraging niches.

The aim of this paper is to place human skill development into a broader comparative context, by examining whether variation in the timing of the acquisition of adult-level skills across a broad array of birds and mammals is caused by (i) the time needed to learn the skills, or (ii) the energy allocated (and thus time needed) to complete full somatic growth and differentiation. Once we have identified the conditions in which time needed to learn skills limit the attainment of maturity, we can explore whether the human pattern arose through a process or a combination of processes also found in other taxa, or instead reflects processes unique to human evolution. This comparative analysis will allow us to dissect the embodied capital hypothesis into two major components, one focusing on the coevolution between the complexity of foraging skills (and thus brain size) and life history, and the other on the role of resource pooling and provisioning.

In this paper, we therefore first ask for birds and mammals in general which factors determine the age at which adult-level foraging skills are reached. We will assume that this point is reached before, or at most around, the age at which reproduction begins, but will later discuss exceptions to this general rule as well. For birds and mammals (figure 2.1), age at first reproduction (denoted here as AFR) is determined by brain size, and not, as might be expected, by body size; humans follow the primate trend in this respect. However, this correlation is consistent with two distinct processes. First, AFR may be set by the time needed to grow and differentiate the adult brain, which develops before full body size is achieved. Second, AFR may be set by the time to learn the requisite skills. In other words, we can ask whether it is time (skill learning) or energy (growth and differentiation) that generally limits the duration of the immature period among birds and mammals. We can differentiate between these two possibilities by asking, within any given species, at what age adult-level foraging skills (denoted here as Age at Skill Competence, or ASC) are reached relative to the onset of reproduction (AFR). The focus is on ecological skills, in particular foraging, because they are known to be directly related to fitness[109], whereas social skills, including parenting, are best practiced while performing them, and are not improved by delaying reproduction [110]. Once we have a general answer, we can explore the third possibility: that ASC is reached after AFR. We expect this to depend on provisioning or food sharing among adults, because weaned mammals or fledged birds, let alone reproducing ones, must under normal conditions be able to sustain themselves.

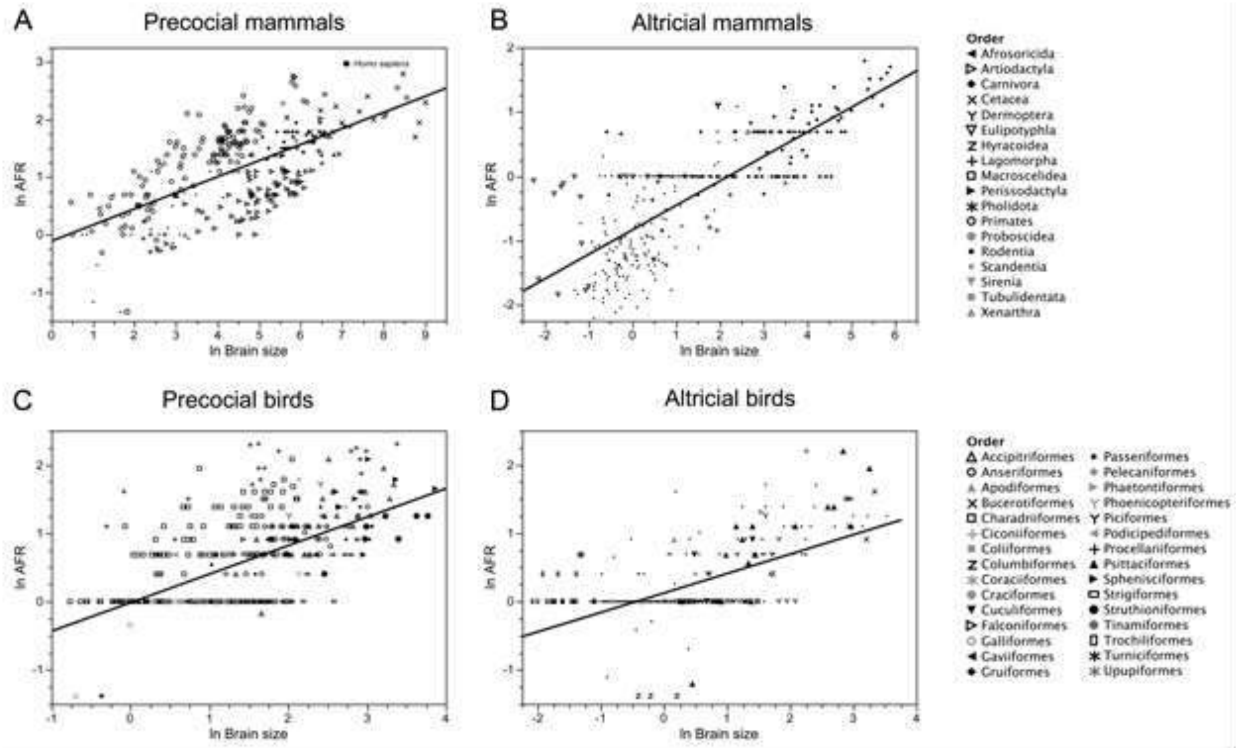

Figure 2.1. Age at first reproduction (AFR) versus brain size in mammals and birds, depicting non-phylogenetic least-squares regression lines. Humans were not included in the calculations, but are shown for comparison. The analysis was phylogenetic multiple least-squares regression (PGLS) with ln AFR as response variable, ln brain size and ln female body mass as effects: A) precocial mammals (N=301 species, brain: ß=0.26, p<0.001, body: ß =0.03, p=0.542); B) altricial mammals (N=312, brain: ß =0.25, p=0.030, body: ß =0.05, p=0.506); C) precocial, semiprecocial and semialtricial birds (N=419, brain: ß =0.25, p=0.008, body: ß =0.13, p=0.018); D) altricial birds (N=392, brain: ß =0.21, p=0.019, body: ß =0.09, p=0.143).

The needing to learn hypothesis was originally developed for birds. Probably due to intensive provisioning by both parents, altricial bird nestlings grow very rapidly, much faster than even provisioned mammal offspring, and reach adult body size before or soon after fledging [111, 112], perhaps because reaching adult size and locomotor competence is important to avoid predation[113]. Nonetheless, in many species the onset of breeding is delayed for months or even years [114]. Ashmole[115] first proposed that immature birds lack important foraging skills for their maintenance. A variety of studies have since confirmed this proposal (reviewed by [116]).

We can visualize the hypothesis and its main prediction as follows (figure 2.2 a). Adult body size is reached before ASC. Thus, AFR is limited by the time to reach ASC. This is expected where there is a combination of high somatic growth rate, as in birds, and a skill-intense foraging niche (in either birds or mammals).

Among mammals in general, support for this idea appears to be limited [39, 49], because they are generally thought to reach adult-level skills well before reaching maturity, i.e. ASC << AFR. With respect to nonhuman primates, empirical studies have been inconclusive: although some provide support for the needing to learn hypothesis [117, 118] most do not [39, 119]. Most mammal species must be self-supporting right after the age of weaning, as there is no post-weaning provisioning of immatures. Consequently, they must have enough skills to be at least self-sufficient, although this does not necessarily mean that these juveniles have reached adult-level skill competence [38], because they are still smaller than adult and non-reproducing. The fact that they still keep growing until shortly before the onset of reproduction [38] strongly suggests that skill competence is reached earlier. This argument implies that the timing of maturity in most mammals is limited by the time needed to reach adult body size.

This second explanation for the correlation between brain size and development time stresses the *energetic constraints* of development. We expect that full growth and differentiation of the brain must necessarily precede that of the body to guarantee a functional organism, which is indeed observed[46]. The unusually high energy costs of brain tissue [13] accounts for the slower development in large-brained species, especially among monotokous precocial mammals that cannot reduce litter size (the expensive brain framework [42, 43]). We can visualize this hypothesis and prediction as follows. Age at adult-level skill competence (ASC) is reached before adult body size, and consequently the energy allocated to (and thus time needed) to develop brain and body determines age at first reproduction (AFR) (figure 2.2 b). This pattern is expected where the skill intensity of the niche is low relative to development rate.

The third possibility is where adult level skills are reached well after age at first reproduction (figure 2.2 c). This implies a complex foraging niche, because otherwise AFR would be reached sooner, and thus assumes that time needed to learn acts as the constraint on reaching AFR. But in addition it must assume some form of food sharing among adults [25], because otherwise reproduction could not be supported. This is the pattern consistent with the embodied capital hypothesis.

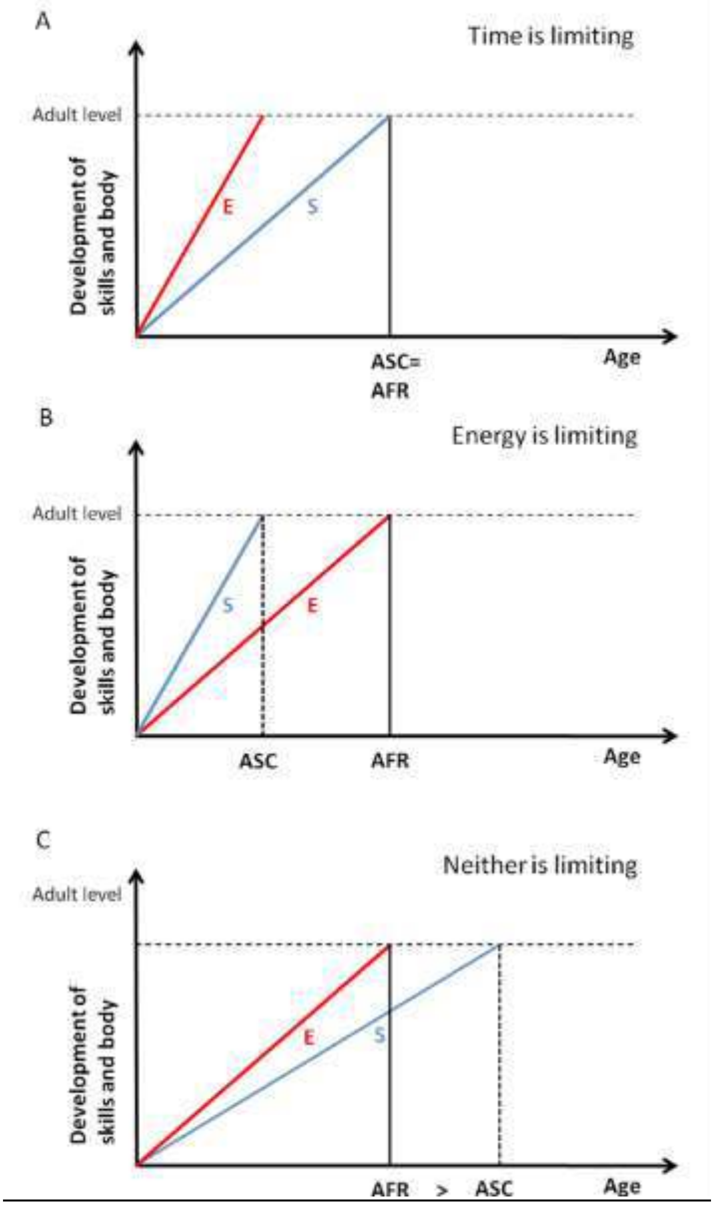

Figure 2.2. Both energetic tradeoffs and the time to learn skills have the potential to influence the length of the immature period. As soon as both adult-level skills and adult body size are reached, successful reproduction is possible. AFR= age of first reproduction, ASC= age of skill competence, E= pace of development, S= rate of skill acquisition. A) Time to acquire adult skill level determines age at onset of reproduction. B) Energy to reach adult body constitution determines age at onset of reproduction. C) Highest skill levels are reached after onset of reproduction.

Predictions tested

This analysis of the factors limiting the age at which sexual maturity is reached leads to three straightforward and testable predictions. The first prediction focuses on the difference between mammals and birds. In contrast to mammals, birds not only complete their physical growth early in their development (and are therefore unlikely to be limited in the timing of maturity by energetic constraints) but also generally live in a skill-intensive foraging niche relative to mammals [120]. We expect the ASC/AFR ratio to be around 1 in most birds, whereas ASC/AFR should necessarily be less, and usually far less, than 1 in most mammals (prediction 1).

The second prediction concerns the relation between the ASC/AFR ration and the complexity of the feeding niche among mammals. If prediction 1 is supported empirically, there will be a time gap between ASC and AFR in most mammals. We expect that those species that need to learn more skills would take longer to reach ASC, so their ASC/AFR ration should eventually approach 1. Thus, we predict an increase in the ASC/AFR ratio with increasing skill intensity of the niche (prediction 2).

The third prediction concerns the possible conditions allowing evolutionary increases in the ASC/AFR ratio, i.e. the evolution of a more complex foraging niche. We predict that in mammals, a species can afford to reach ASC after weaning when juveniles have an energetic buffer against potential energy deficits caused by failures during periods of learning, which allows some learning to take place after weaning. Thus, prediction 3a is that increased ASC/AFR has historically been achieved in two basic conditions that reduce the impact of learning failure: slow conservative development and post-weaning provisioning.

Prediction 3b focuses on how it is possible to delay skill competence until *after* age at first reproduction, as seen in humans. If this is accompanied by a skill intense feeding niche, we can attribute the value of ASC/AFR >1 to increase of ASC rather than reduction of AFR. We propose that the only way individuals can start reproducing before they have reached adult-level foraging skill competence is when harvested resources are pooled and shared among all group members, which is only expected in (some) cooperative hunters.

So far, no systematic comparative test of these predictions has been undertaken. Here, we collected literature data on skill ontogeny of different mammal and bird species to test them. In this, as in previous studies[25], the development of foraging skills was used as a measure of skill competence.

Methods

We compiled a dataset on the development of foraging skills and age of first reproduction of 23 bird and 34 mammal species (13 primates, 13 carnivores, 5 ungulates, 2 bats, and 1 cetacean, see supplementary material). Data on age of first reproduction were taken from an established database (K. Isler, unpublished data). We focused on female age at first reproduction only as this is more easily definable. Data on the development of foraging skills was retrieved from published studies.

For each species, an ASC/AFR ratio was calculated by dividing age at skill competence by age at first reproduction. As age at skill competence we took the youngest reported age (or the average age of the youngest age class respectively) that showed no difference in the measured foraging skill to adult (i.e. breeding) conspecifics. The accuracy at which the age of skill competence could be determined varied from study to study depending on how precisely the increase in skills was described (e.g. how broadly age groups were defined). Measures of foraging competence varied for the different species because studies varied in detail: whenever possible, data on foraging efficiency, intake rate and capture rate were used as these measures allow for a precise assessment of when adult like skills are reached. However in some studies only general data on mastery of foraging skills or diet composition were available. Accordingly, measures of foraging competence were divided into "strong" and "weak" predictors of the actual competence level (table 2.1). All statistical analyses were therefore performed on two data sets (see supplementary material): an unrestricted analysis including all mammal species (n=34) and a restricted, more conservative analysis to assure data quality (n=18). The restricted analysis (i) included only taxa for which "strong" measures of skill competence was available (table 2.1), (ii) excluded species for which the age at skill competence could only be broadly defined, and (iii) excluded taxa where the increase in foraging proficiency was likely due to increase in size or strength rather than skills. Graphs generally represent the unrestricted analysis, showing 34 mammal species.

Table 2.1. Validity of the different measures of foraging competence in mammals.

Validity of measure	Measure of foraging competence
Strong	intake rate capture rate processing rate handling time
Weak	diet composition feeding time mastery of foraging techniques

For the bird-mammal comparison, three categories of skill development trajectories were defined: (1) adult level of skills is reached *before AFR:* before 85% of the developmental period is completed, (2) adult levels of skills is reached *around AFR*: after 85% and before 115% of the developmental period is completed, and (3) highest values in skills are reached *after AFR*: after 115% of the developmental period is completed.

According to their breeding and foraging system, mammal species were divided into solitary breeders and cooperative breeders, and also in independent foragers and cooperative hunters. Mammal species were also divided into four niche-complexity categories according to the level of processing needed during food acquisition. Largely following Kaplan et al. [25], category 1 represents the lowest, and category 4 the highest niche complexity (table 2.2). All analyses were done in R 2.13.1[121] and BayesTraits (available on http://www.evolution.reading.ac.uk). To correct for the impact of phylogenetic non-independence, phylogenetic generalized least square (PGLS) regression was used in the R package caper [122]. All graphs are meant for illustrative purposes only, because the significance is always based on the complete statistical models.

Table 2.2. Niche complexity categories in mammals based on level of processing needed for food acquisition.

Niche complexity	Species	Level of processing
1	Folivores and grazers	No processing
2	Frugivores and insectivores	Low-level processing
3	Extractive foragers and mobile prey catchers	High-level processing
4	Big game hunters	High-level processing and risk

Results

The first prediction concerned the broad bird-mammal difference. Among birds, 20 of the 23 species have ASC/AFR of around 1, i.e. reached adult level of foraging competence around the age of first reproduction. All but two (which were cooperative breeders) of the bird species included in the analysis were pair-breeding. In 24 of the 34 mammal species, adult levels of foraging skill competence are reached well before AFR, in eight around AFR, and in two after AFR (figure 2.3). To obtain a phylogenetically informed modal value of the relative age at skill competence in the two radiations, we calculated the ancestral state of the ASC/AFR value for birds and mammals separately by using GLS in BayesTraits [123, 124]. The ancestral ACS/AFR value of birds was estimated to be 0.98 ±0.034 (SD), the one of mammals to be 0.68 ±0.01 (SD).

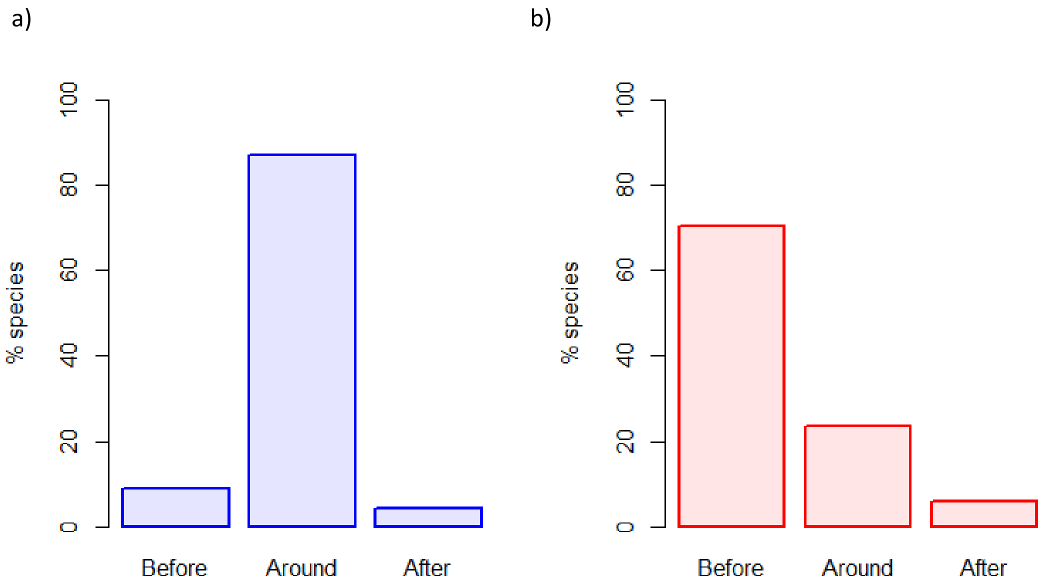

Figure 2.3. Distribution of the different classes of skill development in mammals (a) and birds (b). Before = reaching skills before 85% of the developmental period is completed, Around = after 85% and before 115% of the developmental period is completed, After = after 115% of the developmental period is completed.

The second prediction was that the complexity of the foraging niche should reflect the age at which adult skill level is reached in mammals. As predicted, a PGLS regression showed that the ASC/AFR ratio was positively correlated with niche complexity (Table 2.3). Thus, as the feeding niche becomes more complex, maturing mammals need more time to learn their foraging skills (figure 2.4).

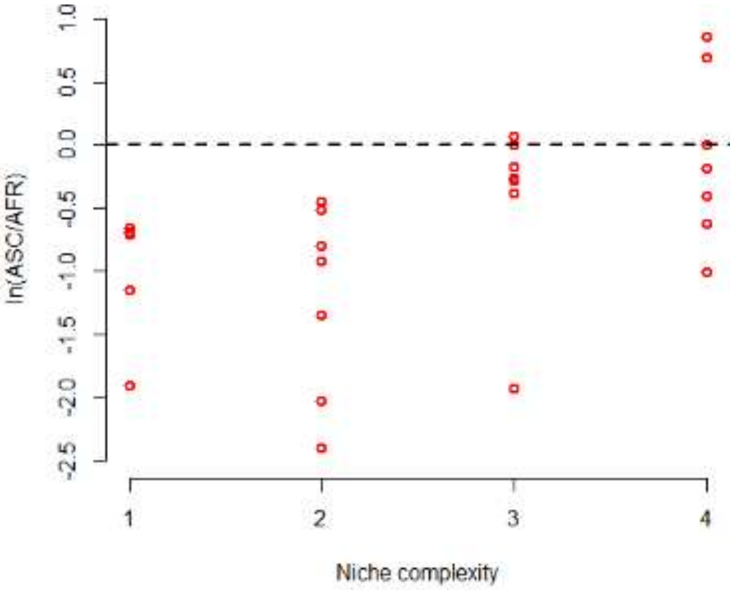

Figure 2.4. Relative age at skill competence as a function of niche complexity in mammals. Values above the dashed line mean that full skill competence is reached after AFR.

The third prediction concerned possible conditions in which the ASC/AFR ratio can be increased by selection. First of all (prediction 3a), we predicted that skill competence should be reached later in development when there is post-weaning provisioning or the species shows a slow, conservative development. A PGLS model showed that both post-weaning provisioning and the pace of development have a significant positive effect on the relative age of skill competence. In the statistical model ln(ASC) was used as response variable, and post-weaning provisioning and development pace as factors. Due to the high correlation between age at first reproduction (AFR) and body mass, we included both relative AFR (the residual AFR vs. body mass) as a proxy of development pace and body mass itself as factors. The model itself was highly significant and so were all effects (Table 2.3, figure 2.5a and 2.5b). Thus, adult-level skills are reached later in mammals that have slow development for their body size or that show post-weaning provisioning.

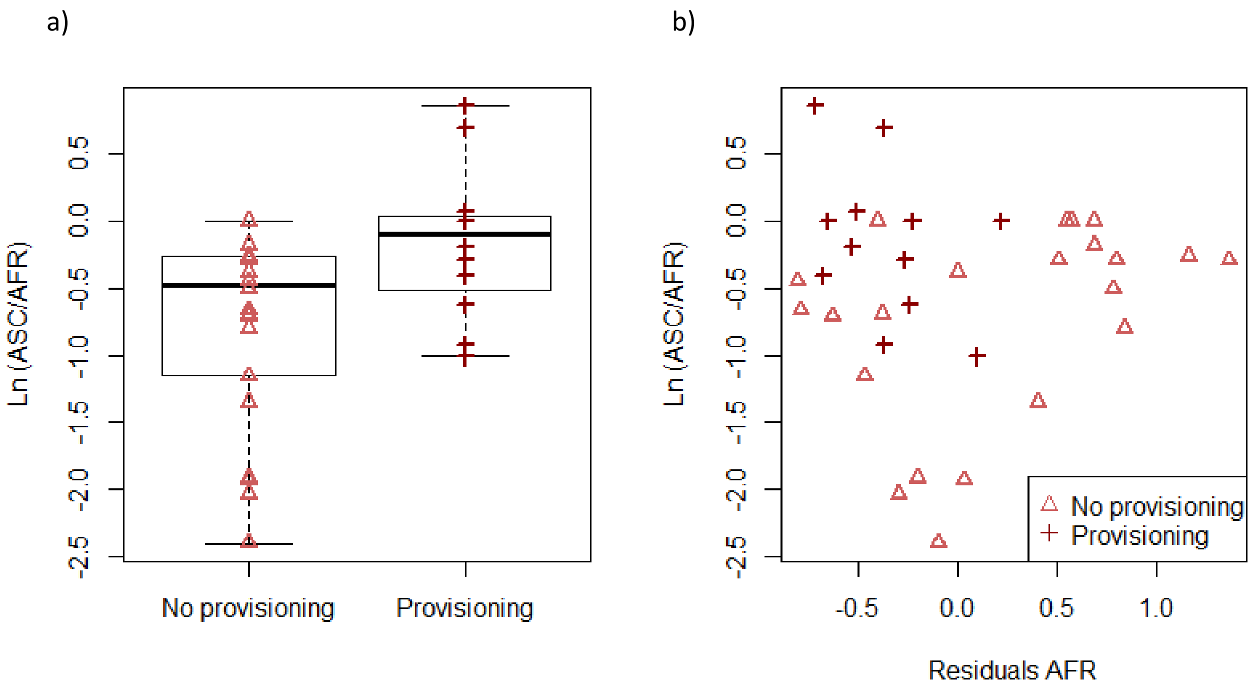

Figure 2.5. (a) Relative age at skill competence of mammal species without post-weaning provisioning versus mammal species with post weaning provisioning. (b) Relative age at skill competence as a function of residuals AFR (as measure of the pace of development) for mammal species without post-weaning provisioning and mammal species with post-weaning provisioning.

Prediction 3b focused on how ASC can be reached after AFR, in other words, how ASC/AFR can become >1. We predicted that this is only possible if there is intensive food sharing among adult individuals. Consistent with our prediction, we found that cooperatively hunting species reach skill competence significantly later than independently foraging species (table 2.3, figure 2.6). Indeed, all cooperatively hunting species in the sample had ASC/AFR ratios between 1 and 2.38 whereas all other independently breeding species showed values less than 1.

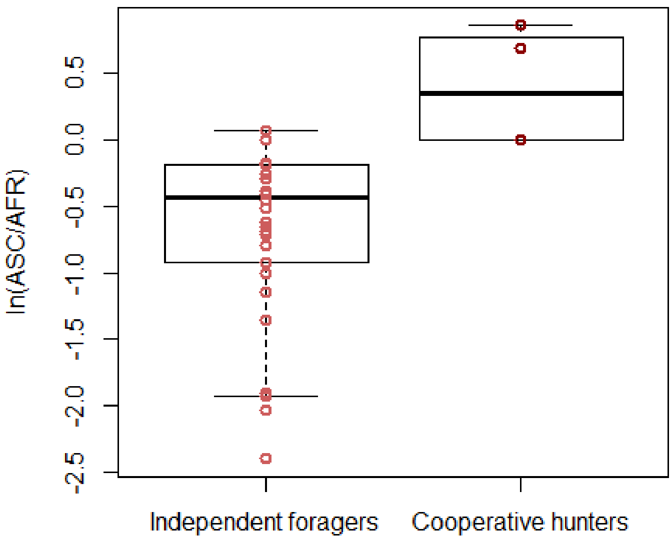

Figure 2.6. Relative age at skill competence of independently foraging versus cooperatively hunting mammal species.

Table 2.3. Summary of the PGLS regression models used to test the different predictions about the effects of different factors on age of skill competence (ln(ASC)) in mammals. Effects are shown in bold face, the other variables are covariates used to control for body size effects. a) unrestricted (N=34) and b) restricted dataset (N=18).

a) unrestricted dataset (N=34 species)

Prediction	P-value model	R^2	F-statistic	Lambda	Effects	P-values effects	ß
2	< 0.001	0.5	17.9	0.54	**Niche complexity**	0.001	0.46
					ln(AFR)	<0.001	0.92
3a	< 0.001	0.5	12.76	0.38	**Residual AFR**	<0.001	1.03
					Provisioning	0.035	0.64
					ln(body mass)	<0.001	0.19
3b	< 0.001	0.5	12.89	0.52	**Cooperative hunting**	0.007	1.07
					ln(AFR)	<0.001	1.07

b) restricted dataset (N=18 species)

Prediction	P-value model	R^2	F-statistic	Lambda	Effects	P-values effects	ß
2	0.002	0.5	8.08	0.55	**Niche complexity**	0.057	0.52
					ln(AFR)	0.013	0.96
3a	< 0.001	0.7	12.98	0.99	**Residual AFR**	0.032	0.91
					Provisioning	<0.001	1.82
					ln(body mass)	0.009	0.21
3b	< 0.001	0.7	22.4	0	**Cooperative hunting**	0.004	1.78
					ln(AFR)	<0.001	1.38

Discussion

Time to grow or time to learn?

In this study, we asked for both birds and mammals whether time at sexual maturity (age at first reproduction, or AFR) is determined by the time when adult body size is reached or when adult-level foraging skills (ASC) are reached, in order to explain the unusually late ASC in humans. We therefore looked at whether energy supply (somatic growth and development) or time to learn vital skills is limiting the duration of the immature period. We predicted a major difference between birds and mammals. Indeed, we found that birds, which reach adult body size very early, reach maturity, i.e. begin breeding, around the time they reach adult-level foraging skills. This confirms that among birds time needed to learn skills is indeed limiting the period of immaturity, and reflects the exceptionally high initial rates of growth and parental investment in altricial birds [113].

In contrast, we found that most mammals reach adult skill levels well before reaching maturity, confirming the traditional view that the immature phase among mammals is best explained by classic life-history theory combined with the notion that the high energy costs of the brain further slowdown overall physical development. Thus, time needed to learn skills does not determine age at first reproduction among mammals in general, most likely because most newly weaned mammals must have the skills to be self-supporting, yet still have much growing to do, being only approximately one third of adult body size [125]. Because failures during periods of learning may have severe consequences for growing organisms (as they lead to lower food intake and consequently carry the risk of brain starvation[43], it is very likely that many species have reached skill competence by the age of weaning.

Among mammals, there is nonetheless much variation in the age at which adult skill competence (ASC) is reached relative to the age at first reproduction (AFR). We found that this variation was related to the complexity of the species' foraging niche. As this complexity increases, adult-level foraging skills are reached later, indicating that living in a complex niche requires learning over a relatively longer time span. The analysis thus clearly showed that some mammal species have found ways to prolong the period of learning until long after the age of weaning. The modal value of mammal's ASC/AFR, controlled for phylogenetic relatedness, was estimated as 0.68. This may seem high, but it Is likely that this value is biased because our data set included a disproportionally high number of species living in rather complex niches (primates, carnivores) and only a few of the many species that live in simple niches (such as ungulates or rodents). This publication bias probably exists because studies of skill learning are not considered interesting in species with simple foraging niches.

The next step was to look at the actual mechanisms that allow for learning after weaning and therefore allowed species to evolve into a complex niche. We could envision three conditions in which the age of adult-level skill competence can be delayed towards age of first reproduction (figure 2.7). The first condition may be most common but quantitatively least important, because it favors only the diet choice part of the ecological skills rather than food finding and processing. Stable gregariousness allows juveniles to continue to associate with adults post-weaning, enabling them to follow knowledgeable adults to food sources they might not have discovered on their own. Such copying of diet choices may account for some of the variation in our data set: especially in group-living primates skill competence does not necessarily have to be reached right at the age of weaning even though there is no post-weaning provisioning.

Figure 2.7. Evolutionary pathways that enable the evolution into a skill-intensive foraging niche.

The second condition, exemplified by the great apes or capuchin monkeys, is where due to very low rates of unavoidable mortality, physical growth has become so slow, perhaps because selection favors conservative growth rates[39] that reduced food intake rates due to imperfect skills do not endanger survival. Thus, enough time is created under normal (non-starvation) conditions to learn many skills. Among Sumatran orangutans, for example, which are weaned at around age 8, adult skill levels are reached around age 12, which is well after weaning but still well before they start to breed, around age 15.5 [90, 126].

The third condition is post-weaning provisioning, which buffers against lack of foraging competence and thus risk of occasional starvation of incompetent foragers, and consequently allows them to learn complex foraging skills. In these species, the ASC/AFR ratio can approach 1, which allows species to inhabit more complex niches, although this is obviously not inevitable.

The final step is the explanation of the fact that in some species ASC is reached well after the onset of reproduction (AFR). In addition to humans, we found that ASC/AFR consistently exceeded 1 in cooperative hunters, with values ranging from 1 and 2.38. This supports the hypothesis that a cooperative hunting system is associated with very late ASC. Thus, systematic food sharing among adults due to cooperative hunting may be the key variable to explain this unexpected phenomenon: Individuals don’t have to exhibit full hunting proficiency to be successful adults and reproduce.

Skill learning and human evolution

Having gained this overview of the factors determining ASC relative AFR in mammals, we can return to the unusually late ASC in humans. Humans combine all three possible causes for late ASC. Humans do not just show the gregariousness and slow development inherited from our great ape ancestor, but modern foragers are also cooperative breeders and hunters, with both intense provisioning of juveniles and obligate sharing of all harvested and hunted food among adult individuals[26]. Therefore, in contrast to great apes and most other primate species, but as in other cooperatively hunting carnivores, human foragers can afford to reach adult-level foraging skills well after the onset of reproduction. Furthermore, humans show a cooperative breeding system with extensive support of the breeders from other group members. All this strongly suggests that the complexity of the human foraging niche, and our great intellectual ability and unusually large brain size in general, coevolved with the combination of food sharing and provisioning [18, 127], which developed on top of a great ape-like life history. We have suggested elsewhere that this life style began relatively early in human evolution, with the emergence of *Homo erectus* [20, 128]. Thus, cooperative breeding and hunting enabled the gradual increase in the complexity of our foraging niche, and thus our brain size.

These results help to place the embodied capital hypothesis [25, 37] into a broader context, by suggesting that this hypothesis, developed specifically to explain the human condition, combines two distinct elements that can be seen as broadly independent biological processes: (i) the coevolution between brain size and life history, including both development time and total lifespan, and (ii) intergenerational transfers.

In the form it is generally presented (e.g. [129]), the first element provides an alternative but equivalent formulation of the basic life-history explanation for brain-life history coevolution (cf.[49]). This coevolution can be explained with reference to the costs of growing a larger brain[43, 44], which thus leads to delayed maturation. However, this only produces a viable demography in species that have a sufficiently increased adult lifespan (due to the survival benefits bought by the larger brain). The nature of these development costs is not specified in this hypothesis: both a slowdown of overall somatic growth and an increase in time needed to acquire the necessary skills can produce the same correlation between brain size and life history.

This first element is effective, but on its own falls short in explaining why humans are so extreme in both brain size and longevity relative to all other mammals. The reason that mammals are limited in how far these two variables can be increased is that they hit a gray ceiling[128, 130]. At the highest skill levels, and thus probably the largest brain sizes, the delay in AFR increases, and as we noted, this is increasingly due to the time needed to learn vital skills. The delay in AFR is counteracted by the increase in adult lifespan, but this compensation is increasingly inadequate as brain size increases because the increase in lifespan is limited due to unavoidable mortality, and in addition birth rates generally go down rather than up with increasing brain size[43]. Demographic non-viability would therefore result if brain size were to increase any further. Brains and maximum lifespan therefore remain stuck at some moderate level: the gray ceiling. In great apes, for instance, brains are roughly one third of those of humans and lifespan roughly two decades less [131].

The second element, intergenerational transfers, is therefore critical to explain how hominins broke through this gray ceiling. In mammals in general, allomaternal inputs increase the reproductive output of adults to improve demographic viability, and thus allow the gray ceiling to be moved up: cooperative breeders have larger brains than their independently breeding relatives [21]. However, this process will still continue to be limited by the constraint that ASC cannot exceed AFR. This is where the intergenerational transfers come in: they allow ASC > AFR, and thus continuing evolution of more complex niches. The only other organisms in which intergenerational transfers are seen are cooperative hunters, which share widely. Thus, the combination of immature provisioning and continued food sharing in hominins allowed brains to increase well beyond the relative size seen in other mammals. In addition, intergenerational transfers further improve survival of both immatures and adults (because it involves sharing among adults as well), which in turn enables the evolution of even longer lifespan [26]. Finally, as skills became more complex, adult productivity increased to levels well beyond what is necessary, thus making the transfers possible and sustaining the coevolutionary cycle.

Conclusion

In sum, the human lifestyle with the complex foraging niche is made possible by two processes: (i) the mammal-wide correlated evolution between brain size and life history and (ii) the intergenerational resource transfers made possible by cooperative breeding and hunting[25, 36]. By adding intergenerational food transfers to a system of relatively complex foraging niches (extractive foraging, some cooperative hunting), hominins could make the niche more complex and allow learning times to exceed the time needed to reach sexual maturity.

Acknowledgements

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Supplementary Material

Table S2.1: Mammal data including adult female body mass, AFR (age at first reproduction in females), niche complexity (as defined in Table 2), post-weaning provisioning, cooperative hunting, ASC/AFR ratio (age at first reproduction divided by age at skill competence), classification of the measure of foraging competence (see Table 1) and whether the data was used in the unrestricted analysis only (U) or also in the restricted analysis (U&R, based on the criteria described in the methods).

Species	Female body mass [kg]	AFR [y]	Niche complexity	Post-weaning provisioning	Cooperative hunting	ASC/AFR ratio	Measure of competence	Analysis	References
Cetartiodactyla									
Cervus nippon	20.1	2	1	0	0	0.49	weak	U	[132]
Giraffa camelopardalis	828	4.8	1	0	0	0.15	weak	U	[133]
Odocoileus hemionus	55.7	1.9	1	0	0	0.52	strong	U&R	[134], [135]
Ovibos moschatus	250	3.2	1	0	0	0.32	weak	U	[136]
Ovis canadensis	72	3	1	0	0	0.5	strong	U&R	[137]
Tursiops truncatus	172	5.5	3	1	1	1	weak	U	[138]
Carnivora									
Acinonyx jubatus	43	2.1	4	1	0	0.67	weak	U	[139]
Canis lupus	38.5	2	4	1	1	2.38	strong	U&R	[140-142]
Crocuta crocuta	64.8	3	4	1	1	2	strong	U&R	[143]
Enhydra lutris	23.5	4	3	0	0	0.15	strong	U&R	[144]
Helogale parvula	0.265	1.4	3	1	0	1.07	strong	U&R	[145]
Lutra lutra	6.75	2.7	3	1	0	1	strong	U&R	[146]
Lycaon pictus	22.05	2	4	1	1	1	weak	U	[147]
Lynx rufus	7.5	2	4	1	0	0.83	weak	U	[148],[149, 150]
Meles meles	10.1	1.6	2	0	0	0.64	weak	U	[151]
Mirounga leonina	503	3.6	3	0	0	1	weak	U	[152]
Panthera tigris	130	3.7	4	1	0	0.54	weak	U	[153, 154]
Suricata suricatta	0.72	2	3	1	0	0.75	strong	U	[155, 156]
Ursus maritimus	225	5.5	4	1	0	0.36	strong	U&R	[157]
Chiroptera									
Myotis velifer	0.009	1.2	2	0	0	0.13	strong	U&R	[158]
Pipistrellus pipistrellus	0.006	1.4	2	0	0	0.09	strong	U&R	[159]
Primates									
Callithrix jacchus	0.381	1.7	2	1	0	0.4	strong	U	[160]
Cebus apella	2.52	6.7	3	0	0	0.75	strong	U&R	[118, 161]
Cebus capucinus	2.54	6	3	0	0	1	strong	U	[162]
Cebus olivaceus	2.52	6	3	0	0	0.83	strong	U&R	[163]
Gorilla beringei	97.5	10	2	0	0	0.6	strong	U&R	[164, 165]
Gorilla gorilla	71.5	10.2	2	0	0	0.45	strong	U&R	[166]
Macaca fuscata	8.03	6.1	3	0	0	1	strong	U	[167, 168]
Papio cynocephalus	12.3	6	3	0	0	0.75	strong	U	[169]
Papio hamadryas	9.9	6.1	3	0	0	1	strong	U	[117]
Papio ursinus	14.8	3.7	3	0	0	0.68	strong	U&R	[170]
Pongo abelii	35.8	15.5	3	0	0	0.77	strong	U&R	[126]
Pongo pygmaeus	35.6	13	3	0	0	0.83	strong	U&R	[171]
Saimiri sciureus	0.662	3.9	2	0	0	0.26	strong	U&R	[119]

2. How to explain the uusually late age at skill competence among humans

Chapter 3: 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 [33, 118, 170]. Living in a complex foraging niche may bring palpable fitness benefits [33]. 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 model 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 [25, 34, 35].

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 [172]. Both factors work as an energetic buffer against failures during periods of learning and therefore allow the learning period to be extended (figure 3.1). We also found evidence that species with complex foraging niches (with complexity defined as the level of processing required) reach adult-level feeding skills later in development than those that live in simpler niches [172].

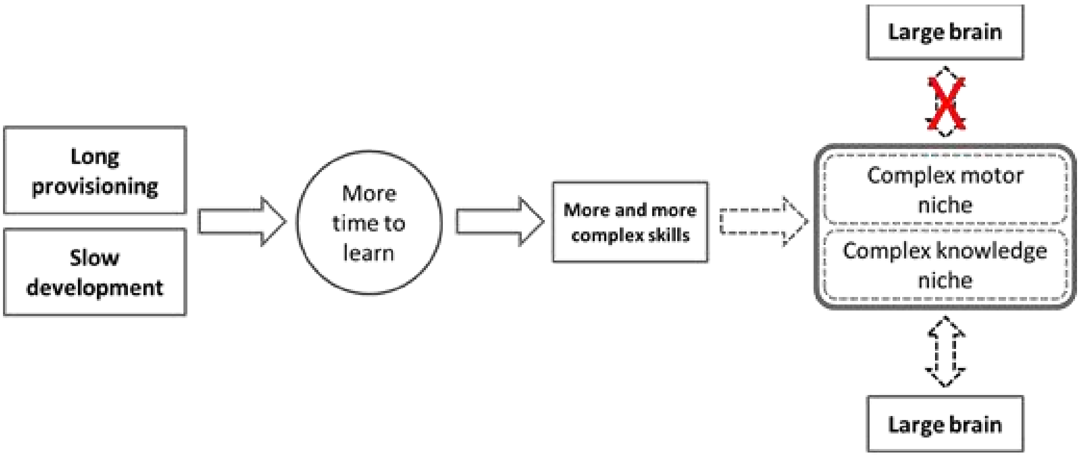


Figure 3.1. Slow development and extended provisioning have been shown to allow for extended periods of learning (later relative age at skill competence[126]). Here we ask in Part I whether the same two factors ultimately allow species to evolve into more complex niches. In Part II we are interested 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 chapter, 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 [39]. 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 [172], 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 [43, 173] and thus reach maturity at a later age, which is compensated for by their improved adult survival [43, 174]. In humans, this tradeoff is responsible for our highly delayed maturation and the adolescent growth spurt[50], although in humans adult-level skills are reached even later [25].

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 [175] or those that engage in extensive extractive foraging or tool use [11, 176, 177]. Second, larger brains are found in species that can maintain a high and stable energy intake all year round [178-180], often as a result of extractive foraging techniques [33] or perhaps because of the ability locate ephemeral food sources[8]. 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 habitat was a driving force in the evolution of human intelligence [10, 11, 181]. 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 [10, 33, 182, 183].

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 (figure 3.1). 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 [126] 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 [25, 117, 184]. 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 [26, 118, 143, 185].

The patterns found in these studies suggest that ecological niche complexity can be divided in 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.[177]). 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.

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. Heldstab, unpublished data; [21, 43, 180]). Data on the different elements of niche complexity were taken from the published literature (see supplementary material). We use measurements on overall brain size as this has been shown to be a very good predictor of cognitive abilities [4, 186] and is a very broadly available measurement in mammals.

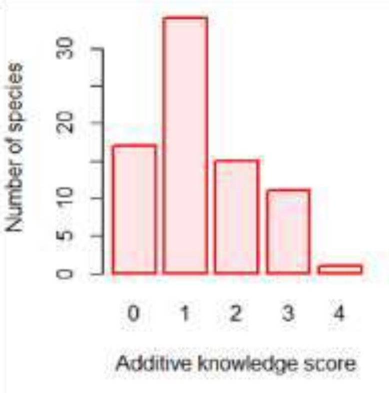
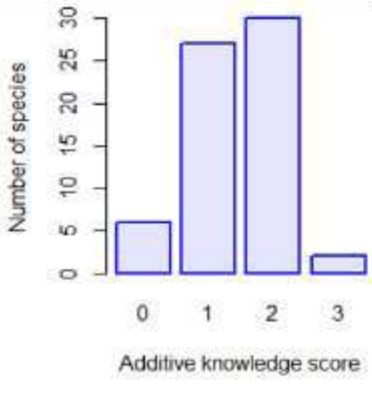
For motor-niche complexity, we divided all species into three complexity categories according to the level of processing involved in food acquisition (Table 3.1). For grazing and folivory, food acquisition generally comprises only one step (bite), whereas for frugivory and insectivory, two basic steps 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.

Table 3.1. Motor niche complexity categories.

Motor 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

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 1 – 2 different classes of food types to 0 (low), and 3 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 3.2).

Table 3.2. Distribution of the different knowledge niche complexity elements and distribution of the additive knowledge complexity score in primates and carnivores.

	Cognitive elements	Primates	Carnivores
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 [121]. More closely related species, in general, show greater similarities in traits because of their shared evolutionary history [124]. 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. [187], as implemented in the package *caper* [122], and phylogenetic logistic regressions (PLR) in the case of binary response variables, as implemented in the package *phylolm* [188]. 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 body mass. 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 (tables S3.2, S3.3, S3.4).

In PGLS, the phylogenetic scaling parameter lambda (λ) [189], 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 [190]. 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 [191, 192]. A nexus file was manually extracted from the information provided in Perelman et al. [192] 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 (table S3.1).

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 3.3a; figure 3.2). 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 3.3b; figure 3.2).

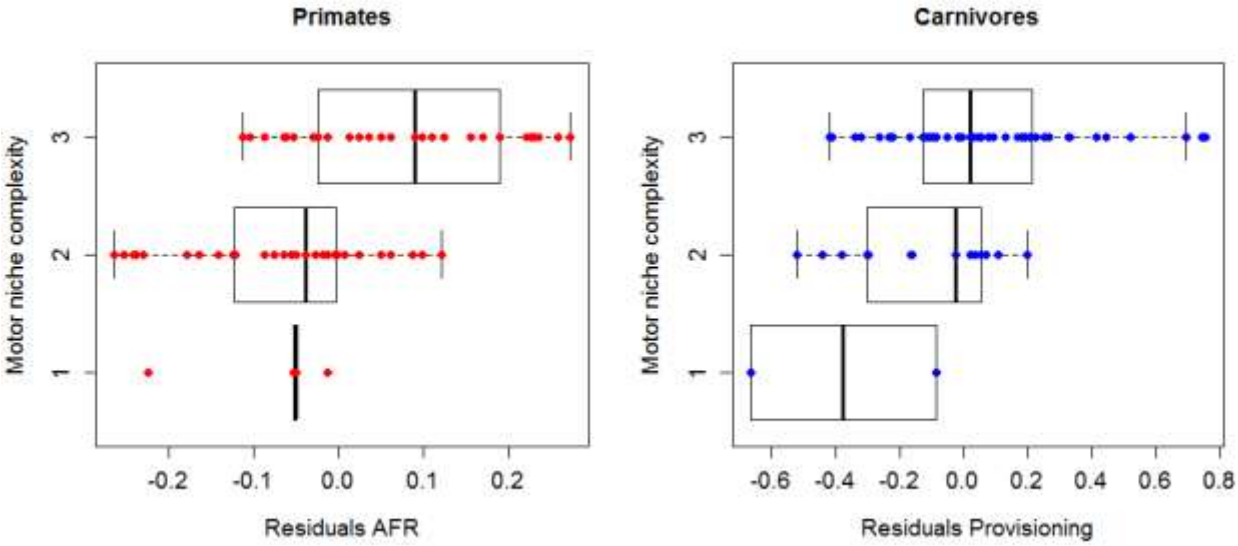


Figure 3.2. Relationships between pace of development (age at first reproduction corrected for body mass) and motor-niche complexity for primates and between length of provisioning (corrected for body mass) and motor-niche complexity for carnivorans.

Table 3.3. PGLS multiple regression models with motor niche complexity as the response variable and body mass, age at first reproduction (AFR) and length of provisioning as the predictor variables, analyzed separately for the a) 78 primate and b) 65 carnivore 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)

Carnivores 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 knowledge-niche 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 3.4a+b; figure 3.3).

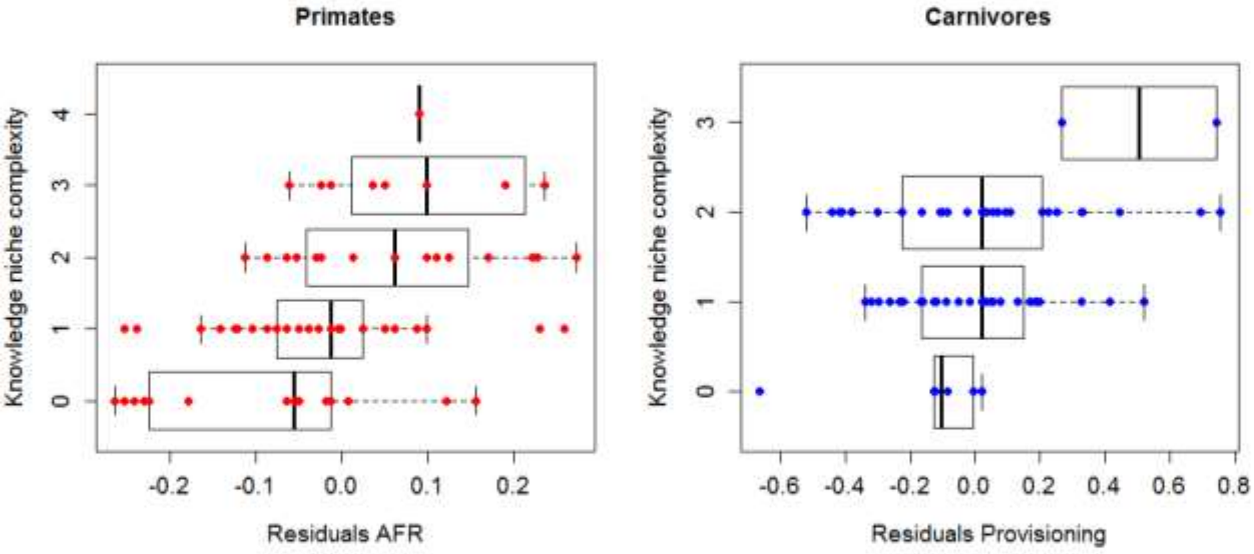


Figure 3.3. Relationships between pace of development (age at first reproduction corrected for body mass) or provisioning (corrected for body mass) and the additive knowledge-niche complexity score in primates and carnivorans.

Table 3.4. Phylogenetic least-square (PGLS) multiple regression models with the additive knowledge score as response variable and body mass, age at first reproduction (AFR) and length of provisioning as predictor variables analyzed separately for the a) 78 primate and b) 65 carnivore species. The 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)

Carnivores 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 (table S3.2a; figure S3.1).

In carnivorans, the length of provisioning had a significant positive effect on diet breadth. For cooperative hunting, there was 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 (table S3.2b; figure S3.2).

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 correlation was 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 table S2a). Detailed statistics on the regression models and further analyses are also shown in (table S3.2 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 3.5b, figure 3.4). Adding the length of provisioning as an additional factor did not change the result (table S3.3b). In primates, in contrast, this correlation is significant (table 3.5a; figure 3.4). However, the correlation between brain size and motor-niche complexity disappears if we control for AFR (table S3.3a).

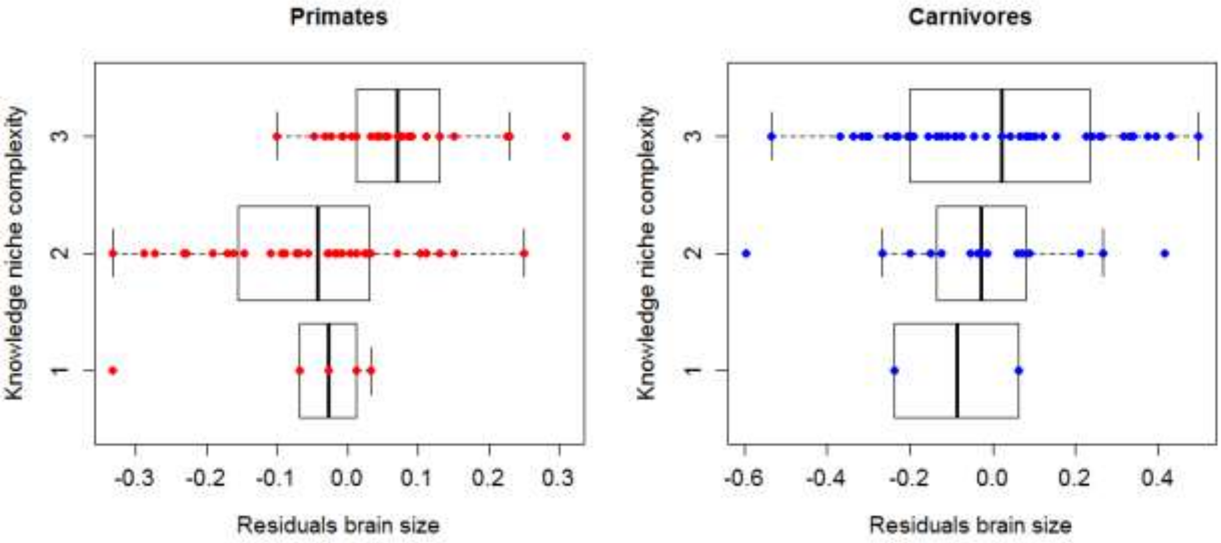


Figure 3.4. Relationships between relative brain size (corrected for body mass) and motor-niche complexity for primates and carnivores.

Table 3.5. PGLS 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 carnivore 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	0.88	0.294	**0.004**

b)

Carnivores N=65

dependent variable	**R^2**	**phylogenetic signal**	**predictor variables**	**estimate**	**std. error**	**p-value**
motor niche complexity	0	lambda=0.87	log body	0.051	0.169	0.761
			log brain	-0.08	0.264	0.764

Knowledge-niche complexity

In primates, the additive knowledge-niche complexity score showed a significant positive correlation with brain size (table 3.6a; figure 3.5). 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 motor-niche complexity or for AFR (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 (table S3.4a, figure S3.3). 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 knowledge-niche 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 3.6b, figure 3.5; table S4b, figure S3.4). Detailed statistics of the regression models of all additional analyses are also shown in (table S3.4a+b).

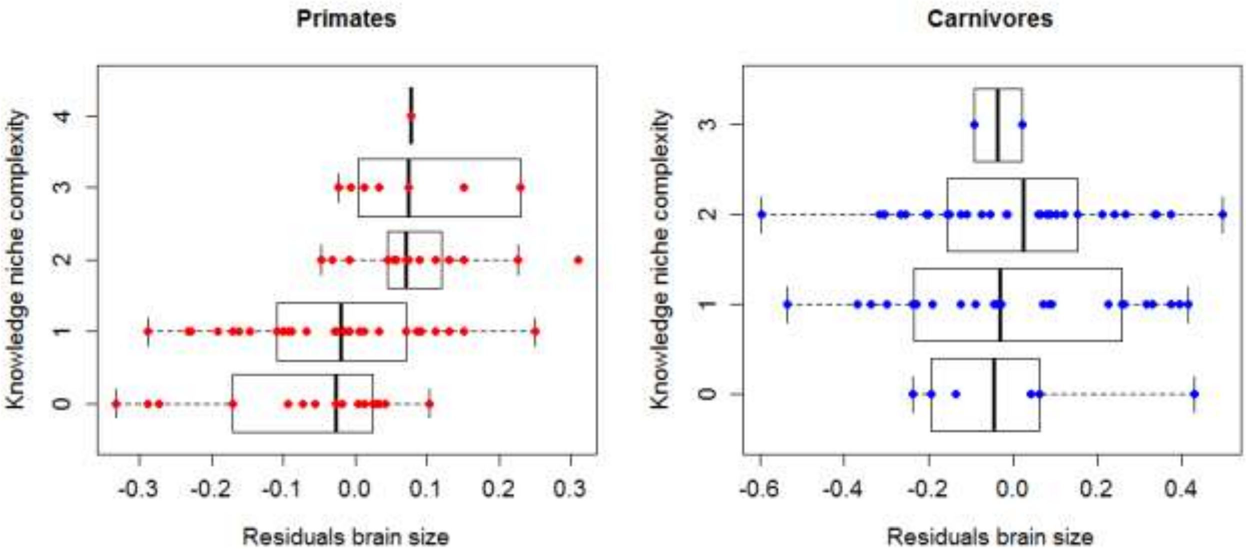


Figure 5. Relationships between relative brain size (corrected for body mass) and additive knowledge-niche complexity score for primates and carnivorans.

Table 3.6. Phylogenetic least-square (PGLS) multiple regression models with the additive knowledge score as response variable and body mass and brain size as predictor variables analyzed separately for the a) 78 primate and b) 65 carnivore species. The 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	3.6	0.654	**<0.001**

b)

Carnivores 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 [172], 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 [39, 43, 50]. 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 pre-reproductive 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 [172].

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 complex motor 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 skill-intense 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* [167, 168]), or in the order of moving from small to large prey in carnivorans and primates [119, 143, 193]. Furthermore, complex foraging elements seem to be practiced throughout ontogeny (e.g. beach hunting in the bottlenose dolphin, *Tursiops* sp. [138]).

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 [185, 194], cooperative hunting in different carnivorans and chimpanzees [142, 143, 195] and extractive foraging in various primates [117, 161, 172].

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 [177]. 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 [40, 42, 196] 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 [173], 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 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 [177] and Reader and Laland [176], 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' 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 supplementary material 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[39]. 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 [173]. 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 [197]. 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 into certain directions [198, 199].

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 [25]. 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 [25, 26].

Obviously, when a lineage shares food and has slow development, evolving into a knowledge-complex niche is more likely. Thus, the most likely explanation for the evolution of a foraging-niche 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 [23, 200], 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 [21, 23, 27]. 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 [172].

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[5, 6, 177]. 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 [10, 11].

Acknowledgements

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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[201]:

In primates, for motor-niche complexity and diet breadth we relied on various references given table S3.1. 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 nice complexity as they mainly rely 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 [202] who used a three point scale which we, in order to make it consistent with the carnivore data, dichotomized into a binary variable (absent/ present), whereby 1 and 2 by Jaeggi and van Schaik [202] was coded as present. Species in our data set that were missing in the Jaeggi and van Schaik[202] compilation were classified according to their definition which is originally based on Gibson [33], defining extractive foraging as "feeding on foods that must first be removed from other matrices in which they are embedded or encased" (Gibson [33], p 96). Extractive foraging was counted as present only in case 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 case these are actively excavated, whereas eradicating plants such as grasses or small scrubs was not accounted as such.

For tool use we based our classification on Bentley-Condit and Smith [203], 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 none of the species that were not available in Bentley-

Condit and Smith [203], we found evidence for regular tool use in the literature and we therefore classified them as non-tool-users.

In carnivores, the classifications into motor-niche complexity, extractive foraging and diet breadth were also based on various references given in table S1. As 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 are predominantly feeding 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 carnivores hunting for mobile prey (excluding insects) were assigned the highest complexity level (level 3) since this prey first needs to be pursued, caught, killed and eventually dissembled before ingestion.

We classified carnivore species as extractive foragers if they crack bones to access marrow (e.g. spotted hyenas, *Crocuta crocuta*) and break 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 [203], following the same rules as described for primates (see above) and for cooperative hunting on Smith et al. [204]. Also in carnivores, for species that were missing in these compilations, literature research showed no evidence for the presence of tool use and 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 those 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 [17, 21, 180] and complemented by unpublished data compiled from the literature by K. Isler, S. M. Graber and S. Heldstab. Additional endocranial volumes (ECV) of adult female museum specimens were measured by S. M. Graber and S. Heldstab using glass beads.

Table S3.1. Data on motor niche complexity, cooperative hunting, diet breadth, extractive foraging, tool use, knowledge score as well as life history parameters and brain size used for the analyses for the 65 carnivore and the 78 primate species.

Species	Motor Complexity	Cooperative hunting	Diet breadth	Extractive Foraging	Tool use	Knowledge Score	AFR (d)	Food dependence (d)	Body mass (gr)	Brain size (ml)	References foraging niche elements
Acinonyx jubatus	3	0	1	0	0	1	865.4	549	43000	111.0	[205]
Ailuropoda melanoleuca	1	0	0	0	0	0	2278.5	457.5	87500	236.0	[206]
Alopex lagopus	3	0	1	0	0	1	355.7	165.5	3415	41.0	[207]
Canis latrans	3	1	1	0	0	2	374.8	225	9760	89.1	[208]
Canis lupus	3	1	1	0	0	2	731.2	365	31100	123.6	[209]
Canis mesomelas	3	1	1	0	0	2	379.3	270	6600	53.6	[210]
Caracal caracal	3	0	1	0	0	1	499.6	288.8	9680	47.7	[211]
Chrysocyon brachyurus	3	0	1	1	0	2	731.8	213.5	23250	110.3	[212]
Conepatus leuconotus	2	0	1	1	0	2	365.4	152	2010	17.4	[213]
Crocuta crocuta	3	1	1	1	0	3	1114.4	914.5	57800	154.6	[214]
Cryptoprocta ferox	3	0	1	0	0	1	1323.4	365	6775	31.0	[215]
Cynictis penicillata	2	0	1	0	0	1	724.4	119	571	8.5	[216]
Eira barbara	3	0	1	0	0	1	733.7	200	3500	40.8	[217]
Enhydra lutris	2	0	0	1	1	2	1462	210	23600	117.9	[218]
Felis chaus	3	0	1	1	0	2	612.4	274.5	5050	37.9	[219]
Felis nigripes	3	0	0	0	0	0	613.4	106.75	1100	20.5	[215]
Felis silvestris	3	0	1	1	0	2	364.7	167.75	4130	25.4	[215]
Genetta genetta	3	0	1	0	0	1	727.9	126	1820	12.8	[220]
Gulo gulo	3	0	1	0	0	1	891.6	182.4	10600	71.7	[221]
Helogale parvula	3	0	1	1	0	2	505.7	153	267	4.2	[213]
Herpestes ichneumon	3	0	1	1	0	2	610.7	365	3265	19.6	[213]
Hyaena hyaena	2	0	1	1	0	2	1003.2	365	36300	103.1	[213]

Ictonyx striatus	3	0	1	0	0	1	365.1	126	713	8.0	[213]
Leopardus pardalis	3	0	1	0	0	1	993.6	213.5	10750	63.2	[213]
Leptailurus serval	3	0	1	0	0	1	895.3	200	10400	54.0	[222]
Lontra canadensis	3	0	1	1	0	2	792	182.4	7850	52.3	[213]
Lutra lutra	3	0	1	1	0	2	974.6	238	6750	36.6	[146]
Lycaon pictus	3	1	1	0	0	2	729.5	391	22050	133.0	[213]
Lynx lynx	3	0	1	0	0	1	739.6	304	17200	88.6	[223]
Lynx rufus	3	0	1	0	0	1	731.6	243.2	7500	61.8	[224]
Martes pennanti	3	0	1	1	0	2	577.9	137.25	2250	30.7	[225]
Meles meles	2	0	1	1	0	2	574.4	183	10100	44.0	[226]
Melursus ursinus	2	0	1	1	0	2	1215.8	547.5	99750	272.5	[227]
Mephitis mephitis	2	0	1	1	0	2	376.2	84	1790	10.4	[213]
Mustela frenata	3	0	1	1	0	2	189.1	84	165	4.0	[213]
Mustela nivalis	3	0	1	1	0	2	156.1	73.5	60	2.3	[228]
Mustela putorius	3	0	1	0	0	1	353.1	91.5	689	6.0	[213]
Mustela sibirica	3	0	1	0	0	1	365.2	91.5	395	5.7	[215]
Nasua narica	2	0	1	1	0	2	790.5	152	3700	39.4	[213]
Neofelis nebulosa	3	0	0	0	0	0	881.9	304	19490	72.0	[213]
Nyctereutes procyonoides	3	0	1	1	0	2	364.7	121	4020	28.5	[229]
Otocyon megalotis	2	0	1	1	0	2	367	197.6	4075	30.3	[230]
Panthera leo	3	1	1	0	0	2	1418.8	775.2	124000	211.3	[213]
Panthera onca	3	0	1	0	0	1	1012.1	501.6	77700	167.7	[213]
Panthera pardus	3	0	1	0	0	1	1033.6	365	31500	129.8	[231]
Panthera tigris	3	0	0	0	0	0	1346.9	577.6	130000	258.1	[213]
Parahyaena brunnea	2	0	1	1	0	2	1157.3	427	39300	118.1	[232]
Potos flavus	2	0	1	0	0	1	928.5	121.6	2800	27.1	[233]
Procyon lotor	2	0	1	1	0	2	603.4	140	5620	41.9	[213]
Proteles cristatus	1	0	0	0	0	0	747.5	122	8820	41.5	[234]

Pteronura brasiliensis	3	0	0	0	0	0	798	288.8	24000	104.5	[235]
Puma concolor	3	0	1	0	0	1	1006.6	304	42700	119.6	[213]
Suricata suricatta	2	0	1	0	0	1	738.4	90	725.5	10.3	[236]
Uncia uncia	3	0	1	0	0	1	1374.9	547.2	32500	111.2	[213]
Urocyon cinereoargenteus	3	0	1	1	0	2	361.4	122	4010	35.8	[224]
Urocyon littoralis	2	0	1	0	0	1	365.2	152	1896	29.7	[237]
Ursus americanus	2	0	1	1	0	2	1734.5	503.25	84700	221.7	[238]
Ursus arctos	3	0	1	1	0	2	1928.3	645	182000	340.8	[239]
Ursus maritimus	3	0	1	1	1	3	2128.9	881.6	225000	429.9	[240]
Viverricula indica	3	0	1	0	0	1	371.4	127.5	2660	17.4	[241]
Vormela peregusna	3	0	1	0	0	1	365	64.5	447.5	5.8	[242]
Vulpes chama	3	0	1	0	0	1	325.7	152	2955	35.8	[243]
Vulpes rueppellii	3	0	1	1	0	2	356.9	121.6	1575	25.3	[213]
Vulpes velox	3	0	1	0	0	1	361.2	152	2345	31.3	[244]
Vulpes vulpes	3	0	1	0	0	1	356.3	225.5	4210	42.3	[245]
Alouatta caraya	2	0	0	1	0	1	1350.5	325	4240	47.5	[246]
Alouatta palliata	2	0	1	0	0	1	1460	365	5350	49.4	[246]
Alouatta seniculus	2	0	1	0	0	1	1898	380	5210	53.5	[246]
Arctocebus aureus	2	0	0	0	0	0	438	115	200	5.7	[247]
Arctocebus calabarensis	2	0	0	0	0	0	401.5	115	309	6.8	[247]
Ateles paniscus	2	0	1	0	0	1	1825	1094	8070	107.0	[246]
Avahi laniger	1	0	0	0	0	0	949	153	1207	9.2	[248]
Cacajao calvus	2	0	1	0	0	1	1314	638	2880	71.7	[249]
Callimico goeldii	3	0	1	0	0	1	547.5	67	483.5	11.0	[250]
Callithrix jacchus	3	0	1	1	0	2	620.5	182.5	320	7.9	[251]
Cebus albifrons	3	0	1	1	1	3	1460	264	2290	63.8	[252]
Cebus apella	3	0	1	1	1	3	2445.5	265	2500.7	62.0	[253]
Cebus capucinus	3	0	1	1	1	3	2190	517	2436.5	66.8	[254]

Cebus nigritus	3	0	1	1	0	2	2555	450	2215	61.9	[255]
Cebus olivaceus	3	0	1	1	1	3	2190	547	2633.3	67.7	[256]
Cercocebus atys	2	0	1	0	0	1	1715.5	126	6200	83.8	[257]
Cercopithecus ascanius	3	0	1	1	0	2	1825	577.5	2901	54.7	[258]
Cercopithecus campbelli	2	0	1	0	0	1	1277.5	365	2544.4	53.0	[258]
Cercopithecus cephus	2	0	1	0	0	1	1825	365	2880	58.6	[258]
Cercopithecus diana	2	0	1	0	0	1	1971	365	3900	55.3	[258]
Cercopithecus mitis	3	0	1	1	0	2	2372.5	316	4628	63.6	[258]
Cercopithecus neglectus	2	0	1	0	0	1	1825	365	4130	58.8	[258]
Chlorocebus pygerythrus	2	0	1	0	0	1	1861.5	259	3575.8	57.8	[258]
Chlorocebus sabaeus	2	0	1	0	0	1	1460	165	3700	57.3	[259, 260]
Colobus angolensis	2	0	1	0	0	1	2190	365	7570	69.8	[245]
Colobus guereza	1	0	1	0	0	1	1752	334	7505.6	70.1	[261]
Colobus polykomos	1	0	0	0	0	0	2007.5	365	6708.9	68.5	[262]
Daubentonia madagascariensis	3	0	1	1	0	2	1277.5	205	2555	43.2	[263]
Eulemur fulvus	2	0	1	0	0	1	985.5	183	2291.7	23.9	[264]
Eulemur macaco	2	0	0	0	0	0	803	135	2350	21.9	[265]
Eulemur mongoz	3	0	1	1	0	2	912.5	152	1212.4	17.3	[264]
Galago moholi	2	0	0	0	0	0	438	84	148.4	3.6	[266]
Gorilla gorilla	2	0	0	1	0	1	3723	1680	71500	418.4	[267]
Hapalemur griseus	2	0	0	0	0	0	1204.5	121	709	13.3	[268]
Lemur catta	2	0	1	0	0	1	1168	179	2210	21.3	[269]
Leontopithecus rosalia	3	0	0	1	0	1	1314	91	609	12.4	[251, 270]
Lepilemur mustelinus	2	0	0	0	0	0	584	75	804	8.0	[271]
Lophocebus albigena	2	0	1	0	0	1	2190	213	6010	87.5	[272]
Loris lydekkerianus	2	0	0	0	0	0	547.5	145	273	6.1	[273]
Loris tardigradus	2	0	0	0	0	0	511	135	192.5	5.3	[273]

Macaca fascicularis	3	0	1	1	1	3	1898	231	3517.9	58.8	[274]
Macaca fuscata	3	0	1	1	1	3	2226.5	195	8030	93.4	[274]
Macaca mulatta	3	0	0	1	0	1	1825	192	5670.5	81.4	[275]
Macaca nemestrina	3	0	1	1	0	2	1423.5	237	6539.2	94.7	[276]
Macaca nigra	3	0	0	1	0	1	1971	214	5470	77.5	[277]
Macaca radiata	3	0	1	1	0	2	1642.5	365	3855.7	68.1	[278]
Macaca silenus	3	0	1	1	1	3	1788.5	456	6100	75.3	[279]
Macaca sylvanus	3	0	1	1	0	2	1752	213	9625	89.7	[274]
Mandrillus sphinx	2	0	1	0	0	1	1825	307	12800	131.3	[280]
Microcebus murinus	3	0	1	0	0	1	657	49	65.1	1.5	[281]
Nasalis larvatus	2	0	1	0	0	1	1825	456	9729.6	81.9	[282]
Nycticebus coucang	2	0	1	0	0	1	547.5	183.2	652.5	9.7	[283]
Otolemur crassicaudatus	2	0	1	0	0	1	657	134	1150	11.4	[284]
Otolemur garnettii	2	0	0	0	0	0	584	140	1188	10.5	[285]
Pan paniscus	3	0	1	1	0	2	5183	1642.5	33200	315.0	[286]
Pan troglodytes	3	1	1	1	1	4	4854.5	1643	40366.7	344.4	[286]
Papio anubis	3	0	1	1	1	3	2518.5	420	13300	149.9	[287]
Papio cynocephalus	3	0	1	1	0	2	2190	456	12000	144.3	[287]
Papio hamadryas	3	0	1	1	0	2	2226.5	480	10300	133.5	[287]
Papio ursinus	3	0	1	1	1	3	2482	502	14800	159.3	[287]
Pithecia monachus	2	0	0	0	0	0	1095	365	2292.7	34.7	[288]
Pithecia pithecia	3	0	1	1	0	2	1460	150	1639	30.3	[289]
Pongo abelii	3	0	1	1	1	3	5621	2555	41148	334.1	[290]
Pongo pygmaeus	3	0	1	1	1	3	5730.5	2008	36947.6	326.0	[290]
Presbytis thomasi	2	0	1	0	0	1	1971	579	6350.4	62.4	[291]
Propithecus diadema	2	0	1	0	0	1	1934.5	183	6130	37.0	[292]
Propithecus edwardsi	2	0	0	0	0	0	1825	365	5790	36.1	[293]
Pygathrix nemaeus	1	0	0	0	0	0	1752	330	8440	91.6	[294]

Saguinus fuscicollis	3	0	1	1	0	2	985.5	91	350.5	8.0	[295]
Saguinus geoffroyi	2	0	1	0	0	1	730	75	516.9	9.8	[296]
Saguinus midas	2	0	1	0	0	1	730	70	535	9.5	[253]
Saguinus mystax	2	0	0	0	0	0	474.5	90	584	9.9	[297]
Saimiri sciureus	3	0	1	1	0	2	1423.5	330	742	22.7	[298]
Tarsius bancanus	3	0	0	0	0	0	584	76	110.7	3.1	[299]
Theropithecus gelada	1	0	0	0	0	0	1460	450	11700	120.2	[300]
Trachypithecus obscurus	2	0	1	0	0	1	1642.5	365	6764.8	57.2	[282]
Trachypithecus vetulus	2	0	1	0	0	1	1569.5	228	5103	57.8	[282]
Varecia variegata	2	0	1	0	0	1	839.5	135	3575	29.2	[301]

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 S3.2a; figure S3.1).

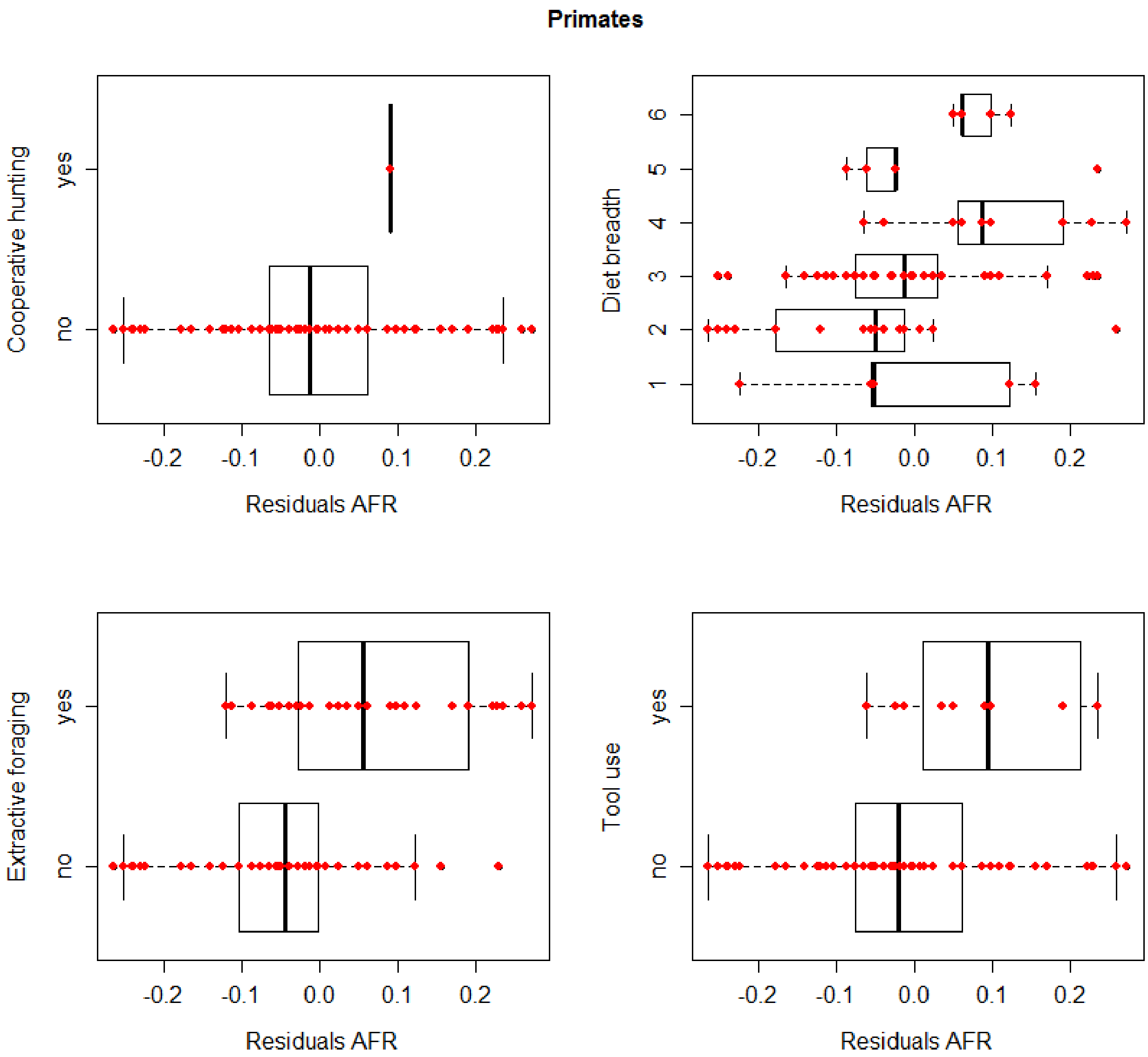

Figure S3.1. Relationships between pace of development (age at first reproduction corrected for body mass) and the different elements of knowledge-niche complexity in primates.

In carnivores, 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 S3.2b; figure S3.2).

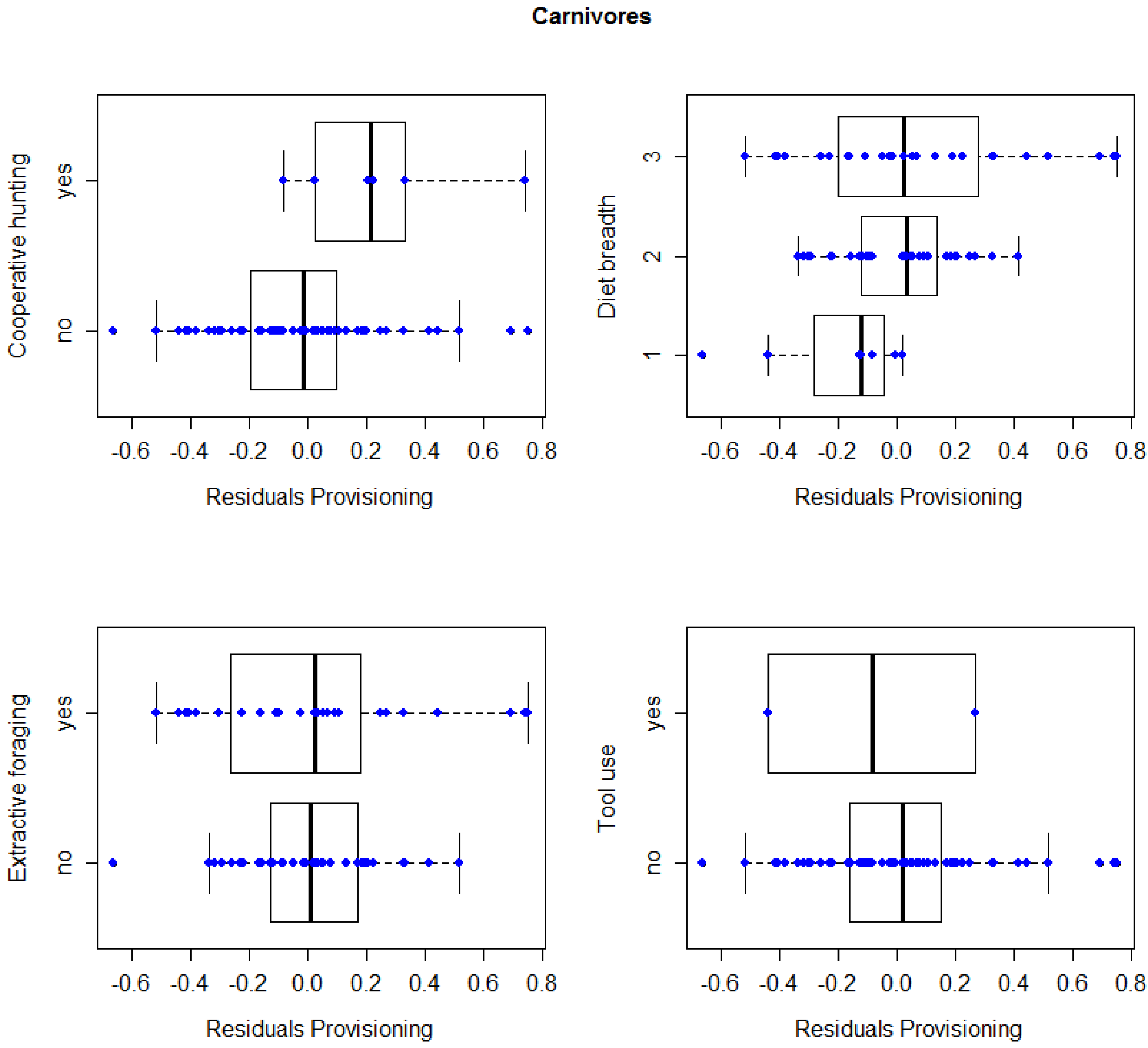

Figure S3.2. Relationships between length of provisioning (corrected for body mass) and the different elements of knowledge-niche complexity in carnivores.

Since we found a positive correlation between knowledge-niche complexity and motor-niche complexity in primates (but not in carnivores), 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 S3.2a).

Table S3.2. Relation between life history and knowledge-niche elements as well as controlling for possible 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 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 (PGLS) and phylogenetic logistic (PLR) 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 (AFR) and length of provisioning as predictor variables for the 65 carnivore 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	0.44	0.472
				log AFR	3.394	1.09	**0.003**
				log provisioning	-0.819	0.671	0.226
		0.19	lambda=0.29	log body	-0.068	0.441	0.878
				motor 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**
				log provisioning	-0.185	1.468	0.9
		-	alpha=0.01	log body	1.535	0.905	0.09
				motor complexity	10.19	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 complexity	0.768	0.264	0.004
				log AFR	2.184	1.125	0.052
Knowledge niche complexity	PGLS	0.73	lambda=0.00	log body	0.229	0.222	0.305
				motor niche	1.109	0.117	**<0.001**
				Log AFR	1.142	0.541	**0.038**

b)

Carnivores 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	0.11
				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	0.52
				log provisioning	0.273	0.794	0.732
cooperative hunting	PLR	-	alpha=0.01	log body	3.31	2.62	0.207
				log AFR	-15.492	7.779	**0.046**
				log provisioning	8.899	4.986	0.074

Brain size and foraging niche complexity

In primates, age of fist reproduction (AFR) has been shown to be correlated with both brain size [40, 196] 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 S3.3a). 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 [173]. In carnivores, adding the length provisioning as an additional factor did not change the results (table S3.3b).

Table S3.3. Relation between brain size and motor-niche complexity - controlled for AFR 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 (PGLS) 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 carnivore 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)

Carnivores 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	0.25	0.515

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 S3.4a). Adding AFR as an additional factor to the regression model (since it has been shown to be correlated with both brain size [40, 42, 196] 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 S3.4a, figure S3).

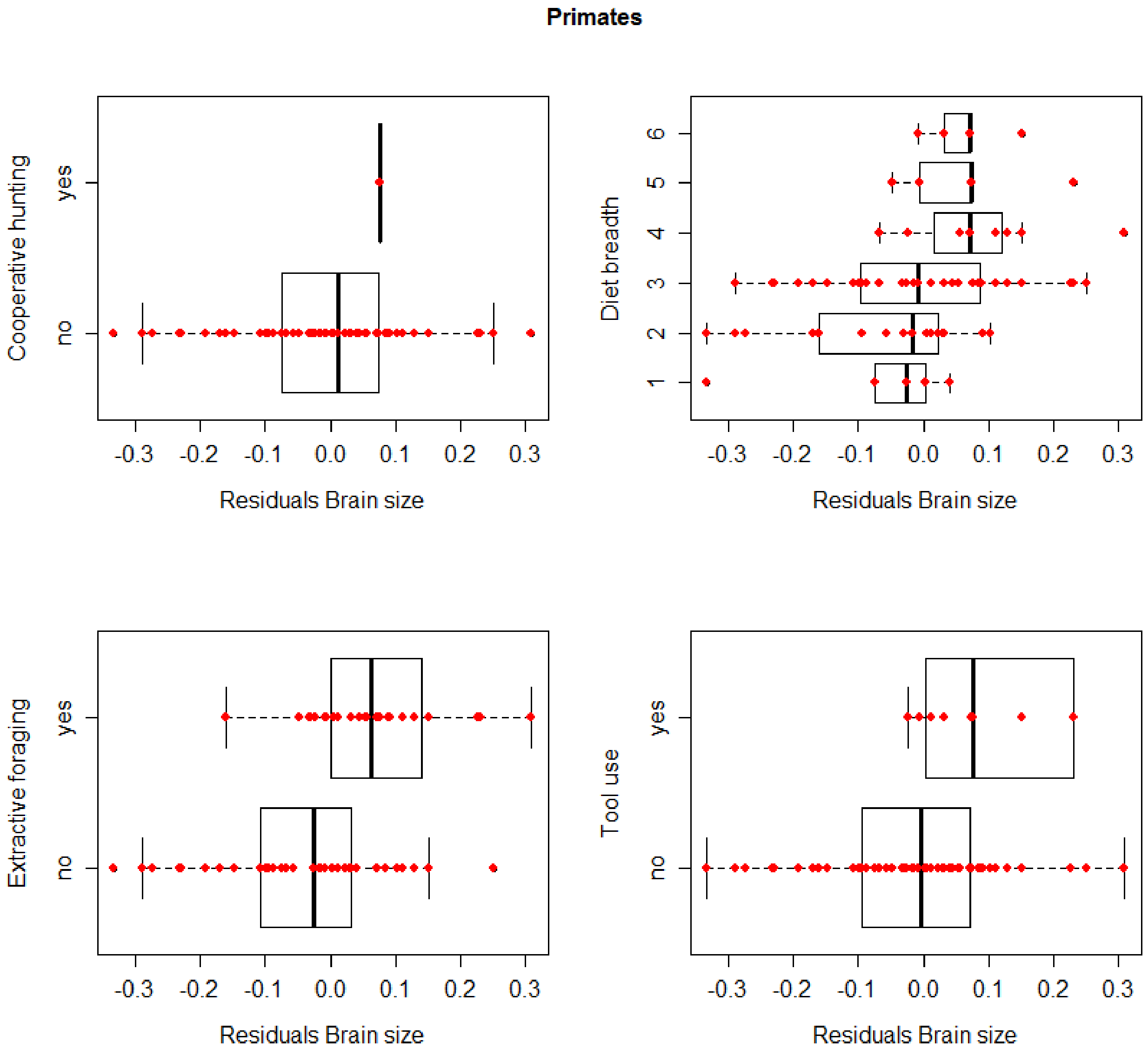

Figure S3.3. Relationships between relative brain size (corrected for body mass) and the different elements of knowledge-niche complexity in primates.

In carnivores, 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 S3.4b, figure S3.4). 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 carnivores) mostly did not change the results. Only in the case of cooperative hunting a significant positive correlation with brain size emerged (table S3.4b).

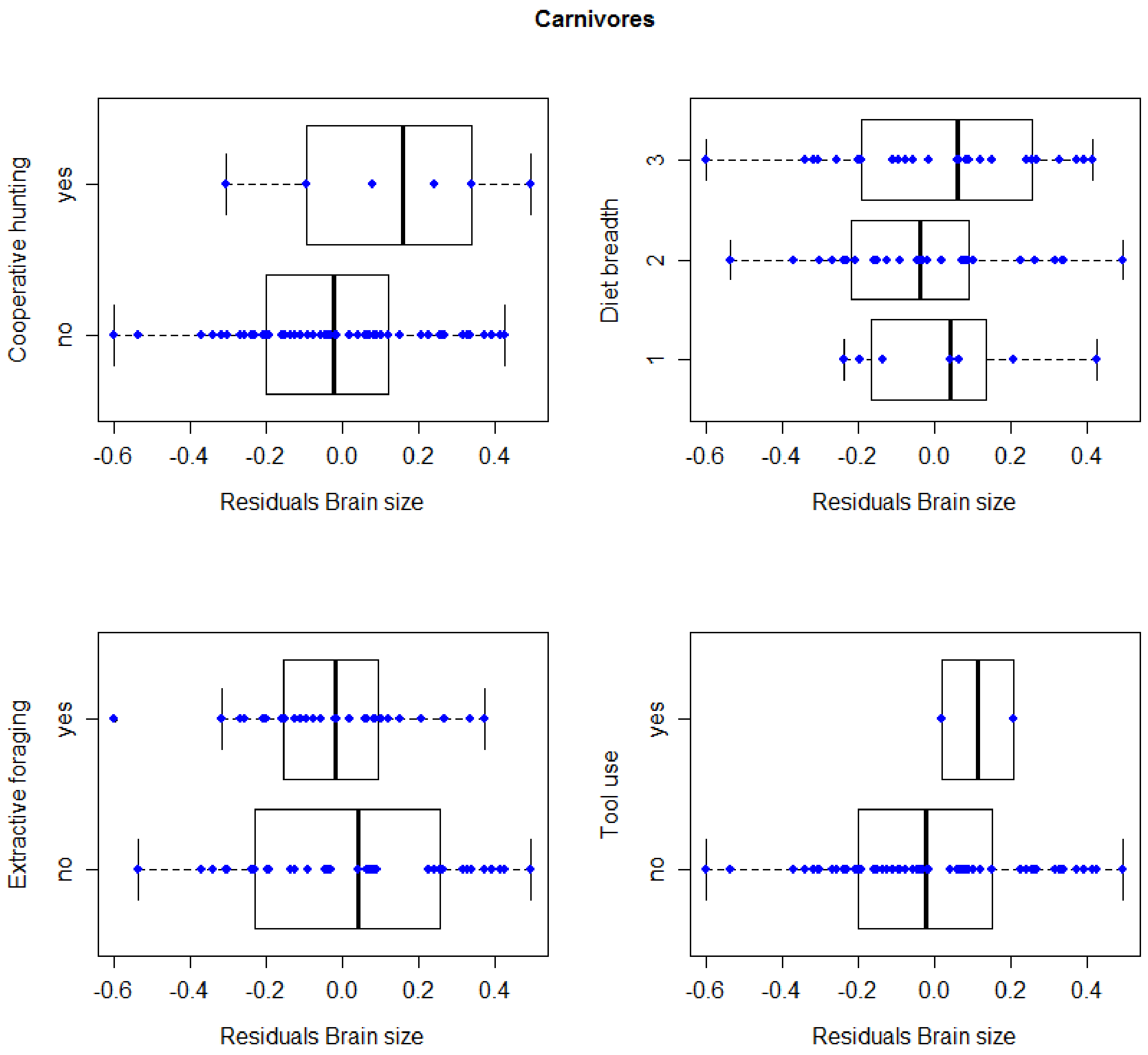

Figure S3.4. Relationships between relative brain size (corrected for body mass) and the different elements of knowledge-niche complexity in carnivores.

Table S3.4. Relation between brain size and knowledge-niche elements - controlled for AFR, 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 (PGLS) and phylogenetic logistic (PLR) 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 carnivore 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
		0.3	lambda=0.00	log body	-0.239	0.355	0.503
				motor complexity	0.559	0.224	**0.015**
				log brain	0.683	0.433	0.119
extrractive 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	1.1	**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 complexity	9.817	3.149	**0.002**
				log brain	0.278	2.508	0.912
tool use	PLR	-	alpha=0.61	log body	-3.6	1.432	**0.012**
				log brain	6.092	2.177	**0.005**
		-	alpha=0.02	log body	-2.727	1.14	**0.017**
				log AFR	2.048	1.36	0.132
				log brain	3.767	1.586	**0.018**
		-	alpha=0.0009	log body	-1.601	0.724	**0.027**
				motor complexity	1.324	0.638	**0.038**
				log brain	2.873	1.019	**0.005**
knowledge niche complexity	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	1.1	0.112	**<0.0001**
				log brain	1.318	0.493	**0.009**

b)

Carnivores 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	0.48
		0.1	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	0.31
		-	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	1.52	0.926
				log brain	0.549	2.396	0.819
		-	alpha=0.01	log body	-7.38	3.249	**0.023**
				log provisioning	7.673	3.523	**0.029**
				log brain	9.31	4.202	**0.027**
knowledge niche complexity	PGLS	0.13	lambda=0.29	log body	-0.0003	0.26	0.999
				log provisioning	0.802	0.287	**0.007**
				log brain	-0.308	0.377	0.417

Chapter 4: Development of foraging skills in two orangutan populations: needing to learn or needing to grow?

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Abstract

Orangutans show one of the slowest-paced life histories of all mammals. Whereas life-history theory suggests that the time to reach adulthood is constrained by the time needed to reach adult body size, the needing to learn hypothesis instead suggests that it is limited by the time needed to acquire adult-level skills.

To test between these two hypotheses, we compared the development of foraging skills and growth trajectories of immature wild orangutans in two populations: at Tuanan (*Pongo pygmaeus*), Borneo, and Suaq Balimbing, Sumatra (*Pongo abelii*). We collected behavioral data on diet repertoire, feeding rates and ranging competence during focal follows, and estimated growth through non-invasive laser photogrammetry.

We found that adult-like diet repertoires are attained around the age of weaning and that female immatures increase their repertoire size faster than their male peers. Adult-level feeding rates of easy techniques are reached just after weaning, but several years later for difficult techniques, albeit always before adulthood. Independent immatures show higher feeding rates for easy to process items than their mothers, with male immatures reaching higher feeding rates faster than females. Sumatran immatures reach adult-level feeding rates 2-3 years later than their Bornean peers, in line with their higher dietary complexity and later weaning. The range-use competence of independently ranging weaned immatures was similar to that of adult females.

In conclusion, unlike in humans, in orangutans, all ecological skills are in place before reproduction starts. Growth trajectories suggest that energetic constraints rather than skills best explain the length of immaturity. However, the need to acquire sufficient skill competence for dietary independence is reached

later where the adult niche is more complex, which is consistent with the relatively later weaning age with increasing brain size found in primates in general, and apes in particular.

Introduction

Compared with other primates, great apes show an exceptionally long period of development, even after controlling for the effects of body size [302, 303]. Among them, with a developmental period of almost 20 years, humans are the most extreme case [304]. So far, the reasons for this delay of the reproductive period remain poorly understood. According to classic life history theory, although the developmental period is needed to grow body and brain to adult size, the reproductive phase should be reached as soon as possible in order to maximize reproductive outcomes. Thus, the relative length of the immature phase is determined by the optimization of developmental and reproductive schedules in the face of allocation tradeoffs and externally imposed mortality [304-306]. However, this leaves quite some remaining variation unaccounted for, including the extreme cases of all great ape species.

Much of this remaining variance is explained by brain size. When controlled for body size, larger-brained species have a relatively longer period of development than smaller brained species [42, 304], [173]. The prolonged immature period of the large-brained great apes is largely in line with this. However, the question remains why such a correlation exists in the first place. Two main theoretical frameworks have been proposed to explain the correlated evolution between the length of the developmental period and brain size.

First, it has been suggested that larger-brained animals show an extended developmental period because they need time to acquire more and increasingly complex skills required for adult survival and reproduction (*needing-to-learn hypothesis [40]*). In this view, the length of the developmental time is constrained by the number and complexity of skills a species has to acquire. This hypothesis therefore predicts that at least some vital skills needed for adult survival reach adult levels just before the age at first reproduction. This prediction seems to hold among birds, where adult-level foraging skills are attained around the time of first reproduction [115, 116, 172]. In most mammals, however, skill competence is reached well before the age at first reproduction [39, 172] In contrast to birds, due to the lack of post-weaning provisioning, most mammals need to be self-supporting right after weaning. Since the consequences of failures during food acquisition are especially severe during development[39], at weaning skills must have reached a level sufficient to support the smaller but growing juvenile body. It is thus likely that in most mammals, even though skill acquisition does not directly constrain first reproduction it might determine the timing of weaning [304].

The alternative hypothesis is that energetic constraints of large brains on somatic development prolong the length of the developmental period (e*xpensive brain framework* [43, 44]). This framework encompasses several hypotheses proposed earlier, including the effects of maturational constraints and malnutrition avoidance (reviewed in [49]). Brain tissue is among the most energetically expensive tissues to maintain [13] and requires even more energy to grow and develop [14]. Also, because developing brains are especially susceptible to temporary energy shortages [45], brain development must be conservative so it can be constantly sustained by sufficient energy. Brain growth is completed before somatic growth [47, 48]. Accordingly, high energetic investment of larger-brained species into brain development during infancy and juvenility result in a delay in the physical development of the body and thus a delayed onset of the reproductive period [43, 49, 50]. The *expensive brain framework* is in line with the interspecific correlation between large brains and delayed maturation. Within species, it predicts that body growth is only completed around the age of fist reproduction, particularly in females.

A comparative study has shown that in most mammals, foraging skills are in place well before the age of first reproduction and thus unlikely to be limiting on the onset of reproduction [172]. Data on chimpanzees (*Pan troglodytes*) and gorillas *(Gorilla gorilla beringei and Gorilla gorilla gorilla)* suggest that adult-like diet repertoires and feeding rates are reached around the age of weaning. Most other primate species seem to follow this pattern: competence in foraging skill roughly coincides with weaning in mountain baboons (*Papio ursinus* [170]), bonnet macaques (*Macaca radiata* [278]), common marmosets (*Callithrix jacchus* [160]), squirrel monkeys (*Saimiri sciureus* [119]) and Mayotte brown lemurs (*Eulemur fulfus* [307]). In very few primate species, foraging competence is reached significantly later than weaning, such as in brown capuchins (*Cebus apella* [118, 161]), or even only around the age at first reproduction as in Japanese macaques (*Macaca fuscata* [167, 168]) or hamadryas baboons (*Papio hamadryas* [117]). However, in those latter cases, lower foraging performance can arguably be attributed to a lack of strength (due to smaller body size of the immatures) rather than lack of skills. Overall, this pattern suggests that in primates, the need to acquire sufficient foraging skills determines the age at dietary independence rather than the age of first reproduction.

Of all primate species, orangutans show the most extreme life history. They show the latest age at first reproduction of any nonhuman primate and the latest age of weaning (and therefore also the longest birth intervals) of any primate species [91]. Furthermore, there is some variation in these life-history parameters between the different orangutan species and subspecies. Immature Sumatran orangutans are weaned around the age of 7.5-9 years, which is 1-2 years later than their Bornean peers [90]. Weaning is followed by a multiyear juvenile period during which individuals are fully self-supporting (see below) but not yet reproducing. Whereas Bornean orangutan females have their first offspring around the age of 13-14 years, their Sumatran peers wait for another 2-3 years until they start reproducing, around the age of 14-16 years [90, 92, 95].

At the same time, compared with other great apes, orangutans show a rather solitary lifestyle, with the degree of sociability ranging from semi-solitary to low level fission-fusion, depending on populations [86-88, 308]. After having been in constant and close associations with their mothers during infancy, juvenile orangutans start to range more and more independently within 1-2 years of complete weaning [90, 93]. Depending on species and population, independent immatures spend 30-80% of their time on their own whereas the remaining time they mainly associate in small peer groups [90, 93, 94]. Unlike most other primates, therefore, orangutans start to range mostly alone soon after weaning, and thus cannot systematically rely on social information for any of the skills they depend on (see below). It is therefore possible that the late weaning of orangutans relative to the general primate pattern, is linked to the need to sustain themselves independently soon afterwards.

The aim of this paper is thus to investigate whether the exceptionally late age at weaning and first reproduction of wild orangutans (*Pongo* spp.) is best explained by the time needed to develop adult-levels skills or by the energetic constraints imposed by competition for energy between brain and body growth and differentiation. Given their lack of coalitions or other complex social interactions, social skills are unlikely to be a constraining factor on orangutan development. For all nonfood subsistence skills (e.g. nest building) competence is already reached during infancy [93]. Thus, probably the most crucial skills immature orangutans have to acquire are foraging skills. Orangutans live in a complex foraging niche: food availability in most orangutan habitats fluctuates during and across years without following any clear seasonal pattern[96]. They show very broad diets and rely on a variety of difficult to process food items. Some populations habitually use tools in the foraging context [97, 98, 309]. Foraging skills can be divided into food selection competence (what to eat), food processing competence (how to eat), and food locating competence (where and when to eat [310]). Given their broad diets, complex processing techniques and highly fluctuating food availability, each of these three aspects may limit orangutan skill development and their ability to compete in the adult niche. For any foraging skill to be potentially limiting development, they must be learned rather than being largely innate. Indeed, it takes immature orangutans multiple years to acquire their foraging skills. Also, there is evidence that they do so by a combination of social- and individual learning [62, 90, 311].

We first test the predictions of the *needing-to-learn hypothesis*. These are that full adult competence is reached (i) around the age at first reproduction if skills levels limit reproduction or (ii) around weaning if skill levels limit the age of nutritional independence. For this we will follow Rapaports and Browns[310] functional division of foraging skills by looking at the development of diet repertoires (*what to eat*), feeding rates (*how to eat*), and ramble ratios of the travel routes, i.e. the actual path length divided by distance between beginning and end of daily path (*when and where to eat*). The *needing-to-learn hypothesis* further predicts that (iii) if foraging skills are learned, more complex skills are attained later than less complex skills, and that (iv) life history differences between the populations will be reflected in skill trajectories, such as that later age at first reproduction or later weaning should go in hand with a later age of skill competence. Finally, since male and female orangutans show different energetic needs and time budgets [312], it is possible that females focus more on the development of ecological skills than males do, and thus that we find sex differences in acquisition trajectories.

In order to test the predictions of the *expensive brain framework* we will estimate growth trajectories of the immatures in the two populations. If, as under the assumptions of the *expensive brain framework,* energetic constraints are limiting on age at first reproduction, immature females should continue growing until at least the age at first reproduction or even thereafter.

Methods

Data were collected at Suaq Balimbing (3˚42'N, 97˚26'E, Aceh Selatan, Indonesia) and at Tuanan (2°09'S, 114°26'E, Kalimantan Tengah, Indonesia), on a population of wild Sumatran (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus wurmbii*), respectively. Both study sites consist mainly of peat swamp forest and show high orangutan densities (7 individuals per km^2 at Suaq and 4 at Tuanan [106]).

To assess skill development we examined 13 immature individuals from Suaq and Tuanan each, using their own mothers as adult references. Details on the focal individuals are summarized in the supplementary material (table S4.1). We distinguish two categories of immatures: dependent immatures (infants), who are between birth and weaning; and independent immatures (juveniles) who are between weaning and female age at first reproduction. Weaning age at Suaq is around 7 - 9 years and at Tuanan around 6 - 7.5 years, whereas female age at first reproduction is around 13 -14 years at Tuanan and 15 – 16 years at Suaq [92] (van Noordwijk and Schuppli unpublished data).

Diet repertoires

Diet repertoires were assessed with the help of long-term behavioral databases compiled at the two field sites. At Tuanan, data have been collected since 2003 and at the time of analysis the database contained 33’200 follow hours on adult females and immatures. At Suaq, data have been collected since 2007, and around 8’400 hours of data have been collected on adult females and immatures. This data are collected during focal follows, following the same protocol for orangutan data collection (http://www.aim.uzh.ch/de/research/orangutannetwork/sfm.html), using focal animal sampling including instantaneous scan sampling at two minutes intervals. Inter-observer reliability was assessed based on simultaneous follows by multiple observers on the same focal animal without verbal exchange about the activity of the focal animal. New observers had to reach an index of concordance of at least 85% with experienced observers before their data was included in the database.

When the focal animal was feeding, we recorded the species as well as the food item. For the analysis, we used the broad categories of fruits, leaves (and other green vegetative matter in the case of vines and lianas), bark, pith (cambium) and insects. Each species – part combination was considered as one specific “food item”. Adult females at Tuanan each have diets comprising around 170 or more food items from around 110 plant species. It takes more than 1500 follow hours collected over multiple years before the recorded repertoire sizes of these females start to stabilize (see figure S4.1) and even after 4000 follow hours, new items are still being recorded. Thus, the development of diet repertoires could only be analyzed at Tuanan where the database is currently far more extensive than at Suaq.

We examined the development of the diet repertoire in 6 immatures at Tuanan (3 females and 3 males) on which we had multiple years of continuous and dense data (at least 400 follow hours for each year of data collection) covering 4.5 -7.5 years of their infancy (for details on the used data set, see table S4.1). The overlap with the mother was calculated for continuous consecutive blocks of 450-500 follow hours, which correspond to 9-13 months each. Since for each data point the overlap calculations are based on data simultaneously taken on the offspring and its mother (followed on the same days), they are based on exactly the same amount of hours for both mother and offspring. However, to correct for the fact that older infants have been followed longer and are compared to a longer follow period of their mothers, we included follow effort as a factor in the statistical model.

Feeding rates

Feeding rates were collected directly during focal follows by CS from 2010-2015 as well as from close-up videos of the focal animals feeding, taken by various observers in 2012 - 2015. We calculated how much time it took an individual to process a food item from picking to ingestion. In the field this was accomplished using a stopwatch. The videos were coded using the interact software (Interact 9). Feeding rates that were taken directly in the field did not differ from those obtained by video coding on the same food item by the same adult focal animal (table S4.2). The complexity of the food items was determined by the number of steps it takes to process an item (for details see table 4.1).

Feeding rates were collected for 11 and 10 immature individuals and their mothers at Tuanan and Suaq, respectively. Rates were averaged over a minimum of five individual samples (of the same individual feeding on the same food item). In order to capture the development of feeding rates with age, if there was a gap of more than five months between two groups of measurements of the same individual feeding on the same species, these measurements were treated as a different data points. To account for the fact that we thus had multiple data point of the same individual feeding on the same food item (at different stages of its development), we analyzed our data using mixed models (see below). To avoid the possible confounding effect of different stages of ripeness of the fruits on feeding rate, whenever possible (60 % of all cases), feeding rates of the immatures were calculated as a percentage of their mothers' feeding rates when feeding in the same tree at the same time. However, in the remaining 40% of the cases (mainly for older, independently ranging immatures), the mother's data were not available and thus the average feeding rate of the adult female feeding on the same food item closest to the measurement date of the immature was taken as an adult reference. The presence or absence of simultaneous samples of the mother had no effect when we included it as a binary variable in the model (see table S4.3).

Ranging competence

We assessed ranging competence by estimating ramble ratios (sinuosity values) of the travel routes, assuming that individuals that struggle to plan their daily resource exploitation schedule would show higher ramble ratios. For this, locations of the focal animals were taken every 30 minutes during focal follows using GPS devices (Garmin models GPSMAP 62s, GPSMAP 60CSx, and GPSMAP 78). Ramble ratios were then calculated in Arc GIS [313], using Hawth's tool [314] and represent the total path length divided by the distance between start and end point of the follow (nest locations for full day follows). Average daily ramble ratios were calculated based on 5 – 17 ($\bar{x}$ = 9) follow days within the same 5 months, in order to capture one specific developmental state of the juvenile individuals. To ensure maximal comparability (e.g. in terms of possible seasonality effects), as adult references, ramble ratios of the mothers followed during the same periods (within the same 5 months) were used. Because this often resulted in >1 data points per individual, we used a mixed model approach (see below).

Body size measurements

For body size measurements, we relied on laser photogrammetry [315, 316] using a camera (Nikon D 90) with 3 parallel lasers attached at a constant distance. The laser points visible in the pictures were used as a reference scale bar. The camera was calibrated by taking pictures of a known reference scale at various distances in the forest before the actual measurements. We focused on three measures of arm length: forearm (elbow to wrist), upper arm (shoulder joint to elbow) and whole arm (shoulder joint to wrist) as a proxy for overall body size.

Laser pictures were taken at Suaq Balimbing in 2013-2014 by various observers. Distances in the pictures were calculated by KL using Paint.net Software. Data points represent averages of 4 – 22 ($\bar{x}$ = 9.1) measurements of the same individual taken within the same 5-month-period. Only pictures showing the arms perpendicular to the field of view of the camera were used. The results presented here are preliminary because only a handful of individuals were available and the standard deviations of the measurements were also still high (see figure 4.4 a). The data from Suaq was compared to data on the Tuanan immatures taken by Abigail Philips in 2009 -2010 on the same focal individuals as observed in the current study and based on the same measurement technique [316].

Dietary complexity

We assessed the dietary complexity of the four adult females on whom we had the most data available at each site (Tuanan: 4098 - 5161 hours, $\bar{x}$= 4644 hours, Suaq: 320 - 1168 hours, $\bar{x}$= 679). We determined the number of processing steps of all the food items that together make up 90% of their diets (in terms of feeding time). Processing steps and examples are described in detail in table 4.1.

Data analysis

All analyses and plots were done using the R programming language [121]. Data were analyzed using general linear mixed models, using lmer as implemented in the package lme4 [317], with individual as a random factor, to account for the fact that data were collected on the same individuals at multiple times, at different stages of their development. Also, in the analysis of the feeding rates, the food item was included as random factor since the same food items occurred multiple times in the data set (eaten by different immatures at different ages). Statistical significance of the fixed effects was assessed using cftest of the multcomp package [318]. Models and their factors were selected based on the Akaike information criterion (AIC). In the case of diet repertoires and feeding rates the best description of age effects was sigmoid, for which we used the pracma package [319].

In the graphs, nonlinear relationships in the data were drawn after the respective general linear model (glm of the stats package, with age as a sigmoid factor), excluding the random factor (individual and species).

Results

1. What to eat: Food selection competence

To assess the development of food selection competence, we examined the immatures' diet composition as a function of age. We found that with increasing age immatures eat an increasing number of food items, and reached a repertoire size that is between 80 and 99% of the size of their mothers' repertoires around the age of weaning. When looking at sex differences, we found a significant interaction effect between age and sex, implying that female immatures attain a broader diet sooner than their male peers, who by the age of weaning seem to reach only 80% of their mother's diet repertoire size (table 4.2, figure 4.1).

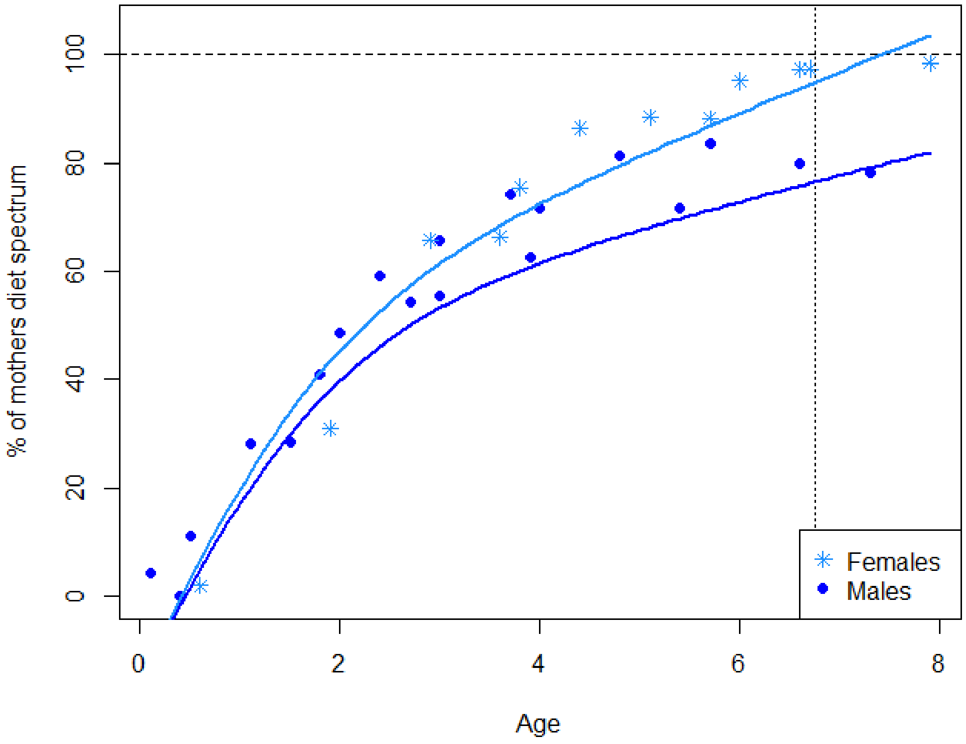

Figure 4.1. Development of diet repertoire at Tuanan: Diet repertoire size in percentage of the mother's diet repertoire size in relation to age (in years) for immatures that are still in permanent associations with their mothers. The dotted vertical line shows mean weaning age at the Tuanan population. The dashed horizontal line marks the mothers' diet repertoire sizes (100%).

Table 4.2. GLMM with diet repertoire size in percentage of the mother's diet as a dependent variable: Effects, estimates, standard errors and p-values as well as number of levels for the categorical variables. The number in parentheses represents the total number of age individual means.

Effect	**Type of effect**	**Estimate**	**Std-Error**	**P-value**	**N (31)**
Age	Fixed	6.84	1.17	**<0.001**	cont.
sigmoid(Age)	Fixed	119.38	9.32	**<0.001**	-
Sex (male= 0)	Fixed	5.26	6.35	0.408	2
Age x Sex (male= 0)	Fixed	-2.67	0.93	**0.004**	-
Follow hours	Fixed	0.001	0.002	0.46	cont.
Individual	Random	-	-	-	6

2. How to eat: Food processing competence

In terms of food processing competence, we tested the effects of age, food processing complexity, sex and site on feeding rates simultaneously, using GLMMs. We found that feeding rates increase with increasing age. For the more difficult to process food items, adult-level feeding speed is reached later than for the easier to process items (table 4.3a, figure 2). Also, immatures start feeding on more difficult to process food items later in their development than on easier items (figure 2), in line with the notion that feeding techniques are learned rather than intrinsic [62, 311]

At both sites, adult-level feeding rates for all processing classes is reached after weaning but well before age at first reproduction (figure 2). We found a trend that, in relation to absolute age, Suaq immatures reach adult-like feeding rates later than their Bornean peers (table 3a). If processing steps are excluded from the model, this difference becomes significant, which shows that especially if not corrected for food complexity, Suaq immatures develop adult-level feeding rates later than Tuanan immatures (table 2b). Excluding processing steps, however, significantly decreases the overall fit of the model, showing that processing complexity of the food explains a significant proportion of the variance in our data (table 3a+b, model comparison: $Chi^2 = 97.6$, $p < 0.001$).

After weaning, at both sites, but more so at Tuanan, feeding rates of independent immatures exceed those of their mothers, especially for easier to process items (figure 4.2). Interestingly, males seem to reach higher feeding rates faster than same-aged females at both sites (table 3a, figure 4.2).

To assess whether lower feeding speed could be caused by a lack of strength of the immatures, we controlled for the effect of overall hardness (Young's modulus) on feeding rates development (see Vogel et al.[320]). Including hardness as a factor led to an insignificant improvement in the overall fit of the model but the effect itself was not significant (table S4.4).

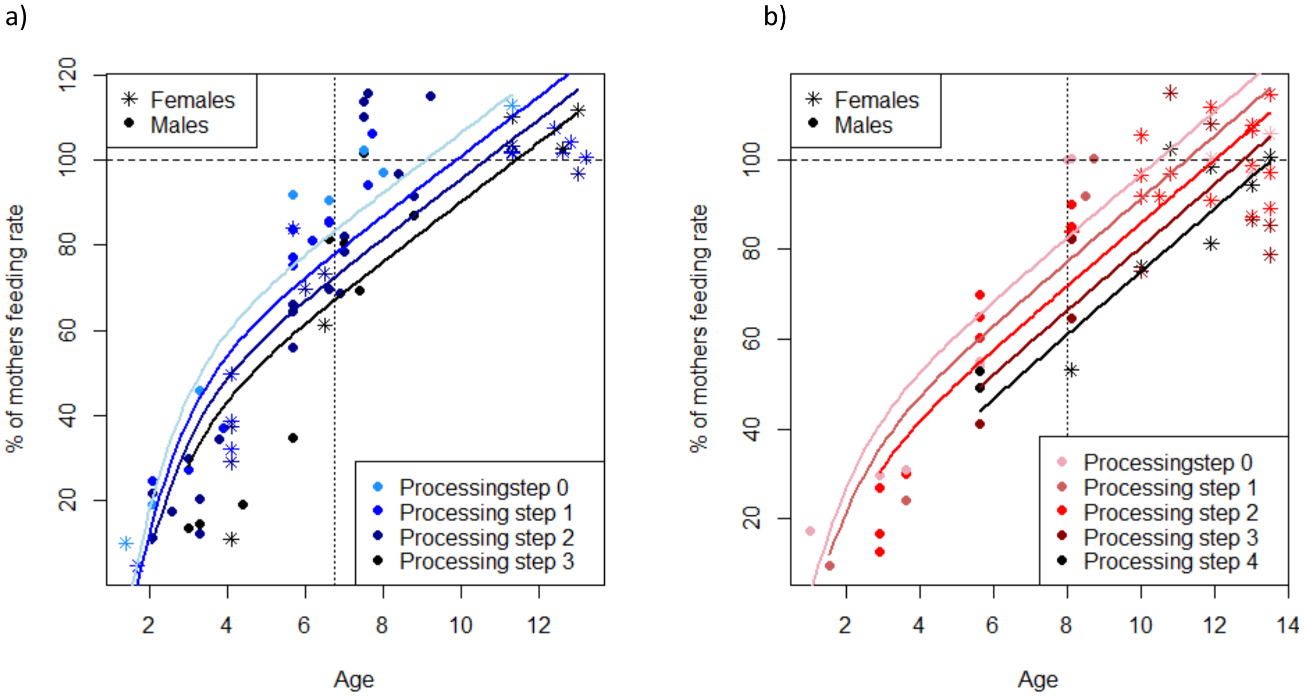

Figure 4.2. Development of feeding rates: Immatures' feeding rates, expressed as percentage of their mother's feeding rates, as a function of age and processing complexity of the food items, at Tuanan (a) and Suaq (b). The vertical dotted line shows mean weaning age at each population. The horizontal dashed line marks adult-level feeding rate (100%).

Table 4.3. GLMMs of feeding rate, expressed as percentage of the mothers' feeding rates, as a dependent variable, with (a) and without (b) including the number of processing steps as an independent variable. Shown are effects, estimates, standard errors and p-values as well as number of levels for the categorical variables and AIC values of the models. The number in parentheses represents the total number of individual - age - species combinations.

a)

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (128)**	**AIC**
Age	Fixed	7.96	0.94	**<0.001**	cont.	
sigmoid(Age)	Fixed	-36.34	56.24	0.52	-	
Processing steps	Fixed	-4.77	1	**<0.001**	5	
Sex (male= 0)	Fixed	-19.58	10.5	0.062	2	
Site (Tuanan= 0)	Fixed	-120.91	70.31	0.085	2	964
Age x Sex	Fixed	4.94	1.27	**<0.001**	-	
sigmoid(Age) x Site	Fixed	126.58	71.67	0.078	-	
Individual	Random	-	-	-	21	
Food Item	Random	-	-	-	34	

b)

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (128)**	**AIC**
Age	Fixed	7.88	0.9	**<0.001**	cont.	
sigmoid(Age)	Fixed	-69.13	55.47	0.212	-	
Sex (male)	Fixed	-21.27	10.09	**0.035**	2	
Site (Tuanan= 0)	Fixed	-130.81	69.44	0.06	2	981
Age x Sex	Fixed	5.56	1.24	**<0.001**	-	
sigmoid(Age) x Site	Fixed	139.4	70.88	**0.049**	-	
Individual	Random				21	
Food Item	Random				34	

3. When and where to eat: Food locating competence

Regarding competence in locating food sources and exploiting them efficiently, we found that ramble ratios of the travel routes of the independently ranging immatures did not differ from those of their mothers: Average daily ramble ratios of the adult females ranged from 1.6 – 3.9 at Tuanan and 2.1 – 3.8 at Suaq, with standard deviations across the different days of the same individual ranging from 0.3 – 1.5 at Tuanan and 0.5 to 2.2 at Suaq. Independent immatures showed average daily ramble ratios ranging from 1.7 - 3.2 at Tuanan and 2.1 – 4 at Suaq, with standard deviations ranging from 0.6 - 2.8 at Tuanan and 0.5 - 1.9 at Suaq. Thus, there is no evidence that independently ranging immatures show higher or more variable ramble ratios in their travel routes than adults (figure 4.3 and S4.2, table 4.4 a). However, there was a significant difference in ramble ratios between the two sites with Tuanan individuals showing lower values and thus more direct travel routes than individuals at Suaq (figure 4.3, table 4.4a). We found no age effect on the average daily ramble ratios among the independently ranging immatures (figure 4.3, table 4.4b): even the youngest and thus newly independently ranging immatures show ramble ratios in the range of the ones of adult females. We also found no difference between mothers and immatures when we tested in a paired design where we compared each independently ranging immature with its mother (figure 4.3).

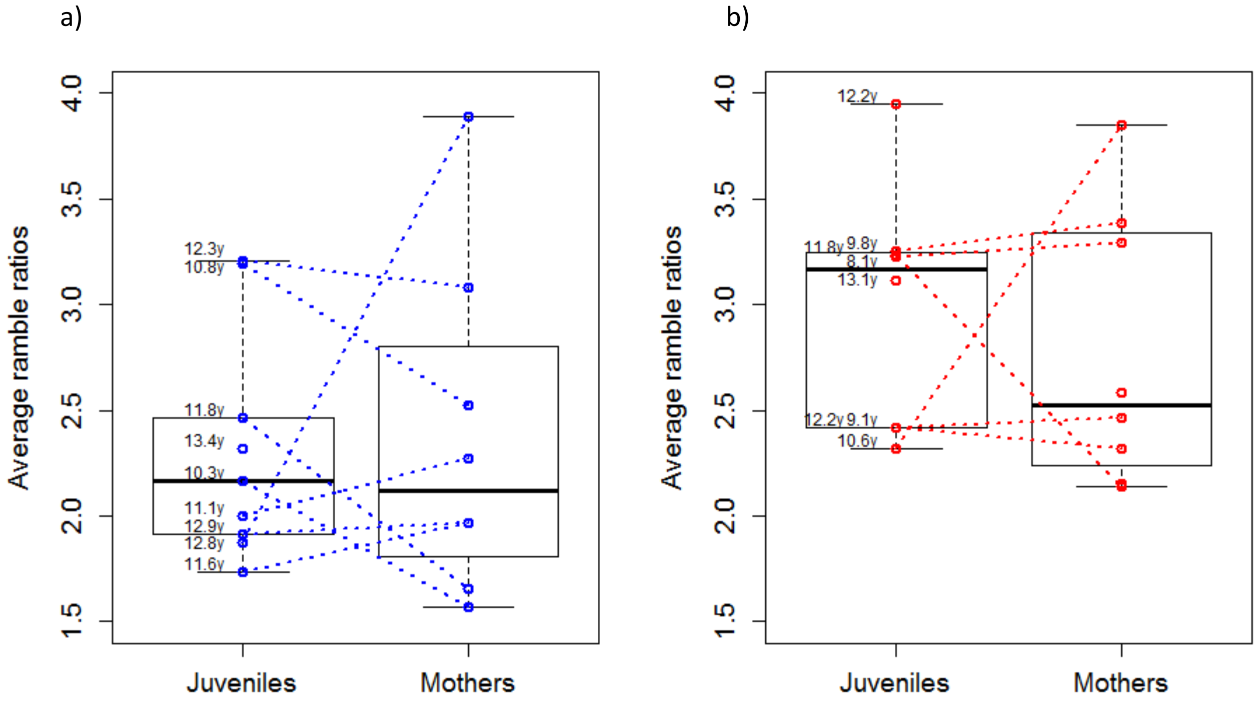

Figure 4.3. Development of ramble ratios: Average daily ramble ratios for independently ranging immatues (juveniles) and mothers at Tuanan (a) and Suaq (b). The numbers next to the juvenile data points indicate ages (in

years). The juvenile points are always paired with a data point of their mother collected in the same 5 month period (in 3 cases this data was not available).

Table 4.4. GLMM with average daily ramble ratio of the mothers and independent immatures as dependent variable, age class and site as fixed effect as well as individual as random effect. Shown are estimates, standard errors, p-values and number of levels for the categorical variables (a). GLMM with average daily ramble ratios of the independently ranging immatures animals as dependent variable, age and site as fixed effects as well as individual as random effect. Estimates, standard errors, p- values and number of levels for the categorical variables (b). The numbers in parentheses indicate the total number of age individual means.

Nr	Effect	Effect type	Estimate	Std-Error	P-value	N
a	Age class (mother= 0)	Fixed	-0.1	0.25	0.672	2
	Site (Tuanan= 0)	Fixed	-0.52	0.25	**0.035**	2
	Individual	Random	-	-	-	15 (32)
b	Age	Fixed	0.02	0.1	0.863	cont.
	Site (Tuanan= 0)	Fixed	-0.69	0.3	**0.021**	2
	Individual	Random	-	-	-	8 (17)

4. *Body growth*

Preliminary data on body growth suggest that immatures grow until around the age at female first reproduction (figure 4.4a + b), even though males are known to continue growing after this age. We discern a trend for Suaq immatures to show smaller body sizes in absolute values as well as relative to the adult female body size than their Tuanan peers after weaning (figure 4.4 c+ d). At the current state, this data is too preliminary to do any detailed statistics.

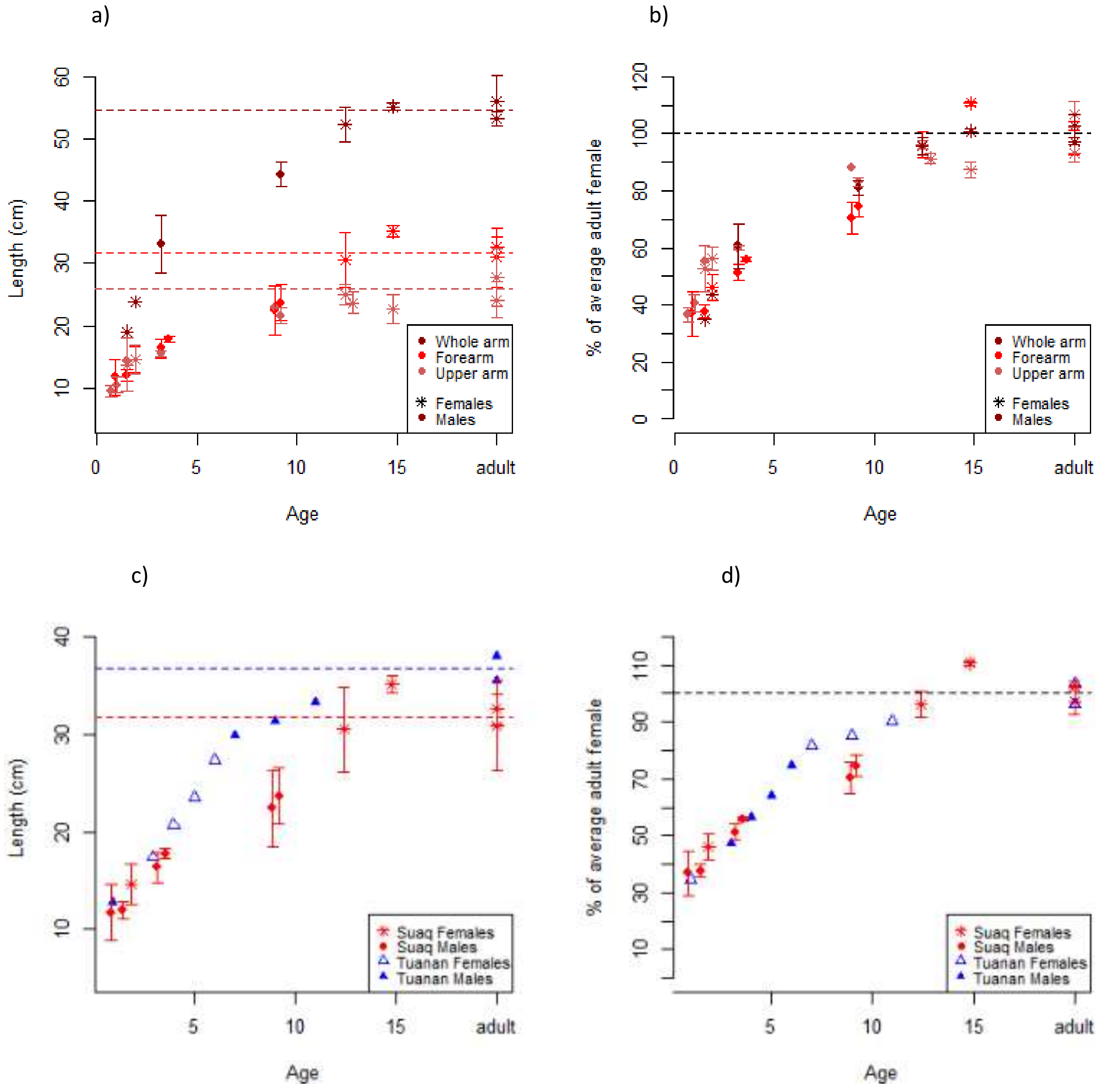

Figure 4.4. Body size development: Measures of whole arm, fore arm and upper arm versus age of the Suaq immatures in absolute values (a) and in percentage of the average adult females (b). Forearm length versus age of the immatures at Tuanan and Suaq in absolute values (c) and in percentage of the average adult females (d). The Tuanan data were retrieved from Chappell et al.[316].

5. Dietary complexity of the two sites

In terms of dietary complexity we found that the two study sites showed different distributions of the frequencies of the different processing steps (figure 4.5). Whereas at Tuanan individuals eat a higher share of items that can be ingested without any processing (steps= 0) than Suaq individuals, the opposite pattern was found for items with 4 processing steps. Moreover, processing requiring 5 steps (tool use) only occurs at Suaq. Frequencies of processing steps 1-3 were very similar for the two sites. Overall, therefore, the relative frequency of a given processing step at Tuanan (its value divided by the corresponding value at Suaq) decreased with increasing processing complexity (Spearman: r=-0.83, p= 0.058, n= 6). The diet at Suaq is therefore more complex than the diet at Tuanan.

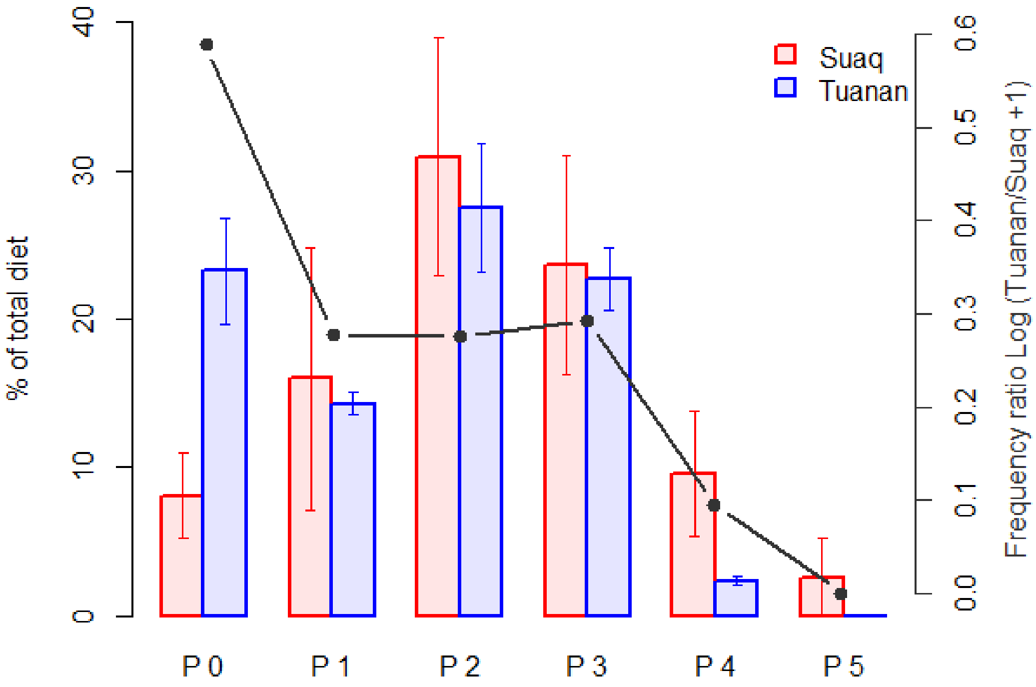

Figure 4.5. Dietary complexity: Distribution of the different processing steps in percent of the total diet (for the food items that form the top 90% of the total diet) of 4 adult females at Tuanan and Suaq each. The black line indicates the site frequency ratio of each given processing step (log (frequency at Tuanan/ frequency at Suaq +1)).

Discussion

Needing to learn or needing to grow?

To investigate whether the late age at first reproduction and the late age of weaning in orangutans is best explained by the time needed to acquire skills or rather by tradeoffs in energy allocations to brain and body, we examined foraging skill development and body growth trajectories of immatures of two populations of wild orangutans. Our results show that in orangutans, the acquisition of foraging skills does not impose a limit on age at first reproduction, as proposed by the classic version of the needing to learn hypothesis: the development of diet repertoire, feeding rates and ramble ratios show that competence in knowing what, how and where to eat is reached long before the age at female first reproduction. However, as predicted by classic life history theory, we found that the need to reach adult body size might determine the length of the developmental period in orangutans: body size measurements showed that immatures continue to grow until female age at first reproduction.

Although reaching adult-level feeding skills doesn’t directly limit the onset of reproduction, we found evidence that foraging skills might play a crucial role for the timing of weaning. In contrast to all other gregarious primates, by the age of weaning, immature orangutans have to be fully self-sufficient: in most populations weaned immatures increasingly range alone and thus can’t rely on social information and are fully dependent on their own knowledge and skills [90, 93]. Weaned immatures must have reached sufficient skill levels to support their small but growing body (see below). The development of the diet repertoire showed that food selection competence is reached around the age of weaning, but that adult-level processing of these foods is achieved later, especially for food items requiring more processing steps. Ramble ratios did not differ between adults and independently ranging immatures. Although these may also be influenced by factors other than food locating competence, such as avoiding or associating with other individuals, the absence of any systematic difference between age classes suggests that independently ranging immatures from the beginning of independence have no difficulty to locate food sources in the forest. This is consistent with the results of an earlier study showing that by the age of weaning, immatures at Tuanan seem to recognize around 50% of their food patches independently[102]. It thus seems that the critical skills for dietary independence in orangutans are competence in food selection and food processing, rather than in food locating.

The diets of adult female orangutans at Tuanan comprise of more than 160 food items of more than 110 different plant species (figure S4.1). These numbers are very comparable to findings of long-term studies on wild chimpanzees (e.g. [321, 322]). However, for the adult females at Tuanan, even after 4000 observation hours, collected over multiple years, new items are still being added (figure S4.1), suggesting there is no such thing as a true diet. This finding also reflects the fluctuating food availability in most orangutan habitats and the lack of consistent seasonal patterns in fruiting [96]. Thus, it is plausible that it takes an immature orangutan multiple years to witness all the items in their mothers' diets and probably even more time to memorize them. In general, juvenile animals are very vulnerable to food shortages[39] (see below). A broad diet is crucial to buffer food scarcities in a habitat with fluctuating food availability. It is unlikely that the incomplete diet repertoires of the immatures are purely an artifact of insufficient processing competence: even though we found that immatures start to feed on more difficult to process items later than on the easy ones, even items of the highest processing classes (including the ones that require tool use) are being eaten by the age of 6 years, albeit at a much lower rate (see also Meulman[194]). Because hardness of the food item does not affect feeding rate (see table S4.5) and the diets of adults and immatures do not differ in their physical properties [312], it is unlikely that strength differences can explain age patterns in feeding rates. However, feeding rates on the more difficult items, but not on the easy ones, increase after weaning, which suggests that learning continues during juvenility. It thus appears that the age of dietary independence is determined by the time it takes to acquire broad enough repertoires and to reach high enough feeding rates to ensure sufficient energy intake during the next phase of immature development.

The developmental trajectories of the feeding rates showed that from a certain age on, independent immatures feed faster than adult females on easier to process food items. In a study on long tailed macaques (*Macaca fascicularis*) it was found that larger body size allows for faster processing of large food items [323]. If gape size in relation to food item size determines feeding speed, a smaller body size may entail advantages for processing smaller items. By weaning, immatures are significantly smaller than adult females. The smaller body size may explain their higher picking rates for small items for which they reached proficiency earlier. Indeed, all of the items in which immatures exceeded the feeding rates of adult females were flowers and small to medium sized fruits.

Growth trajectories obtained by laser photogrammetry showed that by the age of weaning, immature orangutans have only reached around 75% of adult female body size in terms of arm length, which probably corresponds to around 50% of adult volume and weight. Interestingly, this % of adult size at weaning seems highly comparable for immatures at Suaq and Tuanan (figure S4.3). Apart from substantial body growth, there is also considerable brain development during the juvenile period: even though the great ape brain is fully grown by the age of weaning [48, 324], it undergoes a period of synaptic remodeling (overproduction of axons and synapses followed by rapid pruning) and restructuring during juvenility and adolescence [325-328]. Thus, the energetic needs during juvenility imposed by body growth and brain fine-tuning are high [14]. However, constant energy flow to the developing brain is vital since it cannot adjust to temporary energy shortages [45, 49]. Brain starvation is devastating as it causes permanent cognitive impairments and thus reduced adult performance later in life [329, 330]. The optimal body size at the age of weaning and the conservative growth likely act to minimize the risk of starvation but do so at the expense of a longer juvenile period and delayed reproduction [39].

As they reach foraging skills around the age of weaning, orangutans follow the classic primate pattern of skill acquisition in relation to life history [172]. Interestingly however, orangutans seem to attain their foraging skills several years later than chimpanzees and gorillas [164, 166, 331]. Diet repertoire sizes of wild chimpanzees are highly comparable to the ones of wild orangutans [321, 322] and obvious systematic differences in the skill intensity of their diets are also unlikely. It is possible that the age difference in reaching foraging competence is just a side effect of the overall faster development of chimpanzees and gorillas. However, an equally plausible suggestion is that because orangutans cannot rely on social inputs after weaning they have to reach higher levels of competence before they can be weaned.

Sex differences

We found unexpected sex differences in the development of diet repertoires and feeding rates. Whereas female immatures develop broader diets faster than males, male immatures seem to reach higher feeding rates earlier than females. In adult orangutans males in general spend less time feeding than females [290, 312]. Sex differences in various aspects of adult foraging have been found in several other primate species (e.g. [323, 332, 333]). Those differences have been ascribed to either the costs of female reproduction or differing energetic needs associated with sexual size dimorphism [333-336]. Immature orangutan males will, after going through a stage when they are unflanged and at least initially well within the range of female sizes, eventually grow into flanged males, which are much bigger than adult females [337]. In orangutans, where reproducing females increase their food intake relative to basic need by only about 25% [338], older unflanged and especially flanged males most likely require far more food than adult females [312].

Consequently, for males, greater absolute amount, and thus fast intake, of food is crucial to support the growth spurt during secondary development and subsequently for the maintenance of their larger body size. In contrast, as in all mammals, orangutan females have to be able to sustain pregnancy and lactation. During pregnancy, females are probably more dependent on high food quality, in terms of nutrient composition and poison levels. Also, reproducing orangutan females are likely to be more dependent on stable energy intakes than males because their nutritional state directly affects their developing offspring, for which energy shortages are damaging (see below). Thus, female diets are likely to be broader and thus more balanced and less susceptible to fluctuations of food availability, whereas high efficiency in feeding might characterize male diets.

It has been proposed that, depending on the underlying mechanisms, sex differences in foraging are closely correlated with female reproductive status [334]or emerge parallel to the developmental onset sexual size dimorphism [333, 335, 336]. Our findings of sex differences in diet composition and feeding rates among juvenile orangutans are not in line with these predictions. Furthermore, just as in orangutans, immature ring-tailed lemurs *(Lemur catta* [333]), long-tailed macaques [339] and tufted capuchin monkeys (*Cebus nigritus* [332]) show sex differences in several aspects of feeding that match those of adults. Also, immature female chimpanzees acquire proficiency in termite fishing tool use earlier, spend more time watching others termite-fish than their male peers [336]. The most parsimonious alternative hypothesis for many species, namely that sex differences are caused by resource partitioning [333, 340], is unlikely to apply in the chimpanzee example and can be ruled out in the largely solitary Bornean orangutan (see also [312]). In conclusion, in species where repertoires and techniques are learned rather than intrinsic, differences caused by the balance between reproductive load and sexual dimorphism in adult size might already emerge during the juvenile period, suggesting that female and male immatures prepare for sex specific adult niches at this stage of development. In general, to find out what sex differences in immature orangutan diet repertoires and feeding speed mean one would have to look in more detail at sex differences in adults.

Between-site differences

We found that immatures at Tuanan grow faster than at Suaq, in line with their earlier weaning and with a lower overall complexity of the diet. Since the hardness of the food item did not affect feeding rate (see table S5) and immature and adult diets are similar in hardness [312], it is unlikely that differences in feeding rates are due to the smaller body size and thus reduced strength of the immatures. Interestingly, when we controlled for the complexity of the food items by including it as a factor in the model, the difference in age of skill competence (i.e. how fast feeding rates increase as a function of age) between Suaq and Tuanan became non-significant (figure 4.2, table 4.3 a+b). Thus, it seems as if skills of equal complexity develop at a very similar pace at both populations, but that due to the higher complexity of their diet, Suaq immatures have more to learn, so weaning gets delayed. Immatures at both populations seem to be weaned at the same level of feeding skills relative to the overall skill level of the population: by the age of weaning adult feeding rate is reached for the easier items whereas for the more complex items adult-like feeding rate is reached after around two thirds of the juvenile period. The fact that even after controlling for their higher complexity level, there remains a trend that Suaq individuals reach adult-like feeding rates later than Tuanan individuals (i.e. a trend for a positive interaction between site and age on skill competence; see table 3 a) could be the result of investments in acquiring more complex skills which take away time and energy to learn the more basic skills and slow down the learning process of those.

This pattern suggests there has been correlated evolution between a population's dietary complexity, somatic growth and weaning age. This correlation could equally reflect the need to reach greater dietary complexity, which then selected for later weaning, or later weaning being caused by slower life-history pace, which then provided the extended learning period that made the evolution of a greater dietary complexity possible. The fact that the overall level of a population's dietary complexity affects the pace of immature development implies that it is important for individuals within a given population to acquire the full range of skills. However, top-end complexity skills seem to only develop and be maintained in a population under certain preconditions, such as a prolonged mother offspring association or in general increased opportunities for social learning. Perhaps after weaning, juveniles are too busy surviving to focus on learning totally new skills. More generally, this might also apply to the overall complexity level of the diets of different orangutan populations. Our findings are therefore consistent with the finding that there is a correlation between the complexity of the diet niche and (i) the pace of development, as found in primates, and (ii) the relative length of food provisioning, as found in carnivores [341]. More specifically, applied across mammal species, our results suggest a correlation between weaning age in relation to the age at first reproduction and the complexity of the diet as well as body size at the age of weaning.

Conclusion

We could show that in orangutans both the need to learn foraging skills and energetic constraints have severe impacts on life history. Whereas the age at first reproduction seems to be determined by competing energetic investments in brain and body, the age at weaning seems to be connected to how fast foraging skills are acquired. In populations with a higher dietary complexity, immatures have more to learn and thus reach adult skill levels later. At the same time, they seem to grow slower and get weaned later than immatures at populations with a lower dietary complexity, where the minimum skill set to survive seems to be reached earlier. Sex differences in the development of foraging skills suggest that immature female and male orangutans prepare for sex specific adult niches. Thus, the overall adult niche (in terms of the population's overall complexity level of foraging techniques as well as in terms of sex specific foraging complexity) has a significant impact on immature skill development. Applied across different primate species, this implies that weaning should be reached later when there is more to learn.

Acknowledgements

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Table 4.1. Processing steps of food items: the most frequent combinations of the different processing steps, as well as descriptions of the corresponding food items with local and scientific names of example species (T= Tuanan, S= Suaq).

Nr	Processing steps	Food item types	Examples
0	Pick	Fruits and flowers where everything is eaten	Lunuk (*Ficus sp*.; T), Tapuhut Putih (*Syzigium sp.*; T), Nyatoh Puntik (*Palaquium pseudorostrum*; T), Resak Ubar (*Brackenridgea palustris Bartell*; S), Tapis Batu (*Garcinia sp.*; S)
1	a) Pick, bite off	a) Fruits and flowers where a small outer part is bitten off after picking, discarded, and the remaining parts are eaten	a) Medang Baru (*Litsea gracilipes Hook f.*; S), Nyatoh undus buah merah (*Palaquium ridleyi*; T), Katiau (*Madhuca motleyana*; T), Mangkinang Blawau (*Elaeocarpus sp.*; T)
	b) Pick, drop	b) Fruits and flowers where only the sap is ingested and all other parts are discarded after chewing	b) Rewui (*Microcos sp.*; T), Piais (*Nephelium mangayi*; T), Tampang (*Artocarpus dadak*; T)
2	a) Pick, peel, spit out	a) Fruits where the pulp is eaten while the skin and the seed are discarded	a) Puwin (*Sandoricum beccarianum Baill.*; S), Papung (*Sandoricum borneense*; T)
	b) Pick, bite in half, scrape flesh out	b) Hard-shell fruits where pulp and seeds are eaten but the empty pod is discarded	b)Malaka (*Tetramerista glabra*; S), Lewang (*Pouteria cf malaccensis*; T)

	c) Pick, turn repeatedly in mouth, drop seed and skin layers	c) Fruits with edible flesh tightly attached to an inedible seed and thin skin	c) Enyak Beruk (*Syzygium sp*.; T), Nyatoh undus buah besar (*Palaquium cochlearifolium*; T), Tantimun unripe (*Tetrameristra glabra*; T)
	d) Pick, pop pod open, extract seed	d) Fruit pods with an edible seed enclosed	d) Ubar (*Horsfieldia crassifolia*; S), Akar Kamunda (*Leucomphalos callicarpus*; T)
3	a) Pick, bite in half, scrape flesh out, spit out	a) Hard shell fruits where the pulp and seeds are eaten but the empty pod and seeds are discarded	a) Malaka unripe (*Tetramerista glabra*; S), Karandau Putih (*Blumeodendron kurzii*; T), Tutup Kabali (Diospyros pseudo-malabarica; T)
	b) Pick, peel, bite away flesh, remove skin around seed	b) Fruits where the skin around the seed is eaten after removing the inedible skin and flesh	b) Manga Hutan (*Mangifera gracilipes Hook f.*; S)
	c) Pick, pop pod open, extract seed, pop seed open	c) Fruit pods with a seed enclosed; only the internal part of the seed is eaten while the rest is discarded	c) Sepang (*Sterculia sp*.; S)
	d) Collect substrate, scratch or bite open, suck	d) Insects embedded in wood or other substrate	d) Ants (Formicidae; T+S), Termites (*Isoptera*; T+S)
	e) Bite piece of bark loose, rip or strip it off, scrape inner bark off	e) Inner bark (i.e. i.e., cambium/phloem)	e) Maruang (*Myristica lowiana*; T), Pantung (*Dyera lowii*; T), Resak Payo (*Dialium patens Backer.*; S)
4	a) Pick, bite tip off, pull string off of pod to open it, turn pod open, extract seed	a) Bean-like fruits with inedible skin but edible seeds	a) Basong (*Alstonia spatulata BI*.; S)

	b) Pick, pop pod open, extract seed, pop seed open, extract and spit out skin around seed	b) Fruit pods with a seed enclosed; only the internal part of the seed is eaten while the inedible seed skin is discarded	b) Sepang unripe (*Sterculia sp*.; S)
	c) Break dead twig off, examine, bite appart, suck	c) Ants hidden in hollow twigs	c) Ants (Formicidae; S)
5	a+b) Break stick off, peel (optional), chew (optional), insert into tree hole/ nest extract insects or insect product, collect from tool tip	Tool use: a) tree hole b) insect nests	a) Sweat bees (Stingless bees: *Halictidae sp.*; S) b) Ants (Formicidae; S), Termites (*Isoptera*; S), Bees (*Apidae sp.*; S)
	c) Break fruit off, break stick off, peel (optional), chew (optional), insert into tree fruit, extract seed, collect from tool tip, spit out seed skin	c) fruits	c) Cemenang (*Neesia aquatica*; S)

Supplementary Material

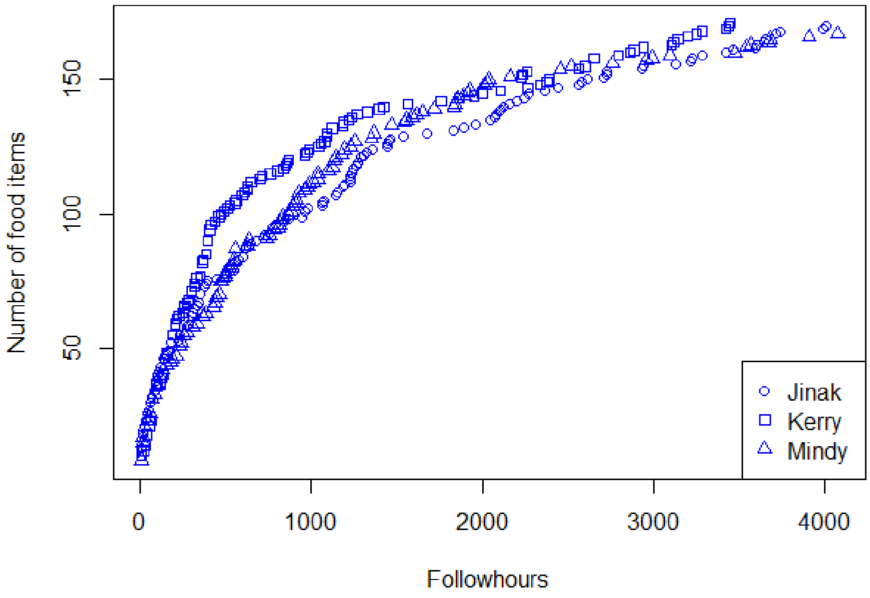

Figure S4.1. Diet repertoire size in relation to follow effort: The number of recorded food items versus the number of hours of follow data collected for the three adult females with the most data available at Tuanan. 500 follow hours correspond to roughly 1 year ($\bar{X}$ = 13.1 months), the overall observation time was 9.5 years. The total number of plant species recorded for each of these females was 109 – 113 ($\bar{X}$ =110.3). For insects we only counted termites, ants, bees (honey) and caterpillars as food items and did not distinguish between the different species. Thus, the number of non-plant food items was 4 for each adult female.

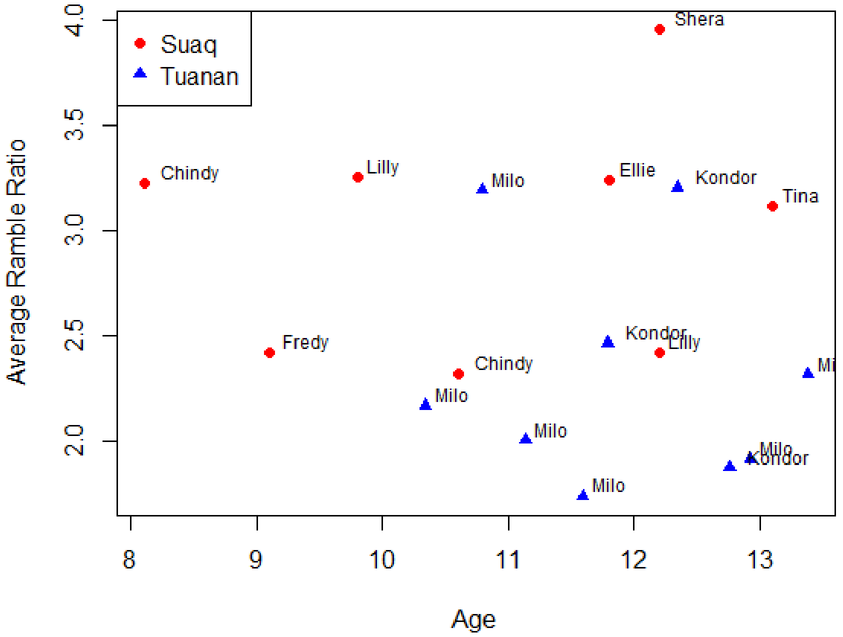

Figure S4.2. Development of ramble ratios over age: Average daily ramble ratios versus age for immatures at Suaq and Tuanan.

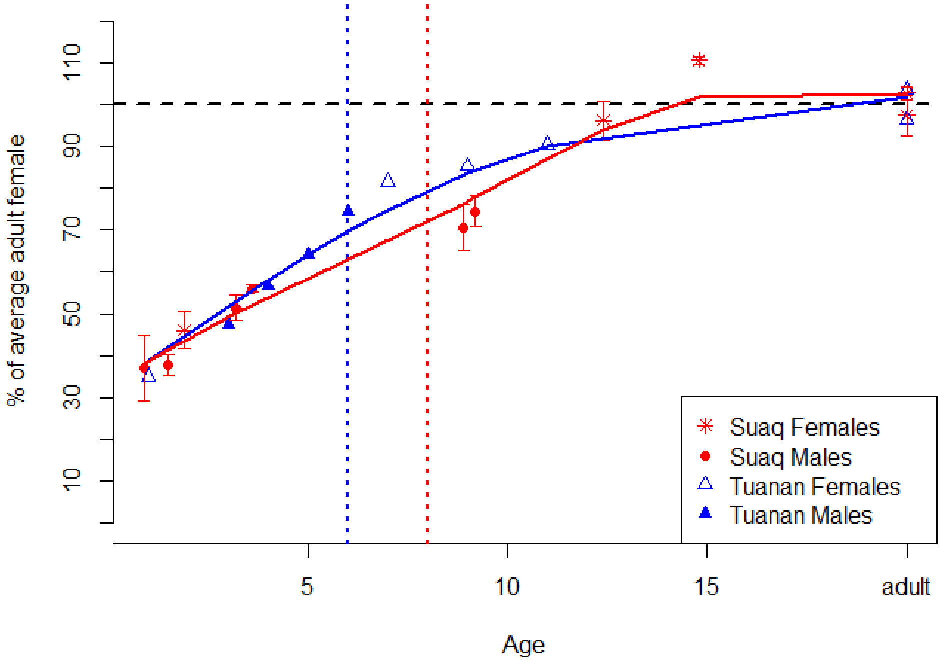

Figure S4.3. Body size comparisons: Growth trajectories bases on forearm measurements for immatures at Suaq and Tuanan. The solid lines were attained via smoothing functions in R (smooth.spline in the stats package). The horizontal lines show average weaning ages at both populations. The Tuanan data were retrieved from Chappell et al.[316].

Table S4.2: GLMM with absolute feeding rate of the adult females as dependent variable. To see if the if there is a difference between feeding rates obtained by video coding as opposed to direct observation this was included as as a binary variable ("Video"). Shown are effects, estimates, standard errors and p-values as well as number of levels for the categorical variables. The number in parentheses represents the total number of individual feeding rates included in the analyses: Only rates of fruits on which we had data from the same individual obtained via video coding as well as via direct observation were included.

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (27)**
Video	Fixed	-3.05	2.19	0.163	2
Species	Random	-	-	-	5
Individual	Random	-	-	-	4

Table S4.3. GLMM with feeding rate in percentage of the mothers feeding rates as a dependent variable. To see if the presence absence of a simultaneous feeding rate taken on the mother has an effect it was included as a binary variable ("Simultaneous mother sample"). Effects, estimates, standard errors and p-values as well as number of number of levels for the categorical variables and AIC values of the models. The number in parentheses represents the total number of individual - age - species combinations.

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (128)**	**AIC**
Age	Fixed	7.99	0.94	**<0.001**	cont.	962
sigmoid(Age)	Fixed	-37.16	56.22	0.51	-	
Processing step	Fixed	-4.71	1.02	**<0.001**	5	
Sex (male= 0)	Fixed	-20.08	10.53	0.057	2	
Site (Tuanan= 0)	Fixed	-123.43	70.44	0.08	2	
Age x Sex	Fixed	4.94	1.27	**<0.001**	-	
sigmoid(Age) x Site	Fixed	129.65	72.04	0.071	-	
Simultaneous mother sample	Fixed	1.11	2.78	0.399	2	
Individual	Random	-	-	-	21	
Food Item	Random	-	-	-	34	

Table S4.4. GLMM with feeding rate of the Tuanan immatures in percentage of the mothers feeding rates as a dependent variable without (a) and with hardness included as a fixed effect (b). Effects, estimates, standard errors and p-values as well as number of levels for the categorical variables and AIC values of the model.

Nr	Effect	Effect type	Estimate	Std-Error	P-value	N	AIC
a)	Age	Fixed	8.07	0.83	**< 0.001**	cont.	535
	sigmoid(Age)	Fixed	92.32	56.49	0.1	-	
	Processing step	Fixed	-6.95	1.58	**< 0.001**	4	
	Sex (male= 0)	Fixed	-18.62	8.49	0.028	2	
	Age x Sex	Fixed	5.56	1.21	**< 0.001**	-	
	Individual	Random	-	-	-	11	
	Food Item	Random	-	-	-	21	
b)	Age	Fixed	7.99	0.79	**< 0.001**	cont.	476
	sigmoid(Age)	Fixed	106.85	58.26	0.067	-	
	Processing step	Fixed	-8.62	1.99	**< 0.001**	4	
	Sex (male= 0)	Fixed	-20.19	8.22	**0.014**	2	
	Age x Sex	Fixed	5.79	1.17	**<0.001**	-	
	Hardness	Fixed	0.63	0.63	0.318	cont.	
	Individual	Random	-	-	-	11	
	Food Item	Random	-	-	-	21	

Table S4.1. Overview of the data used for the different analyses. Study site, focal individual, sex and date of birth of the focal individual, mother of the focal individual, as well as the years in which the different types of data (diet data, feeding rates, ramble ratios and laser measurements) were taken. *= Suaq individuals that were born outside the current but during a former study period (1994- 1999). Those individuals were identified via DNA analyses of them or their mothers from samples taken during both study periods. **= Individuals of which the birth year had to be estimated because they were born outside the study period (before research activities started or during the multi-year break of the research activities at Suaq). P= Data collected by Abigale Philips (published in [316]).

Site	Individual	Sex	Date of birth	Mother	Diet composition	Feeding rates	Ramble ratios	Laser measurements
Suaq	Tina	Female	Early 1998*	Raffi	na	2011	2011	na
Suaq	Shera	Female	Mid 1998**	Chick	na	2010/2011	2010/2011	na
Suaq	Ellie	Female	Early 1999*	Friska	na	2010/11	2010/11	2014
Suaq	Lilly	Female	Early 2001**	Lisa	na	2011	2010/11; 2013	2013, 2014
Suaq	Chindy	Female	2003**	Cissy	na	2010/11; 2013	2010/11; 2013	na
Suaq	Fredy	Male	Early 2005**	Friska	na	2010/11; 2013	2014	2014
Suaq	Sazu	Male	Mid 2005**	Sarabi	na	2014	na	2014
Suaq	Ronaldo	Male	Early 2006**	Raffi	na	2014	na	na
Suaq	Lois	Male	August 2010	Lisa	na	2011; 2013; 2014	na	2013, 2014
Suaq	Frankie	Male	August 2012	Friska	na	2013	na	2014
Suaq	Cinnamon	Female	May 2012	Cissy	na	Na	na	2013, 2014
Suaq	Simba	Male	March 2013	Sarabi	na	Na	na	2014
Suaq	Rendang	Male	March 2014	Raffi	na	Na	na	2014
Tuanan	Kondor	Female	Early 1999**	Kerry	2003- 2007	2012	2010; 2011	2010^{P}

Tuanan	Streisel	Female	Mid 2001**	Sidony	na	Na	na	2009^{P}
Tuanan	Milo	Female	Mid 2001**	Mindy	2003- 2008	2012; 2013; 2014	2011; 2012; 2013; 2014	2010^{P}
Tuanan	Jerry	Male	June 2003	Jinak	2003-2011	2012; 2014; 2015	na	2009^{P}
Tuanan	Deri	Male	July 2004	Desy	na	2012	na	2009^{P}
Tuanan	Jip	Male	February 2006	Juni	2006- 2013	2012; 2013; 2014; 2015	na	2010^{P}
Tuanan	Kino	Male	January 2007	Kerry	2007- 2013	2012; 2013; 2014	na	2010^{P}
Tuanan	Petzy	Male	January 2008	Pinky	na	2012	na	na
Tuanan	Mawas	Female	July 2008	Mindy	2008- 2013	2012; 2014; 2015	na	2009^{P}
Tuanan	Danum	Male	July 2010	Desy	na	2012; 2013; 2014	na	na
Tuanan	Joya	Male	July 2011	Jinak	na	2014; 2015	na	na
Tuanan	Kahiyu	Female	Februrary 2012	Kondor	na	2013	na	na
Tuanan	Jane	Female	July 2013	Juni	na	2014	na	na

4. Development of foraging skills in two orangutan populations: needing to learn or needing to grow?

Chapter 5: Observational social learning and socially induced practice of routine skills in wild immature orangutans

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Abstract

Experiments have shown that captive great apes are capable of observational learning, and patterns of cultural variation among populations suggest that they use this capacity in the wild. So far, the contexts and extent of observational forms of social learning in the wild remain unclear. Social learning is expected to be most pronounced during immature skill acquisition. We therefore examined peering (attentive close range watching) by immatures in two populations of wild orangutans (*Pongo spp*.). A total of 1537 peering events collected during 2571 observation hours were analyzed. We found, first, that peering was most frequent in contexts where learning is expected, namely feeding and nest building. Second, peering in the feeding context was significantly positively correlated with complexity of food processing and negatively with an item's frequency in the mother's diet. Food peering was also followed by significantly increased rates of exploratory behaviors targeting the same food items, indicating it leads to selective practice. Food peering also decreased with age and increasing feeding competence of the immatures. Third, the age of peak peering in the nesting context coincided with the onset of nest-practice behavior, and peering events were followed by significantly increased rates of nest-practice behavior. Fourth, the proportion of peering directed at other individuals rather than the mother increased with age. These findings are consistent with the prediction that immature orangutans learn by observing others in a variety of contexts and that peering is followed by selective practice of the observed behavior. We conclude that observational social learning in combination with socially induced practice over a period of several years is a critical component of the acquisition of learned subsistence skills in orangutans.

Introduction

Social learning is learning that is influenced by observing, associating with, or interacting with individuals or their products [52]. It is the necessary precondition for the emergence and maintenance of traditions and cultures [103, 342]. Also, since the ability to learn socially from others makes learning more efficient, it might be the driving force behind the evolution of intelligence [32, 176]. The simplest forms of social learning are non-observational. This includes social facilitation and local enhancement, where learning is based on the mere presence of conspecifics or their interaction with a specific object at a specific site and thus not dependent on observing the actions of conspecifics. Evidence for non-observational forms of social learning has been found in several fish, reptile, bird, and mammal species, which suggests deep evolutionary roots (reviewed by [310, 343, 344]). However, the effective transmission of knowledge, such as complex food processing techniques (e.g. tool use), may require more efficient and accurate forms of social learning, such as observational social learning, (learning by observing the actions of another individual, including some forms of stimulus enhancement as well as imitation, emulation or observational conditioning [345-347] . Several authors have also pointed out that for many detailed actions competence can only be acquired by individual practice[63, 348], suggesting that observational learning will often need to be accompanied by selective practice.

Communities and populations of chimpanzees (*Pan troglodytes*) and local populations of orangutans (*Pongo spp.*) show behavioral variation that cannot be explained by environmental or genetic differences [79, 104, 342]. Less extensive variation in individual behavioral elements has also been found among wild populations in a variety of primate, bird and cetacean species (reviewed by [349-351]). All these studies concluded that social transmission best explains the observed patterns. Diffusion patterns documented for experimentally introduced knowledge or, in a few cases, newly acquired behavioral variants in the wild are highly suggestive of the operation of social learning in the wild (e.g. [352, 353]reviewed by [354, 355]). Likewise, studies relating behavioral similarity within groups to association patterns are also consistent with social transmission [356, 357].

Most of those field studies could not identify the actual mechanism of social learning at work since they only looked at the results of social learning and not at the process itself. Moreover, they mainly focused on innovative behaviors (e.g. complex feeding techniques or social interactions), which show geographic variation between populations or groups and thus could be most reliably identified as being socially learned. Non-innovative behaviors tend to be more common and do not necessarily result in population differences [346, 358]. However, it is unlikely that the mechanisms of social learning only evolved for the rare case of transmitting novel behavior. The more likely scenario is that social learning evolved in the context of routine skill acquisition (such as basic feeding skills) by immatures. This important idea has so far not been systematically investigated.

Experiments on captive primates have elucidated which social learning mechanisms a species is capable of (reviewed by [351, 355]). Using the two-action paradigm approach [359, 360] numerous studies on a variety of species successfully distinguished between non- observational and observational forms of social learning. This approach demonstrated observational learning under experimental conditions in chimpanzees [361, 362], gorillas (*Gorilla gorilla gorilla* [363]), and orangutans [364-366]. Evidence for observational learning was further found in a few monkey and several bird species (reviewed by [351, 355, 367]).

Important as they are, these studies cannot tell us whether and in what contexts species rely on observational learning as a means of skill acquisition under natural conditions [344]. Most experiments are of extremely short duration relative to the long developmental period of most primates and the time needed in the wild to acquire subsistence skills (e.g. [185]). On the other hand, in captivity, many species show behaviors that are significantly more complex than they do in the wild [105, 368, 369]. Also, species that show social learning in captivity may fail to do so in the wild [370, 371].

Unfortunately, field experiments are difficult to conduct and ethically sensitive. This is why to date few field experiments on social learning in primates have been conducted. Mostly based on the two-action paradigm, field experiments produced evidence for forms of social learning in several taxa (reviewed by [344, 350, 355]). However, field experiments lack ecological validity: even if one can experimentally trigger a behavior in wild animals, this does not automatically imply that animals rely on this behavior in everyday life or it is part of their natural behavior.

Therefore, it remains unclear exactly for what and when individuals engage in social learning in the wild and observational studies on wild populations are needed to resolve this issue. Many species show social influences on foraging behavior in the wild [310, 372]. More specifically, several studies on wild primates and other mammals report a strong connection between the feeding behavior of immatures and their mothers, including mountain gorillas (*Gorilla gorilla beringei* [164]), Japanese macaques (*Macaca fuscata* [373]), howler monkeys (*Alouatta palliate* [374]), red-fronted lemurs (*Eulemur fulvus* [307]), and dolphins (*Tursiops sp.* [375]). Matsuzawa et al. [376] showed that chimpanzees rely on close observation of the mother and others when learning tool-supported nut-cracking, a phenomenon they called “master-apprenticeship”. This interpretation was confirmed by Lonsdorf et al. [185, 377] and Humle et al. [378]).

Similarly, wild chimpanzees and tufted capuchin monkeys (*Sapajus spp.*) selectively seek out skilled individuals to observe during tool-assisted foraging [379-381]. Work on capuchin monkeys (*Cebus capucinus [357]*) and orangutans (*Pongo pygmaeus wurmbii [62])* found similar patterns for other complex foraging techniques.

These studies have shown that in various primates the acquisition of complex skills is socially influenced. However, often, highly complex skills such as tool use seem to be superfluous for an individual's survival, since not all populations of a species show them. Few studies examined whether primates also rely on social learning for the acquisition of the more basic routine skills. Social learning is contrasted with individual learning, which is often treated as the default option for any learning since animals are expected to rely on social information when they are unable to solve a problem independently [382]. However, individual learning is time-intensive and carries the risk of injury or poisoning. In contrast, social learning is more efficient and less risky. Social learning may therefore be more common than previously assumed, and might also be used for the acquisition of routine skills.

The aim of the present study was to examine the role of peering (attentive close range watching) in the skill acquisition process in immature orangutans, including widespread and routine skills, such as the processing of common food items or nest building. We did so by examining peering contexts, choice of experts, and subsequent practice. We further aimed to validate peering as an index of an observational form of social learning in immature orangutans. We used observational data collected during nest-to-nest follows of two populations of wild orangutans, with special attention to indicators of social learning such as peering and different exploratory behaviors. Cross-sectional and longitudinal data composed of a body of more than 1500 peering events by 20 immature individuals allowed us to test detailed predictions about observation rates and contexts.

Orangutans are an appropriate species for this kind of analysis. Wild orangutans live in a complex foraging niche with a diet consisting of many difficult-to-process and hidden food items, many of which require tool use[93]. Also, every evening they build a nest in which to spend the night. These nests are multi-layered constructions in a tree or combination of trees and made of bent branches to which additional elements such as pillows (small piles of small broken off leafy twigs) or blankets (larger leafy twigs bent or laid over the nest, leaving the head area free) are added [99, 100]. Before being weaned at the age of six to nine years, infant orangutans are in permanent association with their mothers and share her nest [90]. These mother-offspring associations are highly tolerant, including almost permanent body contact for the first two years, followed by a period of constant close distance, also in the feeding- and nest building- context [90]. This should provide immature orangutans with incentives and frequent opportunities for social learning, although in most populations adults lead a rather solitary life and rely on their own knowledge [88].

If immature orangutans acquire their feeding- and nest building skills through peering, we can predict a variety of patterns in their peering behavior. In this strictly observational study we used a correlational approach to test the following predictions:

1. Peering is most likely in contexts where learning is possible, especially feeding and nest building, rather than other contexts.

2. a) Peering rates in the feeding context increase with increasing complexity and decrease with increasing frequency of the food item in the mother's diet; b) Peering in the feeding context is followed by increased rates of exploratory behaviors with the same food item, serving as practice; and c) Peering rates in the feeding context decrease with age due to increasing feeding competence of the immatures.

3. a) Peering in the nest-building context is followed by increased rates of nest practice behavior; b) Hence, the age at which immatures show increased peering in the nest building context coincides with the age at which they show increased nest-practice behavior; and c) Peering rates decrease with increasing nest-building competence of the immatures.

4. With increasing age, because the mother's skills will have been acquired, peering directed at the mother gradually decreases, whereas peering directed at other individuals increases, relative to total peering events.

Methods

Data were collected from 2007 to 2015 on a population of wild Sumatran orangutans (*Pongo abelii*) at the Suaq Balimbing research area (3˚42'N, 97˚26'E, Aceh Selatan, Indonesia) and a population of wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at the Tuanan research area (2°09'S, 114°44'E, Kalimantan Tengah, Indonesia). Both research areas consist mainly of peat swamp forest with relatively high orangutan densities, with 7 individuals per square kilometer at Suaq[106] and 4 at Tuanan [383]. At both study sites behavioral observations had been ongoing for several years (starting 1994 at Suaq and 2003 at Tuanan).

The research protocols were approved by the Ministry of research and technology (RISTEK) (Research Permit No.: 152/SIP/FRP/SM/V/2012) and adhered to the legal requirements of Indonesia. As a strictly observational study on wild animals, we did not interact with our study animals in any way.

Data collection

We collected 2571 hours of behavioral data during full day (nest-to-nest) focal follows. We followed an established protocol for orangutan data collection (http://www.aim.uzh.ch/de/research/orangutannetwork.html), using focal animal sampling with instantaneous scan sampling at two minutes intervals as well as all-occurrence focal animal sampling of certain focus behaviors (see table 5.1, figure 5.1). Data were collected by CS and other observers who all reached an index of concordance of more than 85% during inter-observer reliability testing (based on simultaneous follows by multiple observers on the same focal animal without verbal exchange about the activity of the focal animal). We defined the complexity of the food items by the number of steps it takes to process an item, as shown in table 5.2. We assessed nest-building competence by the proportion of nights immatures build their own night nests: whereas young infants often build small, unstable nests during the day in which they take brief rests at most, only during late infancy or even after the onset of juvenility they start building their own nest to spend the night in[90].

Table 5.1. Definitions of the focus behaviors used as measures if social learning, independent exploration and nest practice.

Behavior	Definition
Peering	Directly looking at the action of another individual sustained over at least 5 seconds, and at a close enough range that enables the peering individual to observe the details of the action (within two meters in the feeding- and within five meters in the nest building context). The peering individual is facing the demonstrator individual and shows signs of following the actions shown by the demonstrator by head movements.
Exploration	Non-repetitive, usually destructive manipulation of objects without apparent feeding purpose, as well as feeding attempts on a food item or any other object whereby the item is taken into the mouth but not properly ingested.
Nest practice	Unsuccessful attempt to build a nest (by bending and intertwining leafy branches) or seemingly successful construction of a nest without using it.

Figure 5.1. Dependent immature peering at its mother in the feeding context (Picture by Julia Kunz).

Table 5.2. Processing steps of food items: Descriptions of the most frequent steps and examples

Processing steps	**Description**	**Example**
0	Pick and eat	Leaves
1	a) Pick, peel and eat;	a) Fruits with indigestible skin
	b) Pick, eat and spit out	b) Fruits with indigestible seed
2	a) Pick, peel, eat and spit;	a) Fruits with indigestible skin and seed;
	b) Pick, bite in half, extract inside, eat	b) Hard shell fruits with edible internal fruit flesh
3	a) Pick, bite in half, scrape out inside, eat, spit out;	a) Hard shell fruits with edible internal pulp and indigestible seed;
	b) Collect, scratch or bite open, suck, eat	b) Insects embedded in wood or other substrate
4	a) Break off, peel, extract inside, eat, spit out	a) Vegetative material ('pith') inside branches and liana;
	b) Break off, examine, bite apart, suck, eat	b) Sucking insects out of dead twigs

5	Break off, peel (optional), chew (optional), insert into tree hole/ nest/ fruit, and then extract, collect insects/ insect product/ seeds from tool tip, eat, spit out (optional)	Tool use (tree hole, insect nests and fruits)

Data sets

We collected data on 20 different immatures (11 at Suaq and 9 at Tuanan) over multiple years. To capture one specific developmental state of the immature animals, we lumped data collected on one individual within a period of four months to create a single age-specific individual mean. This resulted in 19 age/individual data points for Suaq and 12 age/individual data points for Tuanan (table S5.1). Each age/individual data point consists of 50-110 (mean = 83) hours of continuous observation. The age range and mean age of both data sets were comparable (Suaq: 0.5-12.3y, mean = 5.21; Tuanan= 0.4-11.3, mean = 5.20). Here, we distinguish three categories of immatures: (i) dependent immatures, who are between birth and weaning; (ii) semi-independent immatures, who are weaned but still in permanent association with their mothers; and (iii) independent immatures, who are no longer in permanent association with their mothers. Weaning age at Suaq is around 7 - 9 y years and at Tuanan around 6 - 7.5 years (van Noordwijk and Schuppli unpublished data).

Data analysis

All analyses and plots were done using R [121]. Data were analyzed using generalized linear mixed models using lmer as implemented in the package lme4 [317]. Individuals were included as a random factor to control for the fact that several individuals occurred multiple times in the data set. Unless otherwise indicated sample sizes for each model (*N*) represent the number of age-specific individual means (see above). Statistical significance of the fixed effects was assessed using cftest of the multcomp package [384]. Simultaneous effects of different factors on peering rates were assessed by including them as fixed effects. Models and their factors were selected based on the Akaike information criterion (AIC). The best description of age effects was either linear or quadratic, depending on the response variable.

A total of 1536 peering events, mostly in the feeding- and nest building context could be included in the analysis. There were more peering events recorded at Suaq (*N*= 1280) than at Tuanan (*N*= 256) mostly because peering rates in the feeding context differed between sites. Thus, the more detailed analyses for the feeding context were only conducted with the Suaq data set. Even though definitions and data collection methods were the same across years and sites, data collection gradually became increasingly detailed. For instance, measurement of the timing of peering events and activities around the peering event were only available for data collected after 2010. Therefore, not all analyses include all data. Details on the statistical models and sample sized can be found in table S5.2.

Results

To investigate whether immature wild orangutans rely on peering for the acquisition of their subsistence and social skills, we analyzed all-occurrence data on peering and exploration gathered during nest-to-nest follows. We first excluded the possibility that peering did not serve to gather information, but instead to receive food from the individual at whom the peering was directed. One could, however, also reasonably argue that begging and receiving food may also facilitate learning [102], and thus still qualify as social learning. We found that 15.6 % of all food peering events were followed by food begging. Thus, begging cannot be responsible for any major patterns seen in peering. Moreover, in the following analyses, including or excluding begging did not alter the results. Nonetheless, for the test of prediction 2.b we excluded begging because after successful begging the immature obtains the item the mother is feeding on, and increased exploration rates with those items would thus not be conclusive in those cases.

Prediction 1:

We found that at both sites most peering happened in the feeding context, followed by nest building. Less than 5.5 percent of peering events took place in a social context, such as mating, displaying at another individual, grooming or peering, or during other, non-social activities, including moving, resting, defecating and urinating or scratching (figure 5.2a). This finding is in line with the rarity of social interactions in orangutans [290].

When focusing on actual rates of peering (peering events of dependent immatures directed at the mother divided by the time the mother engaged in the peered-at activity), we found that activities in the social context as well as nest building were most frequently peered at, followed by feeding. Suaq immatures showed significantly higher peering rates than Tuanan immatures in the feeding context (GLMM: n=16, $b_{SiteTua}$= -0.75, $t_{SiteTua}$= -3.51, $P_{SiteTua}$< 0.001; b_{Age}= 0.23, t_{Age}= 2.20, P_{Age}= 0.028; b_{Age^2}= -0.03, t_{Age^2}= -2.35, P_{Age^2}= 0.019; figure 5.2b), whereas there was no significant difference in the other contexts (figure 5.2b).

We analyzed peering events in the feeding- and nest building context in more detail to test the predicted function of peering in social learning. For all other contexts, the number of peering events was too low for any detailed analysis.

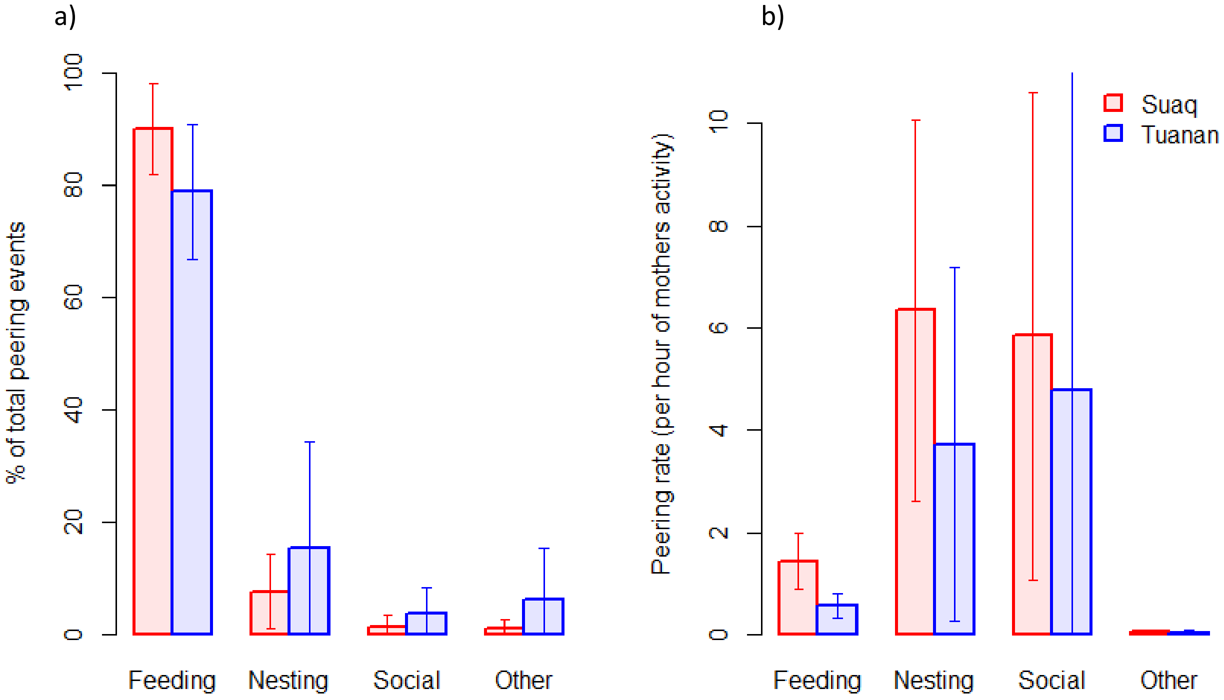

Figure 5.2. Peering contexts: Feeding, Nesting, Social interactions and others (all other, non-social activities), in percentage of total peering events for the different immatures at Suaq and Tuanan (a). Peering rates: Peering events at the mother per hour the mother spent doing the respective activity for the different dependent immatures at Suaq and Tuanan (b).

Prediction 2 a:

We predicted peering rates to reflect the learner's state of ignorance, and thus to increase with increasing processing complexity or increasing rarity of the food item. We examined peering of the Suaq dependent immatures at their mothers in the feeding context in relation to the number of steps needed to process the food item ("complexity"; table 5.2) as well as the frequency of the food item in the mother's diet (in percentage of total diet, "frequency"). To correct for the fact that food items are fed on for different amounts of time and therefore the offspring has varying opportunities to peer, we calculated peering rates by dividing the number of peering events recorded for a given food item by the time the mother was feeding on this item during mother-offspring associations. We long-transformed the predictor variable "frequency" and the response variable (peering rate) in order to reach randomly distributed model residuals. We found that dependent immatures peer significantly more frequently with increasing processing complexity of the item and with decreasing frequency, whereas age had a significantly negative effect on peering rates (table 5.3, figure 5.3 a+b).

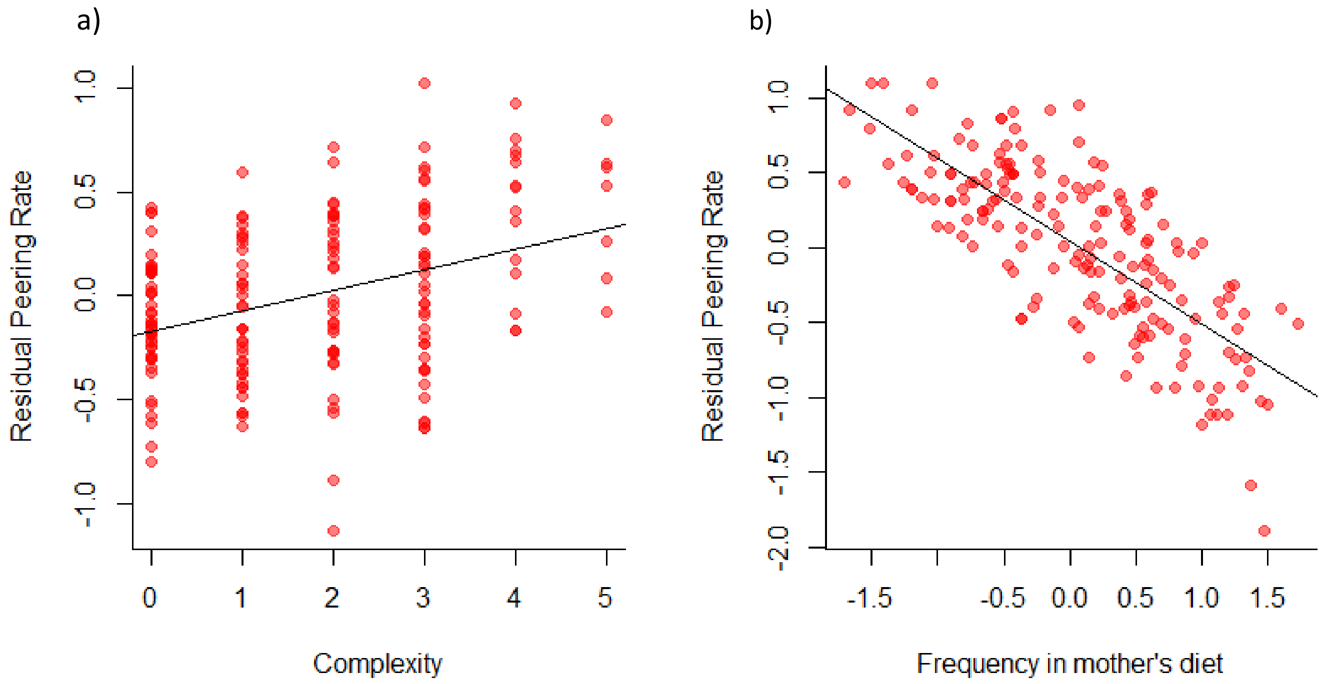

Figure 5.3. Peering in relation to food complexity and frequency in mother's diet: Residual peering rates (corrected for frequency) versus complexity (a) and residual peering rates (corrected for complexity) versus frequency in the mother's diet (log transformed, b) for dependent Suaq immatures peering at their mothers in the feeding context. Residuals and regression lines calculated based them were used for illustrative purposes only.

Table 5.3. GLMM with processing complexity of the food item ("Complexity"), frequency of the food item in the mothers diet (log transformed; "Frequency") as well as age as fixed effects and individual as random effect: estimates, T statistics, p-values and number of levels for the categorical variables (N), where cont. refers to continuous variables. The number in parentheses represents the total number of individual – food item combinations.

Effect	**Type of effect**	**Estimate**	**T statistic**	**P-value**	**N (180)**	**95% CI**		
Complexity	Fixed	0.10	5.89	<0.001	6	0.068	to	0.139
Log(Freq. in mothers diet)	Fixed	-0.58	-17.12	<0.001	cont.	-0.642	to	-0.509
Age	Fixed	-0.04	-2.76	0.03	cont.	-0.068	to	-0.005
Individual	Random	-	-	-	9	-		-

Prediction 2 b:

If immature orangutans learn by observing others, peering should be followed by increased levels of exploratory behaviors or feeding attempts with the same food item, especially in unskilled foragers (dependent immatures). To investigate the effect of peering on exploratory behavior, we determined the number of exploration events with the food item before and after each peering event when being in the mother's feeding patch (see figure S5.1 for a more detailed description of how this was measured). Since peering often happens at the beginning of the mother's feeding bout, the dependent immature has naturally more time to explore after the peering bout, which might bias the results. Thus, to correct for varying opportunities for these behaviors to occur, we calculated peering rates by dividing the number of peering events by the time before or after the peering event, respectively. We only included peering events where the dependent immature was in the feeding patch for at least 2 minutes before and after the peering event.

We found that dependent immatures showed significantly higher rates of exploratory behavior after peering than before peering (GLMM: $N= 14$, $b_{Timing}= 0.11$, $t_{Timing}= 5.5$, $P_{Timing}< 0.001$; $b_{Age}= 0.02$, $t_{Age}= 2$, $P_{Age}= 0.006$; figure 5.4).

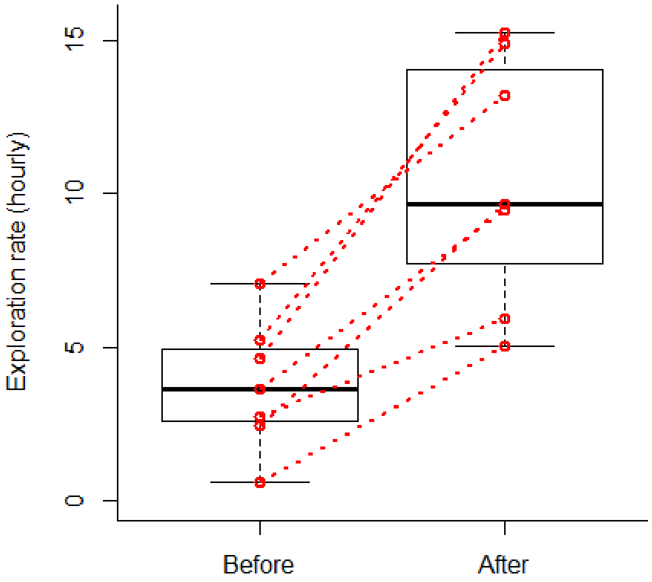

Figure 5.4. Peering and selective exploration: Average hourly rates of exploratory behavior with the same food item before and after peering events at the mother, when being within the same feeding patch for dependent immatures at Suaq. The data points represent exploration rates of the different infants before and after the peering event, averaged over all their recorded food peering events. The dotted lines connect individual average exploration rates of each context.

To examine social influences on selective practice in more detail, we looked at stick exploration by immatures. Adult orangutans habitually use sticks (broken off twigs or dead sticks) only at Suaq, and do so in two feeding contexts: (i) as tools to extracts insect products out of tree holes as well as to get seed out of fruits [385] and (ii) to suck insects out of the ends of dead hollow twigs ("dead twig sucking"). Both feeding techniques involve 'mouthing' the end of the stick. We found a trend that dependent immatures at Suaq explore sticks (using their mouth) more often than dependent immatures at Tuanan (GLMM: N= 16, $b_{SiteTuan}$= -0.45, $t_{SiteTuan}$= -1.93, $P_{SiteTuan}$<0.053; b_{Age}=0.59, t_{Age}=2.64, P_{Age}=0.088, $b_{\text{Age\textasciicircum 2}}$=-0.09, $t_{\text{Age\textasciicircum 2}}$=-2.97, $P_{\text{Age\textasciicircum 2}}$=0.003; figure 5.5a). We also found that in the hour after peering at their mothers using a tool or perfoming dead twig sucking, dependent immatures at Suaq showed significantly increased rates of stick exploration (GLMM: N=10, $b_{Context(AfterPeer)}$= 0.78, $t_{Contex(AfterPeer)t}$= 3.63, $P_{Contex(AfterPeer)t}$< 0.001; b_{Age}= 1.3, t_{Age}= 2.69, P_{Age}= 0.007, $b_{\text{Age\textasciicircum 2}}$=-0.2, $t_{\text{Age\textasciicircum 2}}$=-3, $P_{\text{Age\textasciicircum 2}}$=0.003; figure 5.5a). Also, at Suaq dependent immatures manipulated the end of the stick in a higher percentage of all exploration events on sticks (lm: N=8, b_{Site}= -42.03, t_{Site}= -4.2, P_{Site}< 0.009; b_{Age}= 1.74, t_{Age}= 0.61, P_{Age}= 0.59; figure 5.5b).

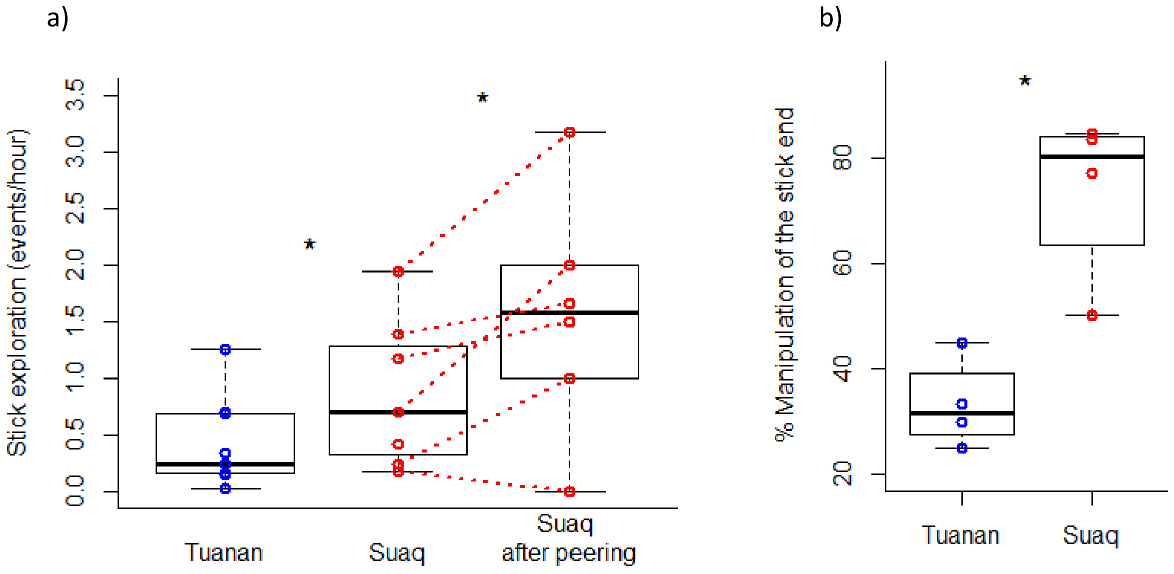

Figure 5.5. Stick use practice. Average hourly rates of exploration events on sticks (using their mouth) for dependent immatures at Tuanan and Suaq over all observation hours, as well as for the Suaq dependent immatures in the hour after they had been peering at the mother using a stick tool or sucking dead twigs (a). Data points represent individual stick exploration rates. The dotted lines connect individual averages for each state. Panel b shows the average percent of exploration events on sticks that were focused on the end of the stick (as opposed to any other part of the stick) for the infants at Suaq and Tuanan.

Prediction 2 c:

Under the assumption that peering is a means of social learning in the feeding context, we predicted that peering rates reflect the learner's competence and should therefore decrease with increasing age and feeding competence. At both sites, peering rates in the feeding context initially increase, as immatures become more active and start to ingest more solid food, peak around the age of three years and then decrease. At the same time, their feeding rates (as a measure of feeding competence) increase. Overall peering rates (directed at adults as well as semi-independent and independent immatures) were significantly higher at Suaq than at Tuanan (GLMM: N= 31, $b_{age\wedge 2}$= -0.01, $t_{Age\wedge 2}$= -4.99, $P_{age\wedge 2}$ <0.001; $b_{SiteTua}$= -0.64, $t_{SiteTua}$= -5.43, $P_{SiteTua}$<0.001; figure 5.6).

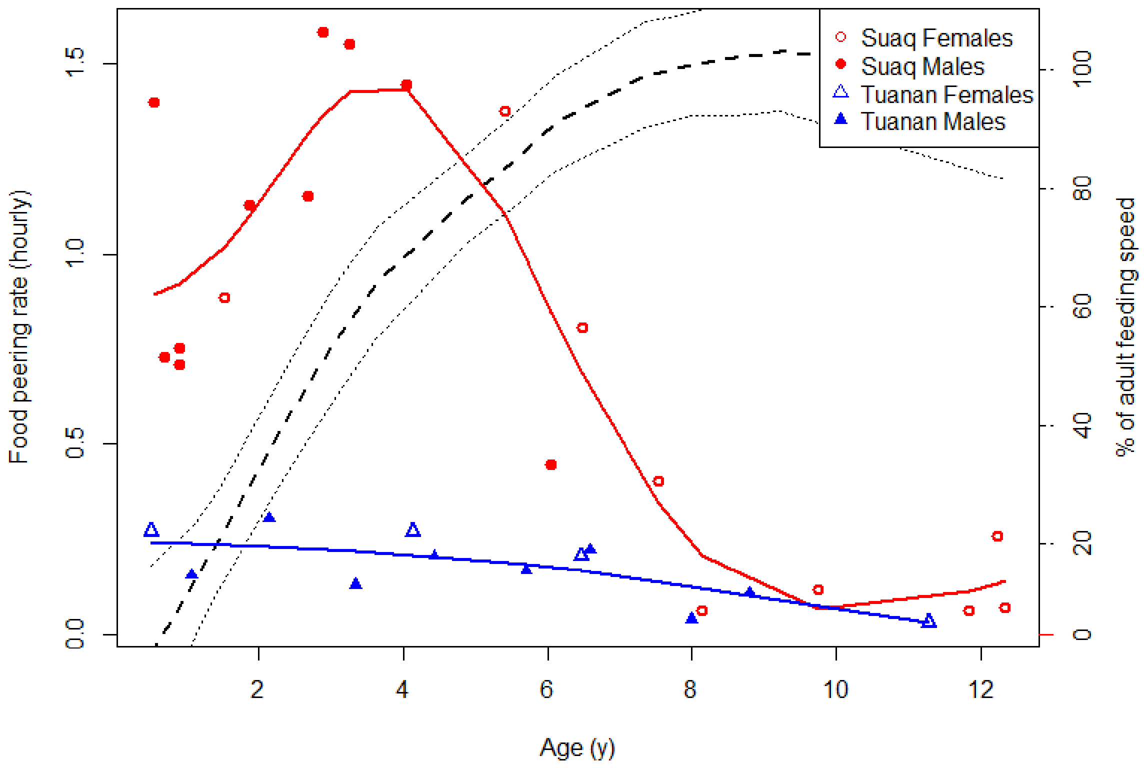

Figure 5.6. Peering in relation to age and feeding competence: Hourly peering rates in the feeding context (at adults as well as semi-independent and independent immatures) versus age (in years). The black solid lines summarize the course of food peering rates versus age for each population, using smoothing functions (smooth spline function of the stats package in R). The red (rising) line shows average feeding rate as a percentage of average adult female feeding speed, with 95% confidence interval, again using a smoothing function (based on chapter 4).

Prediction 3 a:

In the nest-building context we predicted that, as in the feeding context, peering is followed by increased rates of practicing nest building. Consistent with this we found that peering at another individual in the nest-building context leads to significantly increased rates of nest-practice behavior in the peering individuals in the subsequent hour compared to the hour before the peering event (GLMM: N =20, b_{Timing}= 0.25, t_{Timing}= 4.76, P_{Timing}< 0.001; b_{Age}= 0.05, t_{Age}= 1.45, P_{Age}= 0.148; $b_{SiteTua}$= -0.09, $t_{SiteTua}$= -0.61, P_{Site}= 0.542; figure 5.7 a+b).

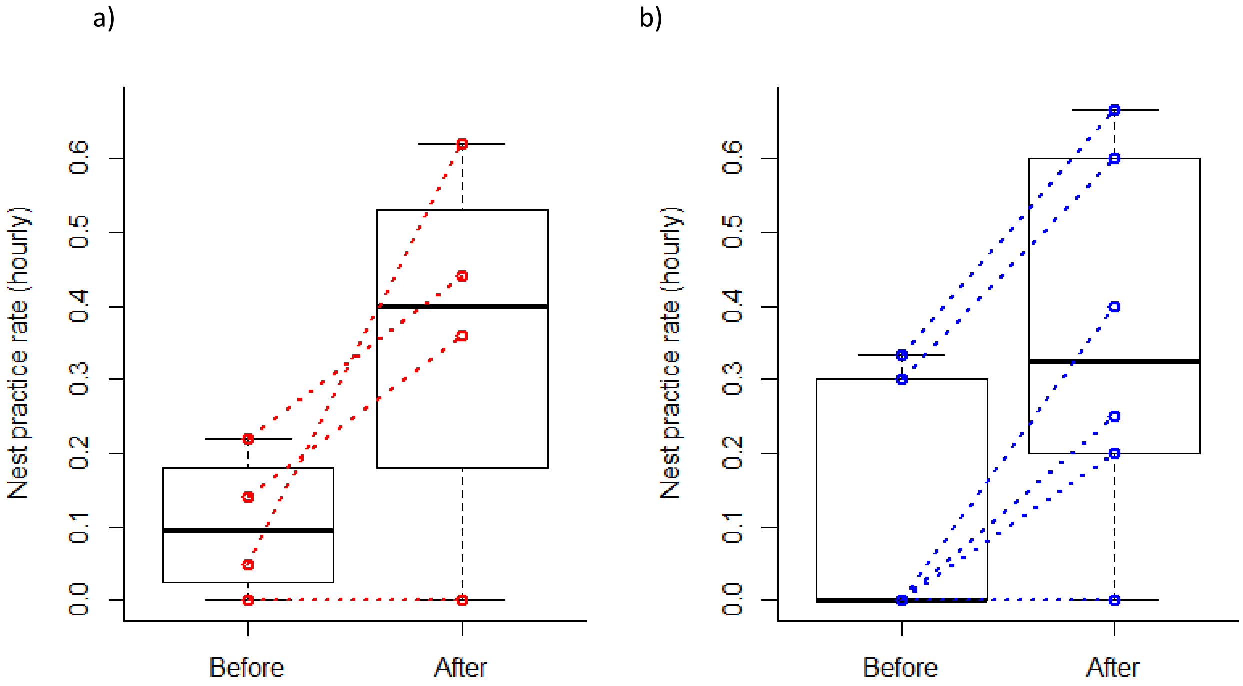

Figure 5.7. **Nest peering and nest practice behavior:** Average hourly rates of nest practice behavior one hour before and after nest peering of dependent immatures at Suaq (a) and at Tuanan (b). Data points represent individual nest practice rates before and after the peering event, averaged over all nest peering events. The dotted lines connect individual averages for each state.

Predictions 3 b & c

Under the assumption that nest peering serves for learning, the age at which immatures start to peer in the nest building context is expected to coincide with the age at which they start to practice nest-building behavior. With increasing nest-building competence of the immature, nest practice behavior is then expected to decrease. Indeed, rates of nest peering were significantly correlated with rates of nest practice behavior. Both nest peering rates and nest practice rates followed the same age trajectory (figure 5.8). We also found that with increasing age and proportion of own night nest building attempts nest peering rates decreased (figure 5.8). There was no significant difference in nest peering rates between the study sites (GLMM (Nestpeering~NestPractice+Site+(1|Individual)): $N= 14$, $b_{NestPractice}= 0.42$, $t_{NestPractice}= 12.5$, $P_{NestPractice}< 0.001$; $b_{SiteTuan}= 0.003$, $t_{SiteTuan}=\ 0.15$, $P_{SiteTuan}= 0.839$).

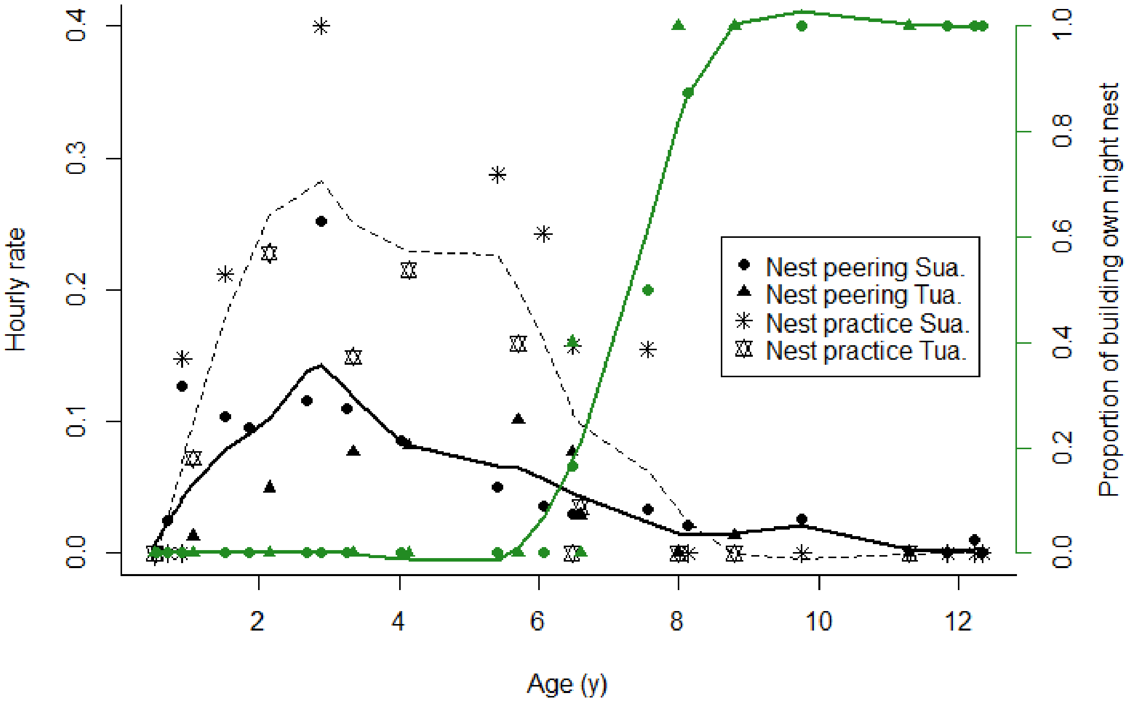

Figure 5.8. Nest peering and nest practice behavior in relation to age and nest building competence: Rates of nest peering and nest practice and the proportion of nights immatures build their own nest (although they do not necessarily spend the entire night in it) as a function of age for the Suaq immatures. The dashed line represents the course of nest practice rates over age, the solid line the course of nest peering over age and the green line the course of proportions of night an own night nest was built over age, using smoothing functions. We obtained all smoothing functions via the smooth spline function of the stats package in R.

Prediction 4:

If peering is a means of social learning, with increasing age immatures should peer more frequently at other individuals with potentially new techniques compared to their (familiar) mothers. To test this, we compared dependent immatures' peering rates at their mothers with those at other adult and independent immature individuals. Because younger dependent immatures rely on their mothers for transportation and thus show a strong bias in association, we had to control for the number of opportunities by including cases where the dependent immature was within two meters of a role model. We therefore calculated the relative proportion of peering directed at the mother versus other role models corrected for the time they spent within 2 meter of each. We only included individuals that had spent at least 60 minutes within two meters of each type of role model over the total follow period to control for lack of opportunities. As predicted, we found that with increasing age, the proportion of peering directed at the mother decreases. From the age of three to four years, when they are fully capable of independent locomotion, dependent immatures prefer other individuals over the mother as peering targets. These other individuals were mainly adult males (which are most likely unrelated), followed by semi-independent and independent immatures (siblings, as well as unrelated immatures) and other mothers (mostly related ones). There was no difference in the relative proportions of peering directed at the mother versus other individuals between the sites (GLMM: $N = 36$, $b_{Age} = -0.08$, $t_{Age} = -4.18$, $P_{Age} < 0.001$; $b_{Site} = -0.02$, $t_{Site} = -0.26$, $P_{Site} = 0.79$; figure 5.9).

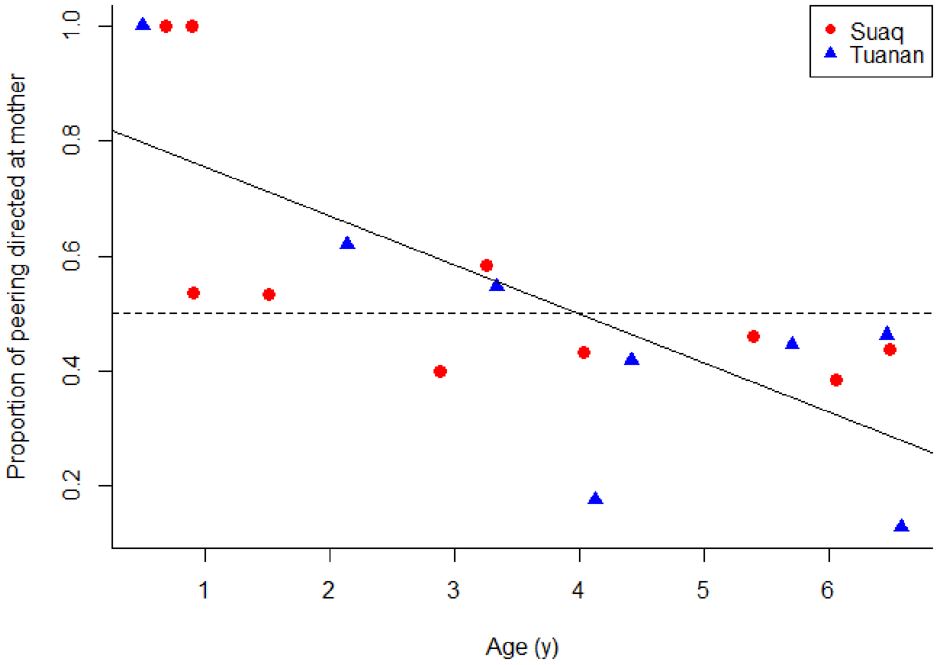

Figure 5.9. Peering at mother versus peering at others: Proportion of peering directed at the mother (versus other individuals) versus age for dependent immatures at Suaq and Tuanan. A value of 0.5 indicates an equal proportion of peering directed at the mother and other individuals.

Discussion

The aim of this study was to test the prediction that immature orangutans, under natural conditions learn their skills by observing conspecifics. To do so we looked at the rates and the context of peering and exploratory behavior in immatures from two populations. It could be argued that the desire to acquire information is not the sole underlying motivation of orangutan peering behavior. However, if information is transferred through peering, irrespective of the original motivation of the peering individual, we expect peering behavior to meet a variety of predictions. In this study we tested these predictions, using a correlational design.

We found that peering is most frequent in contexts in which learning is expected and that peering decreases with increasing competence. The peering data show why it takes immature orangutans multiple years to acquire their feeding skills and more complex feeding skills such as tool use take longest to develop [93, 386, 387]. Similarly, nest building seems to be acquired over multiple years and nest quality only gradually increases [90, 93, 101]. Thus, rather than being developmentally canalized or imprinted, feeding and nest building are acquired through a learning process, using both, social inputs and individual practice. By the age of 12 or 10 years, Sumatran and Bornean orangutan immatures, respectively, have reached adult-like diet repertoires and feeding rates[387]. By that time, peering rates in the feeding and nest building context have strongly declined. However, some peering continues beyond that age, especially when individuals meet unfamiliar associates, which is consistent with the results of experiments on chimpanzee nut cracking [388].

We found that peering rates in the feeding context are lower for the more familiar food items in the mother's diet, consistent with findings on Japanese macaques [373]. This pattern is consistent with several social learning mechanisms, including simple ones, such as stimulus enhancement. As a purely observational study it is difficult to pin down the exact learning mechanism at work: Distinguishing between different forms of observational learning (such as stimulus enhancement, imitation or emulation) goes beyond the scope of the current study. However, because peering rates are significantly higher for food items with greater processing complexity, the use of observational learning is the most plausible, especially given the known capacities of orangutans [364, 366, 389]. We further found significant differences in peering rates and contexts between the study sites, which will be discussed in chapter 6.

If peering is a means of social learning, rates of selective practice should increase following peering, especially for unskilled individuals (younger dependent immatures). Our results confirmed this. First, in the nest building context, peering coincided with the onset of nest-building practice. Furthermore, nest peering led to significantly increased rates of nest practice in the hour after peering. During nest practice immatures show the same types of manipulation of leafy branches as adults do when building their nests. Immature orangutans are surrounded by leafy branches all day long. However, the fact that they only start manipulating those in ways adults do when building nests after observing their mothers doing so, hints towards an observational form of social learning. Second, dependent immatures' rates of exploratory behaviors with the same food item significantly increased after peering: Within the same feeding bout of the mother and when already being within the same feeding patch, exploration rates were significantly lower before the peering event compared to after the peering event. Thus, even though the immatures were already in close proximity of the food items and their mothers, their exploration rates only increased after they had observed their mother feeding on those items. Finally, we found more practice-like stick manipulations at Suaq, the site where adults habitually use sticks in the feeding context, namely during tool use and dead twig sucking. Stick exploration rates were most increased after the immatures had been peering at their mothers using tools or dead twig sucking. In fact, immatures at Suaq were more likely to manipulate sticks at the end part, just as adults do during tool use and dead twig sucking. These patterns strongly suggest that the observed effects were not due to local enhancement or social facilitation but due to observational learning.

The fact that exploration increased after peering also suggests that exploration is partly triggered by attention paid to role models. This is consistent with findings in gorillas (*Gorilla gorilla beringei[164]*) and howler monkeys (*Alouatta palliata* [374]), where immature feeding and exploration behavior is linked to the feeding bouts of their mothers. However, no such link was found in Mayotte brown lemurs (*Euler fulvus* [307]), where juveniles explore food items regardless of their mothers feeding activity.

In conclusion, orangutans, and presumably some, but not all other primate species, learn their foraging and nest-building skills through close observation of these actions by experts. Immature orangutans also show targeted practice of the same actions after observing expert individuals performing these actions. This is consistent with Galef's [63] suggestion that template matching, through an interplay of social and asocial learning helps the learning individual to iteratively produce a match between its performance and the observed actions of a demonstrator, which has recently been confirmed in chimpanzees [64].

We anticipated that older immatures who already acquired most of their mother's skills would show increasing interest in role models other than the mother. Our results supported this prediction: whereas young dependent immatures exclusively peer at their mothers, they increasingly peer at others as they get older. By the age of weaning, immatures show a clear preference for these less familiar role models.

Our result also consistent with the notion that with increasing age, immatures are less reliant on the mother and thus in general, show more interest in other individuals, irrespective of the skills of those individuals. However, the fact remains that immatures bother to peer at those individuals. Wild chimpanzees [388] and Siberian jays (*Perisoreus infaustus* [390]) show a similar pattern under experimental conditions. These findings are also consistent with the phenomenon of social referencing in human infants, who are exclusively oriented towards familiar caregivers in the first few years of life and only gradually extend their interest and trust towards less familiar individuals (e.g. [391]).

Our study suggests that under natural conditions immature orangutans learn by observing others and heavily rely on social learning for skill acquisition. In this species, and perhaps others that need to learn many skills and have intergenerational associations, social learning might in fact be the default mode of learning. This is in line with laboratory experiments that have shown that socially deprived animals show severe deficits in a broad range of skills [74, 76, 392, 393]. Our results are also consistent with the earlier finding that in orangutans, diet must be socially learned since offspring inherit the diet repertoires of their mothers [62]. This study also provides further evidence that observational learning is the mechanism underlying the variation in feeding- and nest building techniques between different orangutan populations [104, 394, 395].

Humans rely heavily on social learning, and do so with uniquely high fidelity [53, 54]. Social learning allows for the accumulation and transfer of knowledge over successive generations [32]. During human evolution, the ability to learn from others enabled our ancestors to occupy a greater variety of habitats than any other mammal species has managed. Strikingly, no individual human being would be able to individually acquire the skills necessary to survive in any of those habitats [51]. It has therefore been argued that the difference in cognitive abilities between us and our closest relatives, the great apes, in itself is not enough to explain the difference in species' success, but that the key must lie in the extent of social transmission [51]. Since we showed that orangutans heavily rely on observational learning under natural conditions, this alone cannot be the cause of the massive difference between humans and great apes. Instead, there are two other likely causes. First, compared to great apes, humans show a much larger network of tolerant experts [396]. Second, humans systematically rely on imitation and teaching whereas great apes don't [347]. However, given the role of practice [63], imitation may not be as critical as previously assumed. Teaching, however, is pronounced in humans [397], and may also be linked to the adoption of extensive allomaternal care by our ancestors [18].

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Supplementary Material

Table S5.1. Study site, name of the focal animal, age and sex class, observation period and age for the 31 age individual data points.

Nr	Site	Focal	Age Class	Sex	Observation	Age
1	Suaq	Lois	Dependent	M	2011	0.5
2	Suaq	Rendang	Dependent	M	2014	0.7
3	Suaq	Simba	Dependent	M	2013/14	0.9
4	Suaq	Frankie	Dependent	M	2013	0.9
5	Suaq	Cinnamon	Dependent	F	2013	1.5
6	Suaq	Ronaldo	Dependent	M	2007/08	1.9
7	Suaq	Fredy	Dependent	M	2007	2.7
8	Suaq	Lois	Dependent	M	2013	2.9

9	Suaq	Fredy	Dependent	M	2008	3.3
10	Suaq	Fredy	Dependent	M	2009	4.0
11	Suaq	Chindy	Dependent	F	2008	5.4
12	Suaq	Fredy	Dependent	M	2010/11	6.1
13	Suaq	Lilly	Dependent	F	2007/08	6.5
14	Suaq	Lilly	Dependent	F	2008/09	7.5
16	Suaq	Chindy	Independent	F	2010/11	8.1
15	Suaq	Lilly	Independent	F	2011	9.8
18	Suaq	Ellie	Independent	F	2010/11	11.8
17	Suaq	Shera	Independent	F	2010/11	12.2
19	Suaq	Lilly	Independent	F	2014	12.3
20	Tuanan	Kahiyu	Dependent	F	2012	0.4
21	Tuanan	Joya	Dependent	M	2012	1.0
22	Tuanan	Danum	Dependent	M	2012	2.1
23	Tuanan	Joya	Dependent	M	2014	3.3
24	Tuanan	Mawas	Dependent	F	2012	4.1
25	Tuanan	Petzy	Dependent	F	2012	4.4
26	Tuanan	Kino	Dependent	M	2012	5.7
27	Tuanan	Mawas	1/2 dependent	F	2014/15	6.5
28	Tuanan	Jip	Dependent	M	2012	6.6
29	Tuanan	Deri	Independent	M	2012	8.0
30	Tuanan	Jip	Independent	M	2014	8.8
31	Tuanan	Milo	Independent	F	2012	11.3

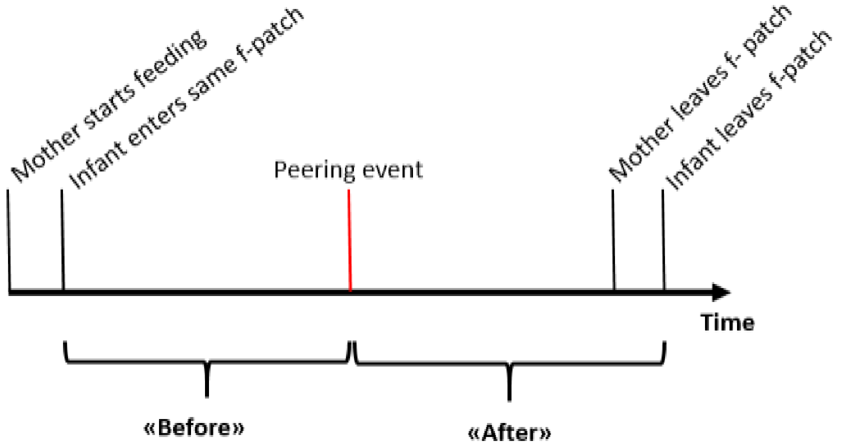

Figure S5.1. Explanation to the analysis of figure 5.4: To see whether exploration rates increase after a peering event, for each of dependent immatures we calculated average hourly rates of exploratory behavior with the same food item before and after peering events. We only included peering events directed at the mother. For each peering event we looked at the immatures' exploration rates for the time they were within the same feeding patch ("f-patch") as the mother. "Before" refers to the amount of time before the peering event, "After" to the time after the peering event

Table S5.2. Details on the statistical analyses for each prediction: model type, dependent variable (with the sample described in parentheses), effects, type of effects, estimates, T statistics, P-values (with significance on the 5% level indicated in bold font), N (where the number in parentheses next to the N individual is the total number of individual – age – timing combinations for each model and cont. refers to continuous variables), and 95% confidence intervals.

Prediction	Model	Dependent variable	Effect	Type of effect	Estimate	T statistic	P-value	N	95% CI		
1	GLMM	Food peering rate (dependent immatures at Suaq and Tuanan)	Age	Fixed	**0.23**	**2.2**	**0.028**	cont.	0.195	to	0.422
			Age^2	Fixed	**0.03**	**-2.35**	**0.019**	cont.	-0.034	to	-0.026
			Site (Tuanan)	Fixed	**-0.75**	**-3.51**	**<0.001**	2	-0.762	to	-0.672
			Individual	Random	-	-	-	12 (15)	-		-
2 b	GLMM	Exploration rate (dependent immatures at Suaq)	Timing (after peer)	Fixed	6.71	4.83	**<0.001**	2	4.103	to	9.32
			Age	Fixed	1.06	2.76	**0.006**	cont.	0.343	to	1.761
			Individual	Random	-	-	-	6 (14)	-		-
2 b (stick)	GLMM	Stick exploration rate (dependent immatures at Suaq and Tuanan)	Age	Fixed	0.59	2.64	**0.008**	cont.	0.187	to	0.991
			Age^2	Fixed	-0.09	-2.97	**0.003**	cont.	-0.148	to	-0.036
			Site (Tuanan)	Fixed	-0.45	-1.93	**0.053**	2	-0.878	to	-0.03
			Individual	Random	-	-	-	13 (16)	-		-
	GLMM	Stick exploration rate (dependent immaures at Suaq)	Timing (after peer)	Fixed	0.78	3.63	**<0.001**	2	0.339	to	1.215
			Age	Fixed	1.3	2.69	**0.007**	cont.	0.687	to	1.917
			Age^2	Fixed	-0.2	-3	**0.003**	cont.	-0.291	to	-0.118
			Individual	Random				5 (10)			
	LM (N= 10)	End manipulations in percent of total stick manipulations (dependent immatures at Suaq and Tuanan)	Age	Fixed	-42.03	0.61	0.568	cont.	-67.79	to	-16.27
			Site (Tuanan)	Fixed	1.74	-4.2	**0.009**	2	-5.58	to	9.05
3a	GLMM		Timing (after peer)	Fixed	0.25	4.76	**<0.001**	2	0.146	to	0.355
			Age	Fixed	0.05	1.45	0.542	cont.	0.049	to	0.071

		Nest practice rate (dependent immatures at Suaq and Tuanan)	Site (Tuanan)	Fixed	-0.09	-0.61	0.148	2	-0.106	to	-0.036
			Individual	Random	-	-	-	9 (20)	-		-
3b+c	GLMM	Nest peering rate (immatures at Suaq and Tuanan)	Nest practice rate	Fixed	0.42	5.56	**<0.001**	cont.	0.279	to	0.572
			Site (Tuanan)	Fixed	0.003	0.2	0.839	2	-0.026	to	0.032
			Individual	Random	-	-	-	18 (26)	-		-
4	GLMM	Proportion of peering directed at mother (immatures at Suaq and Tuanan)	Age	Fixed	-0.08	-4.18	**<0.001**	cont.	-0.122	to	-0.046
			Site (Tuanan)	Fixed	-0.02	-0.26	0.794	2	-0.184	to	0.139
			Individual	Random	-	-	-	18 (36)	-		-

5. Observational social learning and socially induced practice of routine skills in wild immature orangutans

Chapter 6: Developmental effects of sociability on exploration rate in wild orangutans

Caroline Schuppli, Sofia Forss, Ellen Meulman, Carel van Schaik

Submitted

Abstract

It has been hypothesized that opportunities for social learning affect not only the size of the adult skill set, but also learning ability, and thus ultimately innovation frequency. Although it is difficult to test this prediction directly in the wild, innovation is usually preceded by exploration. We therefore compared exploration rates in a highly sociable population of *Pongo abelii* at Suaq Balimbing and a less sociable population of *Pongo pygmaeus* at Tuanan. Immatures at Suaq have increased opportunities for social learning through more frequent associations and increased social tolerance. Suaq immatures showed significantly higher rates of peering (attentive close-range watching), even after controlling for differences in association time and diet complexity, implying that they make disproportionally greater use of their increased opportunities for social learning. As predicted, we found that immatures and adults at Suaq show significantly higher rates of explorative behavior. Although exploration rate also increased when the subject was in association, the difference remained when we controlled for association time, suggesting persistent developmental effects or intrinsic population differences. Moreover, within populations, more sociable mothers had higher exploration rates and also had offspring with higher exploration rates. The difference in exploration rate found between the two populations is in line with a higher mean dietary complexity, as well as a larger set of learned skills at Suaq. Our findings suggest that increased sociability triggers a social learning cascade whereby a higher attentiveness to conspecifics' activities leads to an increased exploratory tendency (and ultimately a higher probability of innovation) in a population.

Introduction

Cultural effects on cognitive development in humans have been described for a long time and have reached the status of common knowledge: social inputs during childhood have a strong effect on the development of the cognitive skill set [80]. Studies on institutionalized children have shown that children raised with limited social inputs show deficits in a variety of domains, including language, social-emotional development and intelligence [67, 68]. Effects of limited social inputs during development are also evident on the physiological and anatomical level, expressed in structural and functional changes of the brain [69, 70]. Recent studies have shown that more subtle differences in the frequency and quality of social inputs during critical periods of early childhood also affect later cognitive performance [398]: increased social interactions during day care [399] a higher degree and consistence of parents' responsiveness during early childhood [400, 401] and early education and care programs were all found to have significant positive effects on cognitive development and later cognitive abilities.

Experiments on a variety of nonhuman species suggest that similar processes might also be at work in other animals, suggesting some degree of evolutionary continuity. On the one hand, extreme social deprivation during development has been shown to lead to smaller adult skill sets and reduced learning abilities in several mammal taxa [74-76, 393]. On the other hand, extreme enculturation (such as during hand rearing) was found to lead to a more rapid development of a broader set of skills as well as increased learning ability in primates, in particular apes [77, 78]. Thus, as in humans, social inputs during development affect the number of skills individuals have acquired by adulthood as well as their cognitive performance. However, neither the underlying mechanisms nor the degree evolutionary continuity in the more fine-grained effects of the quality of social inputs on cognitive development have so far been investigated.

Until now, independent learning has often been regarded as a less complex form of learning compared to social learning. However, recent findings challenge this notion. Experiments have shown that individuals acquire skills faster when exposed to role models as opposed to when they have to rely on independent learning [55, 56]. Also, individuals with more opportunities for social learning acquire more complex skills faster [57, 58], consistent with the hypothesis that social learning is more efficient than independent learning. Social learning leads subjects to focus on relevant information and thus makes it easier for them to acquire valuable skills without time-consuming and potentially dangerous innovation. Furthermore, social learning allows skills to be passed on to the next generation, making them heritable. Skills themselves are a clear target for natural selection as opposed to the learning ability per se, since that will only sometimes result in innovation and thus actual fitness benefits. Consequently, the net benefit per unit brain tissue is higher in lineages with social learning and it should be easier for selection to favor the evolution of increased learning ability in species that rely on social learning [32].

The intraspecific correlation of independent- and social-learning abilities also suggests that the ability for independent- and social learning depend on the same basic cognitive mechanisms [52] . Indeed, social learning most likely includes an element of individual evaluation [63]. In most forms of social learning, only the trigger is social, whereas the association itself is most likely dependent on forms of independent learning. Accordingly, a growing body of evidence suggests that even observational forms of social learning mostly entail a phase of independent practice of the observed behavior [62-64]. Thus, most social learning may indeed largely rely on existing asocial-learning mechanisms [52, 61]. The exception to this is probably blind copying as it has been shown in humans (e.g. over-imitation[65]). Also, experiences and abilities gained through social learning are likely to be transferred to new situations and thus increase overall cognitive performance [32, 81]. Selection on social learning will therefore automatically also favor the evolution of independent learning ability.

The cultural intelligence hypothesis builds up on these observed correlations of social- and independent learning ability and predicts effects of opportunities for social learning on two levels [32, 79]. On the developmental (proximate) level it states that individuals with more opportunities for social learning during their development will have acquired larger sets of learned skills as adults. Through experience effects, as well as based on the cognitive overlap between the two mechanisms, individuals with more opportunities for social learning during development will also have an increased current independent learning ability. On an evolutionary (ultimate) level, the cultural intelligence hypothesis states that species with more opportunities for social learning will over evolutionary time show an increased innate learning ability. In addition, the cultural intelligence hypothesis also predicts that increased learning abilities go hand in hand with higher exploratory tendencies and thus result in an increased likelihood of innovations. Thus, populations which offer more opportunities for social learning should exhibit overall larger and more complex repertoires of learned skills.

The aim of this study is to investigate the effects of varying opportunities for social learning on skill acquisition and cognitive performance in wild orangutans. Orangutans represent the ideal natural experiment for this because their degree of sociability varies significantly between populations. Sociability levels range from semi-solitary to low-level fission fusion with Sumatran orangutans, *Pongo abelii*, generally spending more time in associations than Bornean orangutans, *Pongo pygmaeus* [87, 88, 308]. Depending on the specific population, mother-offspring pairs spend 10-50% of their time in association with at least one other individual [90]. Furthermore, being one of our closest relatives, orangutans show strong domain-general cognition[2, 3] and rely on a broad range of learned skills in the ecological context. Orangutan infants stay in permanent and very close association with their mothers for their first six to nine years and it takes immatures more than ten years to learn the full range of their ecological subsistence skills [90, 93, 387].

Controversially, despite showing broad repertoires of learned skills, wild adult orangutans show low exploration rates and are highly novelty averse [66, 105]. Immature skill acquisition is highly socially mediated, whereby most input comes from the mother [62, 311]. The frequency of inputs from individuals other than the mother varies drastically between different populations. In orangutans, social learning and independent exploration are tightly linked: peering (attentive close range watching of a conspecifics activity) leads to a direct increase of exploration with the same object or food item as the peered at individual is manipulating [62, 311]. Thus, sociability and opportunities for social learning might also have direct effects on exploration rates. It is therefore important to separate the direct effects of associations on exploration rates from those of developmentally induced or innate differences in exploratory tendency between the species.

To test the cultural intelligence hypothesis we will compare two orangutan populations of that differ substantially in their ecologically induced density and thus their potential degree of sociability: the highly sociable Suaq Balimbing population and the less sociable Tuanan population. First, assuming that social learning is more efficient than independent learning, we predict that individuals at Suaq make use of their increased opportunities and show higher rates of indicators social learning (i.e. peering; cf. [311]). Second, we predict that increased opportunities for social learning will result in higher rates of explorative behavior at Suaq. Since immatures are generally more exploratory than adults, these differences should be most pronounced in immatures. To rule out that these differences are not a result of generally increased activity levels in the more sociable population, we will also look at differences in the frequency of other types of object manipulation behavior.

Third, in order to identify the mechanisms at work, we will examine direct effects of associations on exploratory tendency versus developmental effects. If there are direct effects of associations on exploratory tendency, we predict that, individuals will show increased rates of exploration when in association. If increased levels of sociability have lasting developmental or even evolutionary effects, we predict that individuals at the more sociable population will show increased exploration rates even as adults and inclusive when being on their own. Under the assumption of long lasting developmental effects, we further predict that within populations, the level of the mother's sociability will affect her own exploratory tendencies as well as those of her offspring throughout their life. Finally, on the population level, we predict that increased exploratory tendencies will result in a higher likelihood of innovations and thus larger repertoires of learned skills as well as higher skill complexity.

Methods

Study sites

Data was collected from 2007 – 2014 at Suaq Balimbing (3˚42'N, 97˚26'E, Aceh Selatan, Indonesia) on a population of wild Sumatran orangutans (*Pongo abelii*) and from 2012 – 2015 at Tuanan (2°09'S, 114°26'E, Kalimantan Tengah, Indonesia) on a population of wild Bornean orangutans (*Pongo pygmaeus wurmbii*). With 7 individuals per km^2, Suaq shows the highest orangutan density of all studied orangutan sites, whereas Tuanan's density is significantly lower with 4.25 individuals per km^2 [106, 107].These differences in density are thought to be directly related to differences in plant productivity and thus food availability[103].

Data collection

Behavioral data was collected following an established protocol for orangutan data collection (www.aim.uzh.ch/orangutannetwork/Field_Guidelines.html), using focal animal sampling including instantaneous scan sampling at two minutes intervals. Additionally, all object manipulation behavior and indicators of social learning were described in detail, including context, exact description of the type of manipulation and the manipulated object or interaction partner (table 6.1).

Data was collected by CS at both sites as well as by SF, EM and several well-trained observers. Inter-observer reliability was assessed through simultaneous follows by multiple observers on the same focal animal without verbal exchange about the activity of the focal animal. Only data of observers that reached an index of concordance with CS of more than 85% on the frequency of the specific focus behavior were included in the analysis. This led to slight variations in sample size, depending on the observed behavior.

Associations were defined as two or more individuals being within 50 meters to each other. At every two-minute interval during scan sampling, the distance between the focal individual and all association partners (party members) was assessed.

Table 6.1. Definitions and classifications of the focal behaviors.

Class of behavior	Behavior	Definition
Explorative object manipulation	Exploration, Try feeding	Non-repetitive, usually destructive manipulation of, or feeding attempts on objects (such as fruits, sticks, leaves, other plant or material, animal products, etc.), excluding actual feeding.
Playful object manipulation	Object Play	Manipulation of an object without apparent goal and including repetitive movements.
Social learning	Peering	Directly looking at the action of another individual sustained over at least 5 seconds, and at a close enough range that enables the peering individual to observe the details of the action.

Data sets

We followed 22 different immature individuals (13 at Suaq and 9 at Tuanan) as well as 12 (6 and 6) of their mothers as adult references. For the immatures, data collected within 5 months was averaged to create a single age-specific individual mean. This resulted in 19-20 age/individual data points of immatures for Suaq and 11-12 age/individual data points for Tuanan, depending on the observed behavior (see above). For the immatures as well as for the adults, the average rate of each behavior is calculated based on 50-110 observation hours.

Immature individuals were classified as (i) dependent immatures who are between birth and weaning (infants); and immatures after weaning (juveniles). Among the latter we distinguished between (ii) semi-independent immatures, who are weaned but still in permanent association with their mothers; and (iii) independent immatures, who are no longer in permanent association with their mothers. Weaning age at Suaq is around 7 - 9 years and at Tuanan around 6 - 7.5 years.

Data Analyses

All analyses and plots were done using the R programming language (R development Core Team [121], version 3.1.3) using the R studio interface [402]. Data were analyzed with general linear mixed models, using lmer as implemented in the package lme4 [317]. To account for the fact that data was collected on the same immature individuals at multiple times, at different stages of their development, we included the individual as a random factor. Statistical significance of the fixed effects was assessed using cftest of the multcomp package [384]. To test for differences in the hourly rates of the focus behaviors in the immatures, age was included in the model to account for the fact that the rates of these behaviors are strongly correlated with age. Depending on the behavior, the best fit of the age term was quadratic, sigmoid or linear and was determined based on the Akaike information criterion (AIC).

Results

Prediction 1: *Individuals at the more sociable population will have more opportunities for social learning.*

In terms of opportunities for social learning we found that immatures at Suaq have a significantly higher average number of party members than immatures at Tuanan (figure 6.1a, table 6.2a). Also, during associations with party members other than their mother or the dependent or semi- dependent sibling, they spend a higher share of the association time within two meters of that party member (figure 6.1b, table 6.2b).

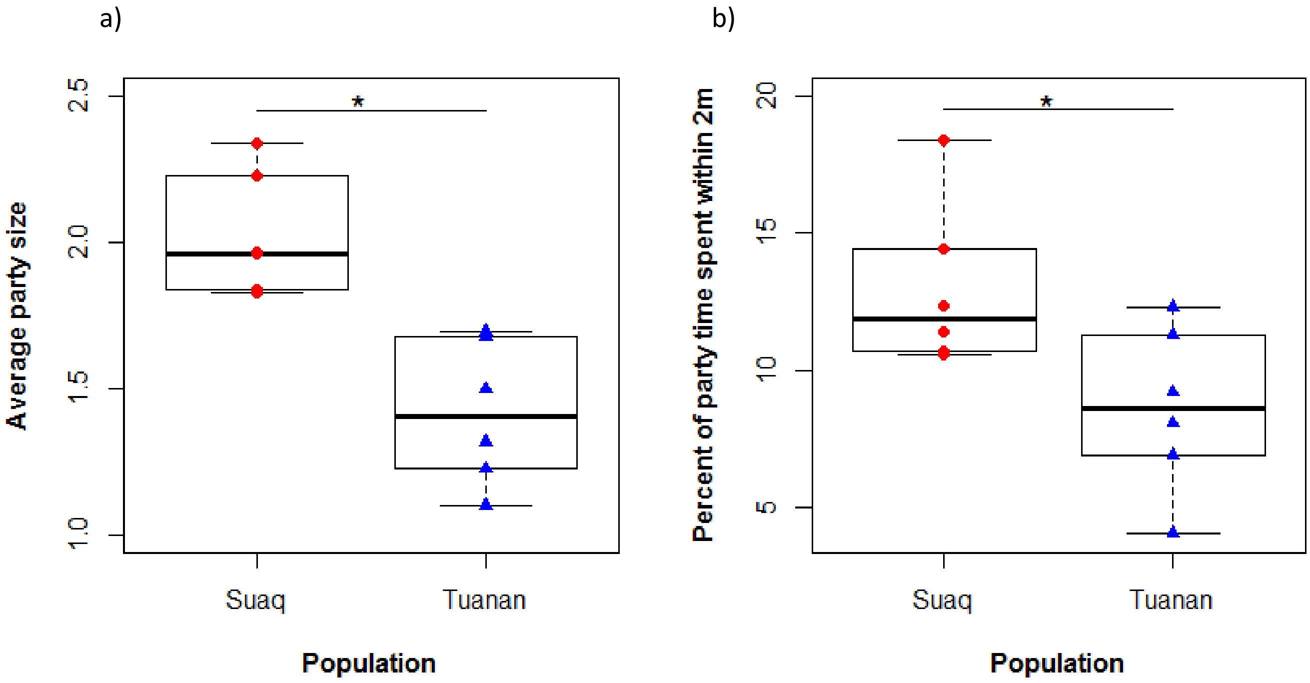

Figure 6.1. Average number of party members (including mother and siblings) for infants at Suaq and Tuanan (a). Percentage of association time spent within 2 meters for the infants at Suaq and Tuanan, when being in association with individuals other than their mothers or dependent or semi-dependent siblings (b).

Table 6.2. GLMs with average association time of the dependent immatures with individuals other than the mother or the semi- dependent sibling (a) and percent of association time spent within two meters of those party members (b) as response variables and age as well as population as effects.

	Response	**Effect**	**Estimate**	**Std-Error**	**P-value**	**N**
a)	**Average association size**	Site (Tuanan)	-0.61	0.131	**<0.001**	12
b)	**% of Association time spent within 2m**	Site (Tuanan)	-4.35	1.73	**0.031**	12

Prediction 2: *Individuals at the more sociable population will make use of their increased opportunities for social learning and thus show higher rates of social learning (i.e. peering).*

To investigate the use of these increased opportunities for social learning, we first looked at the ontogeny of peering behavior. We found that hourly peering rates increased until the age of 3-4 years and then decrease (figure 2 a). In total, immatures at Suaq peered significantly more often per hour than immatures at Tuanan (table 3a, figure 2a). To correct for varying opportunities to peer, we also examined peering rates per time spent in association with different classes of individuals. We found that Suaq immatures peered significantly more per hour they spent in association with at least one adult or immature individual (table 6.3b, figure 6.2b). Peering at their mother per time spent with her showed the same pattern (table 6.3c, figure 6.2c). For peering at party members other than the mother we found that peering rates per hour spent in association with those individuals began increasing from the age of 1.5-2 years, peaked around weaning and then decreased again. There was a trend for immatures at Suaq to peer more frequently at party members other than the mother per hour they spent with them (table 6.3d, figure 6.2d), but the sample size for this last test was low because associations at Tuanan are rare and thus not all individuals could be included in the sample. This may the reason why the difference between the populations in this test did not reach statistical significance.

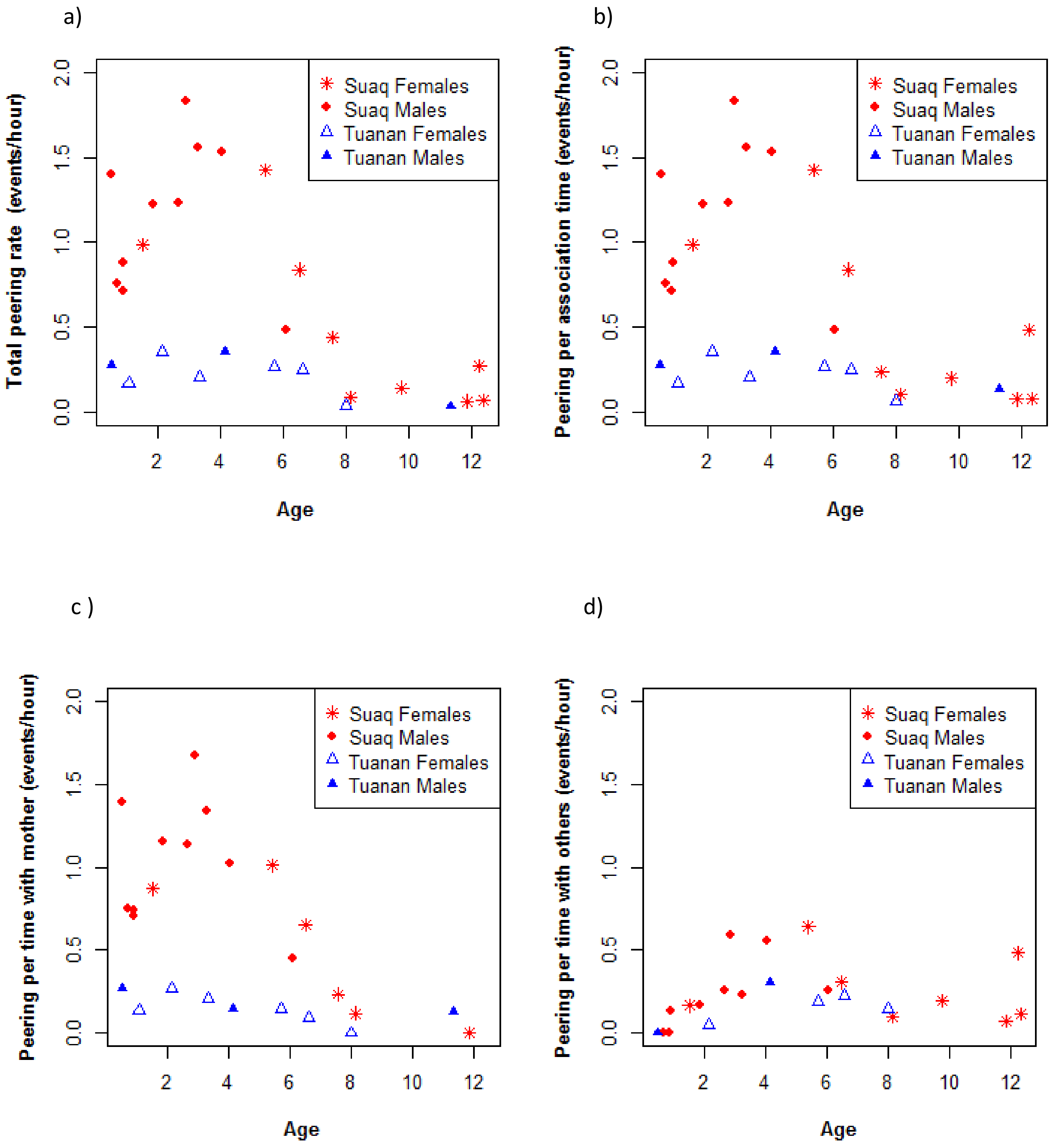

Figure 6.2. Average total peering rates (peering events per hour) versus age in years (a). Peering corrected for total association time (peering events per association hour with at least one adult or immature party member, including the mother) versus age (b). Peering at mother, corrected for time spent with her (peering events at the mother per hour spent with her) versus age (c). Peering at other individuals, corrected for time spent with them (peering events at other individuals than the mother per hour spent with them) versus age (d).

Table 6.3. GLMMs with Peering rate as response variable (total peering events per follow hour (a), total peering events per hour spent in association (b), peering events at the mother per hour spent in association with her (c), peering events at individuals other than the mother per hour spent in association with at least one of them (d)), and age as well as site as fixed effects and individual as random effect.

	Response	Effect	Effect type	Estimate	Std-Error	P-value	N (30)
a)	**Peering events per follow hour**	Age^2	Fixed	-0.01	<0.01	**< 0.001**	-
		Site (Tuanan)	Fixed	-0.68	0.14	**< 0.001**	2
		Individual	Random	-	-	-	19
b)	**Peering events per total association time**	Age^2	Fixed	-0.01	<0.01	**< 0.001**	cont.
		Site (Tuanan)	Fixed	-0.67	0.15	**< 0.001**	2
		Individual	Random	-	-	-	19
c)	**Peering events per time with mother**	Age^2	Fixed	-0.01	< 0.01	**< 0.001**	cont.
		Site (Tuanan)	Fixed	-0.6	0.14	**< 0.001**	2
		Individual	Random	-	-	-	19
d)	**Peering events per time with others**	Age	Fixed	-0.02	0.01	**< 0.001**	cont.
		Sigmoid(Age)	Fixed	1.33	0.38	**< 0.001**	cont.
		Site (Tuanan)	Fixed	-0.12	0.07	0.089	2
		Individual	Random	-	-	-	19

Second, we looked at differences in peering rates of the independent immatures aimed at their mothers in the feeding context. Because food item complexity (number of steps needed to process the food item, “complexity”) and the frequency of the food item in the mother’s diet (in percentage of total diet, “frequency”) had previously been found to be correlated with peering rates (for definitions see [311]), we corrected for these two effects. To correct for the fact that food items are fed on for different amounts of time and therefore the offspring has varying opportunities to peer, peering rates were calculated as the number of peering events recorded for a given food item per unit time the mother was feeding on this item during the observation time. We only included food items that were fed on by the mother for a total of at least 20 minutes during the observation time, to decrease the risk of outliers diluting the results. We included data of 6 infants at each site with a highly comparable age range (at both sites ranging from 0.5-6 y, with an average age of 2.9 and 3.0 y respectively). To reach evenly distributed residuals, the predictor variable “frequency” and the response variable (peering rate) were log transformed. We found, as expected, that dependent immatures peer significantly more frequently with increasing complexity and with decreasing frequency of the food item, but also that, independent of these effects, Suaq infants showed significantly higher peering rates than Tuanan infants (figure 6.3, table 6.4).

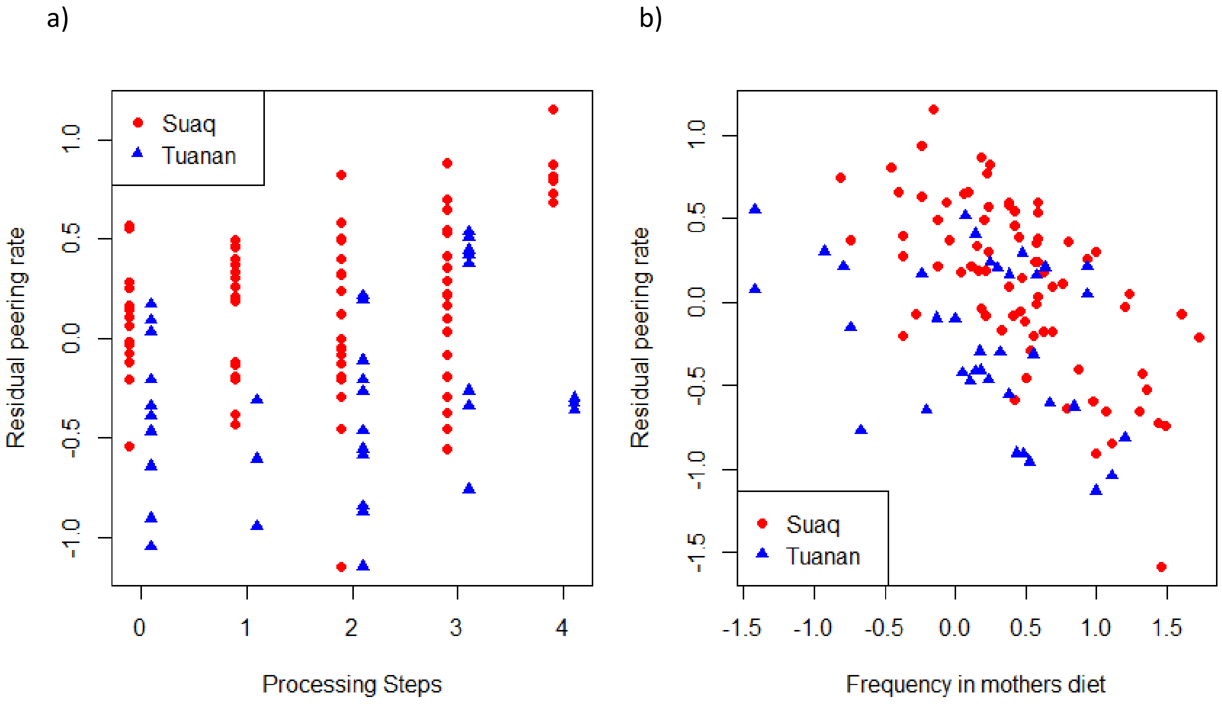

Figure 6.3. Population differences in immatures’ peering rates in relation to food complexity and frequency: Residual peering rates (corrected for frequency) versus complexity (a) and residual peering rates (corrected for complexity) versus frequency in the mothers’ diet (log transformed), b) for dependent immatures peering at their mothers in the feeding context at Suaq and Tuanan. Residuals were used for illustrative purposes only (see Table 4 for statistics).

Table 6.4. GLMMs with Peering rate as response variable (number of peering events per item and time the mother was eating a specific item), processing complexity of the food item ("Complexity"), frequency of the food item in the mothers diet (log transformed; "Frequency") as well as age as fixed effects and individual as random effect: estimates, T statistics, p-values and number of levels for the categorical variables (N). The number in parentheses represents the total number of individual – food item combinations.

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (116)**
Processing steps	Fixed	0.09	0.03	**0.002**	4
Log Freq. in Mothers diet	Fixed	-0.46	0.07	**<0.001**	cont.
Site (Tuanan)	Fixed	-0.46	0.09	**<0.001**	2
Age	Fixed	0.03	0.02	0.237	cont.
Individual	Random	-	-	-	21

<u>Prediction 3:</u> *Individuals at the more sociable population will show higher rates of explorative object manipulation behavior but not necessarily higher rates of non-exploratory object manipulation behavior (e.g. object play). The difference in exploration should be most pronounced in immatures but also be retained in adults.*

Regarding population differences in exploratory tendency in immatures, we found that at both sites rates of explorative object manipulation first increased with age, peaked around the age of 2-3 years and then decreased. By the age of weaning, the rates of these behaviors had dropped to around 0.5 events per hour. Immatures at Suaq showed significantly higher rates of explorative behaviors than immatures at Tuanan (figure 6.4 a, table 6.5 a). To rule out the possibility that this population difference could be caused by an overall higher level of activity of the Suaq immatures, we also looked at rates of object play behavior. The same age trajectory was found as for explorative object manipulation behavior, but the difference between the sites was far less pronounced and did not reach statistical significance (figure 6.4 b, table 6.5 b).

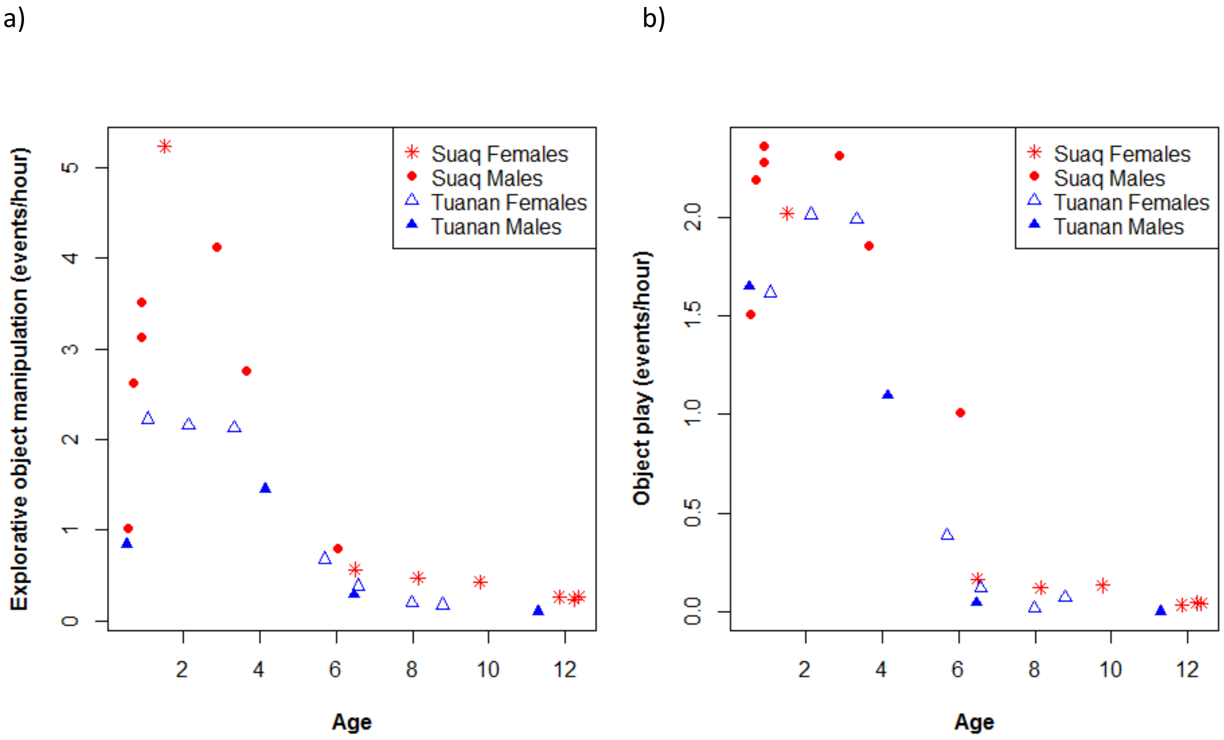

Figure 6.4. Average hourly rates of explorative object manipulation (a) and object play (b) versus age for the immatures of Tuanan and Suaq.

Table 6.5. GLMM with explorative object manipulation (events per hour) as response variable and age as well as population as fixed effects and individual as random effect (a). GLMM with object play behavior (events per hour) as response variable and age as well as population as fixed effects and individual as random effect (b).

	Response	**Effect**	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (29)**
a)	**Explorative object manipulation**	Age	Fixed	-0.28	0.19	0.138	cont.
		Age^2	Fixed	<0.01	0.02	0.89	-
		Population (Tuanan)	Fixed	-0.91	0.4	**0.025**	2
		Individual	Random	-	-	-	22
b)	**Object play**	Age	Fixed	-0.34	0.08	< 0.001	cont.
		Age^2	Fixed	0.01	0.01	0.097	-
		Population (Tuanan)	Fixed	-0.3	0.17	0.087	2
		Individual	Random	-	-	-	22

To assess whether these early differences in exploratory tendency have long lasting effects, we also looked at rates of explorative object manipulation in juveniles and adults. We found that rates of explorative object manipulation were significantly higher in juveniles than in adults and that overall, they were significantly higher in Suaq than in Tuanan (figure 6.5 a+b, table 6.6).

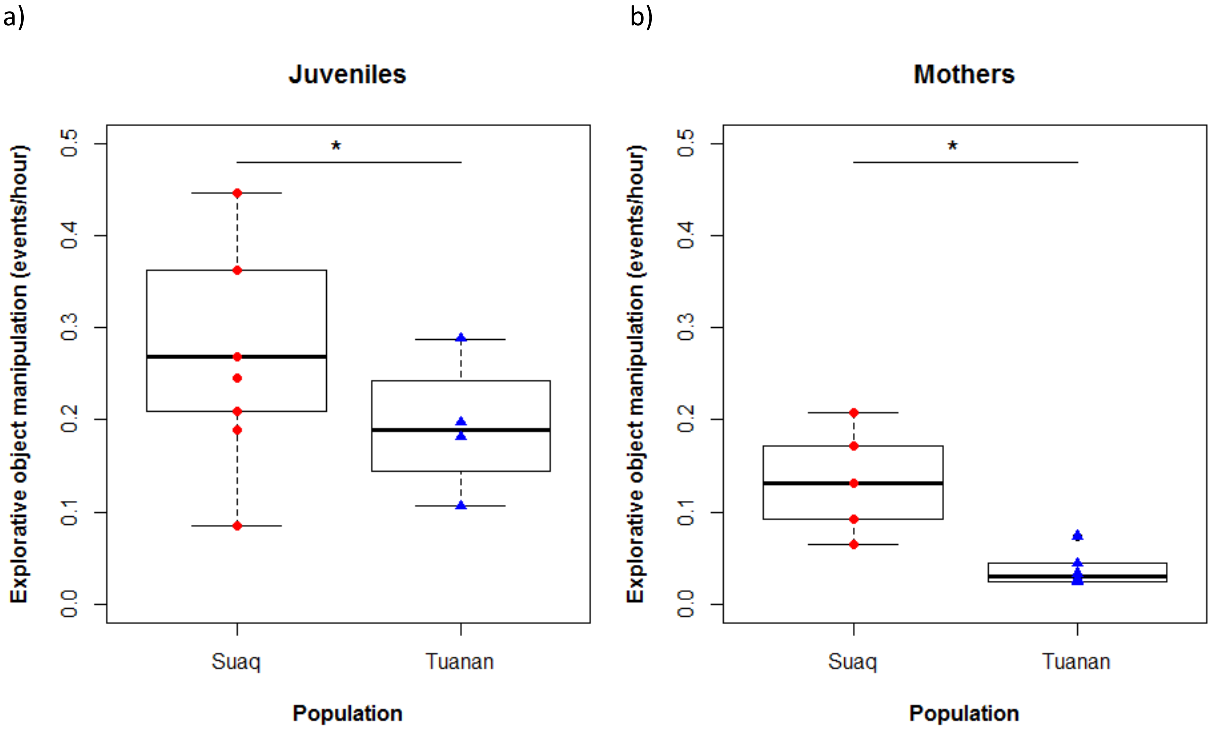

Figure 6.5. Rates of explorative object manipulation (events per observation hour) for juveniles (a) and adults (b) at Suaq versus Tuanan.

Table 6.6. GLMMS with rates of explorative object manipulation (events per hour) as response variable and age class (independent immatures versus adults) as well as population (Tuanan versus Suaq) as fixed effects and individual as random effect. The number in brackets represents the total number of data points.

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (24)**
Class (Juvenile)	Fixed	0.16	0.04	**<0.001**	2
Population (Tuanan)	Fixed	-0.1	0.04	**0.02**	2
Individual	Random	-	-	-	21

Prediction 4: *If assocaitions have direct effects on exploration, exploration rates should increase when being in assocaition. However, under the assumption of developmental effects on explorative behavior, the population difference in exploration should still be evident in the solitary context. Also, within populations, sociability levels of the mothers will correlate with their own exploration rates and the ones of their offspring.*

We found that within associations with individuals other than their own dependent and semi-dependent immatures, both adults and juveniles in both populations showed significantly higher rates of explorative object manipulation than when they were solitary (figure 6.6, table 6.7).

We then tested whether the increased rates of explorative object manipulation at Suaq (see above) merely reflected this immediate result of increased assoctiation frequency rather than developmental differences. We did so by comparing rates of explorative object manipulation of adults of both populations while being solitary. We found that while solitary, adults at Suaq still showed significantly higher exploration rates then Tuanan individuals (Lm: N= 11, B_{site}= -0.07, $Stde_{site}$= 0.02, P_{site}= 0.01, R^2= 0.54), thus confirming a consistent population difference in exploration tendency.

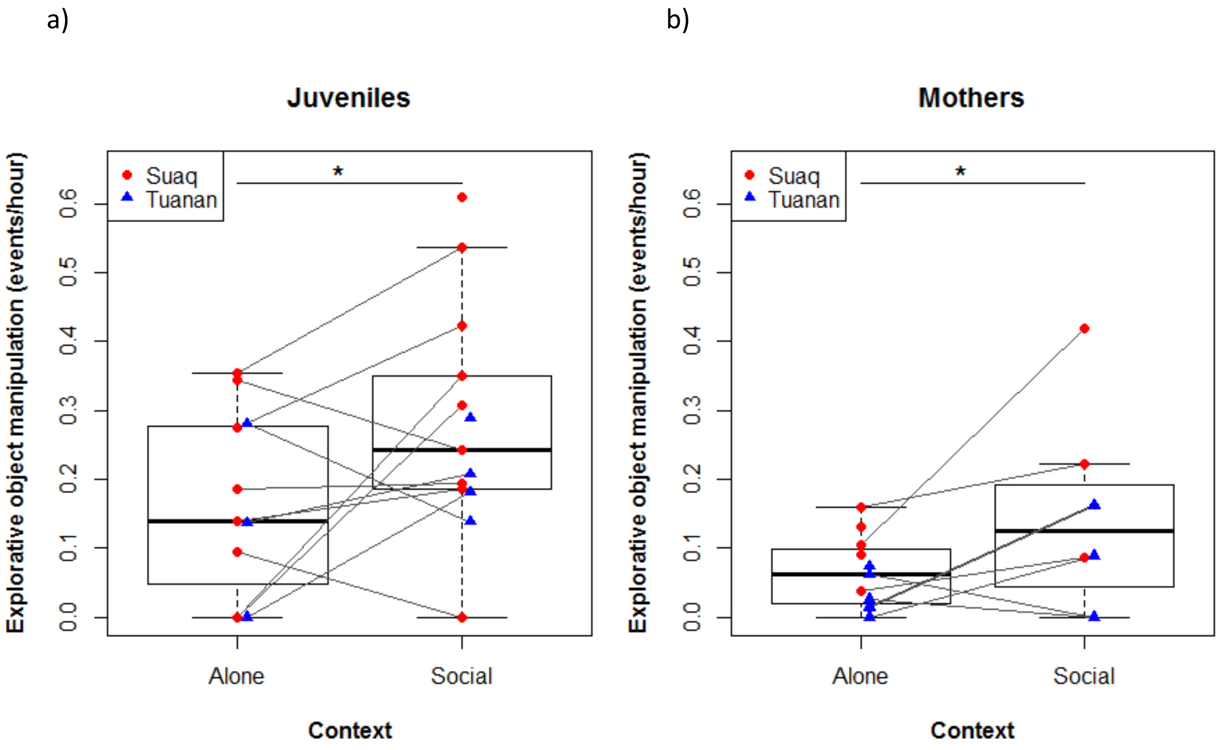

Figure 6.6. Rates of Explorative object manipulation (events per hour) in the solitary context (when being alone or with dependent or semi dependent offspring only, “Alone”) and in the social context (when being with at least

one party member that is not the own dependent of semi dependent offspring, “Social”) for independent immatures at Suaq and Tuanan (a), as well as for adults at Suaq and Tuanan (b).

Table 6.7. GLMMS with rates of explorative object manipulation (events per hour) as response variable and context (alone versus social), age class (juvenile versus adult) and population (Tuanan versus Suaq) as fixed effects and individual as random effect. The number in brackets represents the total number of data points (individual – context combinations).

Effect	**Effect type**	**Estimate**	**Std-Error**	**P-value**	**N (46)**
Context (Alone)	Fixed	-0.1	0.04	**0.003**	2
Class (Juvenile)	Fixed	0.09	0.04	**0.03**	2
Population (Tuanan)	Fixed	-0.09	0.04	**0.03**	2
Individual	Random	-	-	-	21

To assess the extent to which the population differences merely reflected innate differences or also developmental effects, we further tested whether within populations the overall level of sociability of the mother has an effect on her own as well as her offspring’s exploratory tendency. As a measure of overall sociability we took the average number of other adult or independent immature individuals the mother associated per complete follow day (using all the data available of each mother). For the mothers we found a significant correlation between own overall sociability and her total rate of explorative object manipulation (table 6.8a, figure 6.7a). To make sure this effect was not driven by the population differences in both overall sociability and exploratory tendency, we also controlled for these factors by standardizing (z-transforming) the sociability and rates of explorative object manipulation within each population. This yielded a clear trend for a positive correlation between standardized sociability and standardized exploratory tendency (table 6.8b, figure S6.1). More data on a larger number of adult females would be needed to more thoroughly assess such within-population effects.

To assess whether immature exploration rates were affected by those of their mothers, we first calculated residuals from a fitted smoothening function of explorative object manipulation rates versus age for Suaq and Tuanan each (using the smooth spline function of the stats package in R , figure S6.2). We excluded immatures below the age of 7 months since before that age it is unlikely that differences in experienced sociability would affect their behavior, especially since the mothers of young infants in general avoid associations. Whereas we found a positive correlation between the mothers' overall sociability and the offspring's' rates of explorative object manipulation at Suaq, we did not find this correlation at Tuanan (table 6.8 c+d, figure 6.7b).

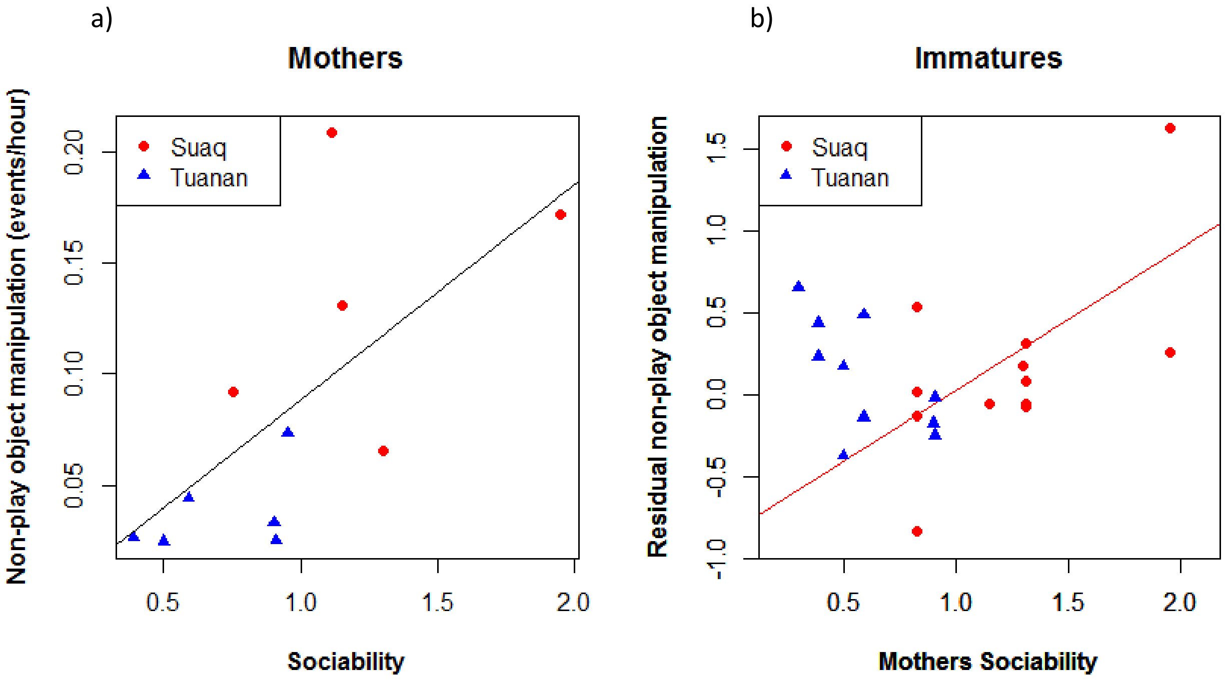

Figure 6.7. Relationship between overall sociability and hourly rate of explorative object manipulation for the mothers at Suaq and Tuanan (a). Relationship between the mother's overall sociability and the age-corrected (residuals of hourly explorative object manipulation versus age) non-play object exploration rate of their immature offspring at Suaq and Tuanan (b).

Table 6.8. Linear models on the correlation of the mothers' rates of explorative object manipulation with their own overall sociability (a), the within-population standardized rates of explorative object manipulation of the mothers and their within-population standardized overall sociability. Also presented are linear models with the residual rates of explorative object manipulation of the immatures as response variable and their mother's overall sociability as well as age as dependent effects for Suaq (c) and Tuanan (d). The residual rates of explorative object manipulation were calculated from a smoothening function of rates of explorative object manipulation over age for Suaq and Tuanan separately.

	Response	Effect	Estimate	Std-Error	P-value	N
a)	**Object manipulation (Mothers)**	Sociability	0.1	0.03	**0.018**	12
b)	**Z (Object manipulation (Mothers))**	Z (Sociability)	0.51	0.27	0.091	12
c)	**Residual Exploration Rate (Immatures at Suaq)**	Mother's Sociability	0.89	0.36	**0.036**	12
		Age	-0.03	0.03	0.392	
d)	**Residual Exploration Rate (Immatures at Tuanan)**	Mother's Sociability	-0.79	0.41	0.094	10
		Age	-0.04	0.03	0.201	

Prediction 5: *Ultimately, higher exploratory tendency will lead to larger repertoires of innovations at the more sociable population.*

To test whether increased exploratory tendencies will result in a higher likelihood of innovations and thus larger repertoires at the level of the population, we compared the number of insect feeding techniques at the two sites. We found that at Suaq individuals habitually use 16 different techniques to feed on insects whereas at Tuanan only 7 techniques occur, which are a near-perfect subset of those found at Suaq. The exception was soaking dead logs in water, which was absent at Suaq, presumably because individuals there spent no time on the ground, reflecting the presence of the tiger (van Schaik 2004). All other techniques are unlikely to be influenced by ecological factors since both the insect types and the relevant substrates occur at both sites. Two techniques were observed on the anecdotal level (observed once or twice by one or two individuals only whereby the technique was performed in a way that did not look proficient) only at one of each of the populations (table 6.9).

Table 6.9. Different techniques to feed on insects (ants, termites, bees and stingless bees): variants, descriptions and occurrence at the study sites. Yes= present at the site, No= never observed at the site, (Yes) = observed on the anecdotal level only (observed once or twice by one or two individuals only whereby the technique was performed in a way that did not look proficient), Ecol= Absent for ecological reasons.

Technique	Variants	Description	Suaq	Tuanan
Bouquet feeding		Picking ants or termites from a fistful of dry or fresh leaves with lips.	Yes	Yes
Dead twig split lick		Splitting hollow twigs lengthwise using teeth and hands and then licking the ants out of them.	Yes	No
Dead twig sucking		Breaking hollow (dead) twigs using mouth and hands, then suck the ants out of the endings.	Yes	(Yes)
Dripping out of nest	a) Hand b) Mouth	Dripping termites or ants out of their nest into the open hand (a) or directly into mouth (b).	(Yes)	Yes
Finger dipping		Catching termites or ants from leaves/ branches by touching the leaves with the fingertips of the stretched hand and letting them crawl onto the fingers.	Yes	Yes
Finger picking		Picking termites or ants off a surface (tree trunk or branches) using the thumb against the side of the index finger.	Yes	No
Fist fishing	a) Side of fist b) Front of fist	Wiping termites or ants with the fist off a surface (tree trunk or branches) using either the side of the fist (along pinkie finger, a) or front of the fist (along curled fingers, b). Then licking the insects off the hand/ wrist.	Yes	No
Fist smashing	a) Front of fist b) Bottom of fist c) Back of wrist	Smashing bees or stingless bees against a surface with the front or the side of the fist or the back of the wrist.	Yes	No
Hollow fist leaf strip		Drawing leaves through the partly closed hand to obtain termites or ants that are on the foliage.	Yes	No

Licking		Licking termites or ants off a surface (tree trunk, branches) with protruded under lip.	Yes	Yes
Lip picking		Picking termites or ants off a surface (tree trunk, branches, leaves, old nest material) with lips (between upper and under lip).	Yes	Yes
Mouth foliage strip		Drawing leaves through the mouth to obtain termites or ants that are on the foliage.	Yes	No
Nest destruction		Rummaging through old orangutan nests for termites or ants, taking the nest apart while doing so.	Yes	
Smashing flying insects into fur		Catching bees or stingless bees by smashing them against own fur (mostly upper arm).	Yes	No
Snatching flying insects in the air	a) Full circle snatch b) Quick snatch	Catching bees or stingless bees in the air by snatching them with hand.	Yes	No
Soaking log in water		Soaking a piece of dead wood into the water of a stream or puddle to get the termites hidden inside to emerge to the surface of the wood.	Ecol	Yes
Sucking out of dead wood	a) Sucking b) Chewing	Eating termites or ants out of dead wood (log or dead tree trunk) by biting or breaking open dead wood, then sucking them out (a) or passing (chewing) pieces of dead wood through the mouth (b).	Yes	Yes
Tool use	Several different variants	Obtaining insects or their products by using tools: mainly inserting processed sticks into tree holes and insect nests.	Yes	No
Total number of techniques			**16 (17)**	**7 (8)**

Discussion

To investigate the effects of sociability on current learning ability, we related population differences in opportunities for social learning to exploratory tendency in adults and immatures of orangutans. First, we found that immatures in the more sociable population (Suaq, Sumatra) did indeed make use of their increased opportunities for social learning by showing significantly higher rates of peering than same-aged individuals at the less sociable population at Tuanan (Borneo). However, this difference in peering rates was not simply a result of greater opportunity: it remained after controlling for differences in opportunities to peer, as Suaq individuals watched their mothers as well as other individuals more frequently per time spent with them than Tuanan individuals did. Second, we found that immatures as well as adults at Suaq show significantly higher rates of exploratory behavior compared to Tuanan individuals. Among immatures, the population difference in exploratory behavior was much bigger than the insignificant difference observed in object play, implying that the difference in exploratory behavior cannot be explained by a generally increased activity level at the more sociable population.

With respect to the mechanism underlying these differences, we found that rates of exploratory behavior were higher when individuals were in association with others than when alone, which implies direct effects of associations on exploration. Experimental studies of effects of the presence of conspecifics on exploration in several mammal and bird species have produced mixed results: some have found negative effects of associations, ascribing them to socially induced neophobia or the possibility that social interactions simply lead to a decrease of the amount of time that can be devoted to other activities [403-406]. Others have found positive effects of conspecifics' presence on exploration, mainly expressed in reduced neophobia. These studies proposed reduced stress under the social condition or social facilitation effects respectively as underlying mechanisms[407-409] (see also: Forss et al. in preparation). Positive effects of associations on exploration rates might also be the result of a vigilance effect where shared vigilance among association partners reduces the overall cognitive load and thus allows for devoting more attention to exploration [410, 411]. Our finding that orangutan mothers' exploration rates only increased when being in association with individuals other than their own dependent or semi-dependent offspring is in line with a vigilance effect: since young immature individuals are unlikely to contribute to shared vigilance, being in with dependent offspring does not lead to reduced vigilance demands on the mother.

Exploration rates of our study animals significantly dropped during juvenility, reaching values of less than one event per day by the onset of adulthood. A study on neophobia showed that wild orangutans are in general very reluctant to approach or touch novel objects [105]. The only exceptions were contexts in which the focal animals had first observed a familiar researcher interacting with the objects, after which they then went to examine the same objects themselves. However, in captivity, exploration levels are highly increased: all great apes in captive settings show a near absence of neophobia, as well as very high innovation tendencies [105, 412]. This well-known captivity effect has been hypothesized to be the result of social facilitation by following social cues provided by human care takers or a reduction of the cognitive load including a reduced need to be vigilant [368, 413]. Ancestral humans are at the very other end of the great ape spectrum of exploratory tendency: whereas for a long time, the rate of change in human technology was remarkably slow, during the upper Paleolithic Revolution, the number and complexity of the artefacts as products of innovations drastically increased [414, 415]. Since then and up to date, the rate of technological change has remained at an incredibly high level. In a recent study it has been proposed that similarly to the captivity effect, the evolution of human innovativeness can be attributed to a reduction in the cognitive load as a result of becoming a top carnivore and thus a reduced need to be vigilant [66].

On top of direct effects of associations on exploration rates, our results also indicated long lasting developmental effects of experienced sociability on exploratory tendency. First, when comparing the two populations, the differences in hourly rates of exploratory behavior remained when controlling for differences in association time: even when solitary, juveniles and mothers at Suaq showed higher rates of exploration compared with the same age classes at Tuanan. Because this result could also reflect possible intrinsic differences in exploratory tendency between the populations, we also examined patterns within populations. Within Suaq, the mother’s level of sociability is correlated with her own exploratory tendency as well as that of her offspring, which clearly speaks for developmental effects (while not excluding innate differences as well). Thus, just as in humans, in orangutans early differences in the frequency of social inputs have an effect of cognitive development: even within a given population, the mother’s level of sociability predicts the exploratory tendency of her offspring, suggesting that in orangutans, subtle differences in quality and frequency of social interactions have significant effects on cognitive development. In line with these finding, rehabilitated great apes, after their release were found to produce various innovations that have never been seen in the wild [416], suggesting that increased social inputs during their time with humans had long lasting consequences.

Our sample size allowed only for testing the effects of the mothers sociability level on the offspring's exploratory tendency to a limited degree: for each of the immatures we only had 1-3 data points on exploratory tendency during immaturity available. It would be interesting to see if these developmental effects within populations also last into adulthood. However, to evaluate this, more long-term data on experienced sociability and cognitive performance is needed. Long-term data would also allow to test at what stage of development the experienced sociability has the greatest effect on later exploratory tendency. It is possible that there is a specific developmental window (i.e. critical or sensitive periods [417]) during which the experienced social inputs decisively affect later performance. Critical or sensitive periods for the development of a variety of socially induced behaviors have been described for a long time in a variety of animal species [418-420]. In humans, there is also evidence for critical periods of cognitive development: the quality of social interaction during early childhood seems to have the most severe effect on later cognitive development, supposedly because during that time cognitive associations develop [401, 421, 422].

Increased levels of exploratory tendency imply higher innovation frequencies, which should ultimately lead to a larger skill pool at the Suaq population, given that those innovations are successfully transmitted. Also, increased rates of social learning at Suaq (as suggested by the increased peering rates) should lead to a faster accumulation of more complex skills in this population [32]. Accordingly, in chapter 4 we found that diet repertoires at Suaq were significantly more complex than the ones at Tuanan. Also, the most complex skills such as tool use can only be found at Suaq but not at Tuanan[86]. In the current study we found further evidence that the repertoire of learned skills is broader at Suaq than Tuanan: we found that Suaq individuals show a bigger repertoire of different techniques of insect feeding than Tuanan individuals.

Although it proves hard to fully exclude ecological differences between two sites as underlying causes for differences in behavioral repertoires, in the specific case of insect feeding it is unlikely that the observed population difference is caused by ecological differences. Both sites show very similar insects with no notable difference in abundances. However, since it has been shown that environmental opportunity drives innovation [423], to fully exclude ecological effects, one will have to quantify the insect abundances between the sites. Most techniques that are absent at Tuanan could well be used there too (e.g. catching flying insects in the air or fist fishing them off branches, see table S2). Also, there is no difference in the opportunities for the use of the most complex insect feeding technique, namely tool use: tree hole abundance and occupancy largely coincide between the two sites (Schuppli unpublished data).

The higher dietary complexity and broader skill sets might be the reason behind the increased peering rates at Suaq: where there is more need to learn, learning will naturally occur more frequently. On the one hand, this might work directly, in that a higher occurrence of more complex technique directly triggers higher watching rates. On the other hand, it is plausible that larger and more complex skill sets caused the evolution of an innately increased social interest: in a population where there is more to learn, increased attention to conspecific will pay off more because the probability of learning a novel behavior or technique is higher. To disentangle these two possibilities, we compared peering rates between the two populations controlling for item frequency and complexity, as in chapter 5, those two factors had been shown to affect peering rates. Our results indicate that even when controlling for complexity and frequency of the food items, immatures at Suaq show significantly higher peering rates. This suggests an intrinsic predisposition of the Suaq immatures to be more attentive to their conspecifics' actions but doesn't rule out early developmental effects where an exposure to more and more complex skills make infants keener to learn and thus explore. However, a recent study showed that Sumatran orangutans in the zoo, despite very similar housing conditions, show showed superior innate problem-solving skills to Borneans, and also differences in exploration style, suggesting at least a some intrinsic species differences. Increased social learning at a more sociable population may then lead to a higher exploratory tendency through an experience effect, and thus also higher innovation frequencies inclusive of a higher probability of innovations being transmitted. Ultimately, this will then cause an expansion of the population skill pool, further increasing the payoff of increased social interest, turning the whole cascade into a positive feedback loop.

To sum up, we found evidence for effects of sociability and opportunities for social learning in orangutans on two levels. First, associations lead to a direct proximate increase of exploration rates. Second, both within and between populations, increased sociability levels during infancy positively affect exploratory tendencies. Third, the between-population effects were shown to last into adulthood. We found that ultimately, this leads to higher innovation frequencies and thus larger and more complex population skill pools in more sociable populations. Our findings suggest that growing up with increased opportunities for social learning from a larger number of role models triggers a cascade, from increased levels of social learning, through increased levels of practice to an increase in exploratory tendency. The more sociable population will ultimately also have a larger skill pool, due to both an increased rate of social transmission and presumably a higher per capita rate of innovation.

Supplementary Material

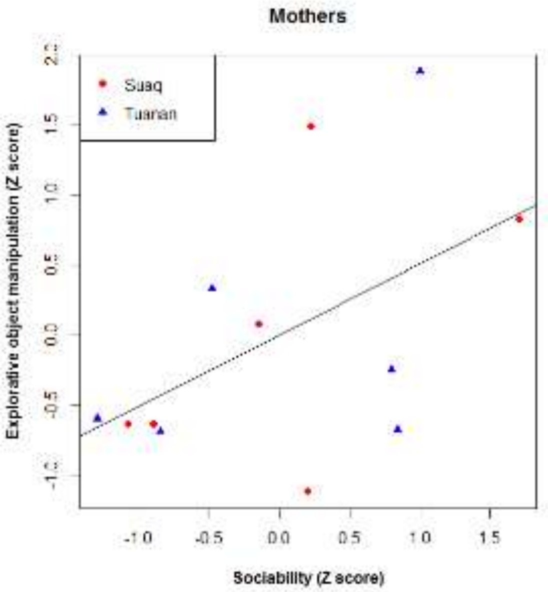

Figure S6.1. Overall sociability (z transformed within each population) versus hourly rates of explorative object manipulation (z transformed within each population) of the mothers at Suaq and Tuanan.

a)

b)

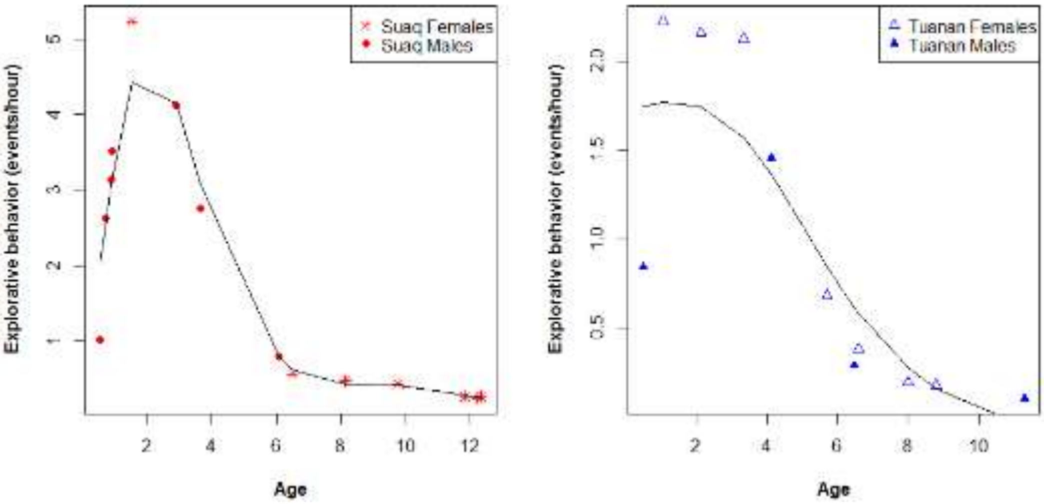

Figure S6.2. Exploration rates (events per hour) versus age for the immatures at Suaq (a) and Tuanan (b) with a fitted smoothing function (using the smooth spline function of the stats package in R).

Chapter 7: General Discussion

Part 1: Skill acquisition, niche complexity and the evolution of cognition

The aim of the first part of this dissertation was to investigate (i) which factors allow species to acquire skills over extended periods of time, (ii) if the same factors ultimately allow them to evolve into complex niches, and (iii) how this is connected to brain size.

The results of chapter 2 showed that most mammals reach adult like competence in their foraging skills well before the age at first reproduction, in contrast to most bird species, which reach foraging competence only around the age at first reproduction. Within mammals we found that two life-history parameters are consistently correlated with later attainment of skill competence: slow conservative development and food provisioning of offspring over extended periods of time. Also, in species with intense sharing of resources (such as cooperative hunters) competence in foraging skills may reach peak values only after the start of reproduction. Furthermore, we found that with increasing niche complexity, the age of adult-level skill competence edges ever closer to the age at first reproduction. The results of chapter 3 complemented the first set of findings and showed that the same two life-history parameters that are associated with later skill competence are also correlated with complex niches: species living in complex niches either develop slowly or continue to provision their young after weaning.

Both chapters can be consolidated into a *niche complexity/ life history framework* whereby provisioning and slow development make possible the acquisition of extensive skill repertoires by either providing immatures with an energetic buffer or by extending the learning period (which usually go hand in hand with reduced efficiency). Longer learning periods allow for the acquisition of a bigger number and more complex skills. A broader skill repertoire then enables species to exploit more complex niches, which provide access to more nutrient-rich and seasonally stable food sources. The new energy sources gained this way can be used for brain size increase, which is positively correlated with skill levels, further boosting this cycle (figure 7.1). However, only in primates was the cognitive dimension of niche complexity correlated with brain size. Thus, the *niche complexity/ life history framework* developed here shows that ecological conditions shape a species' life history in a certain direction, which then leads to a better ecological performance and exploitation of new niches and in some cases larger brains. The exact causality or even the commencement of this feedback loop will be very hard to disentangle. All in all, the most plausible interpretation is that life history, brain size and niche complexity coevolve.

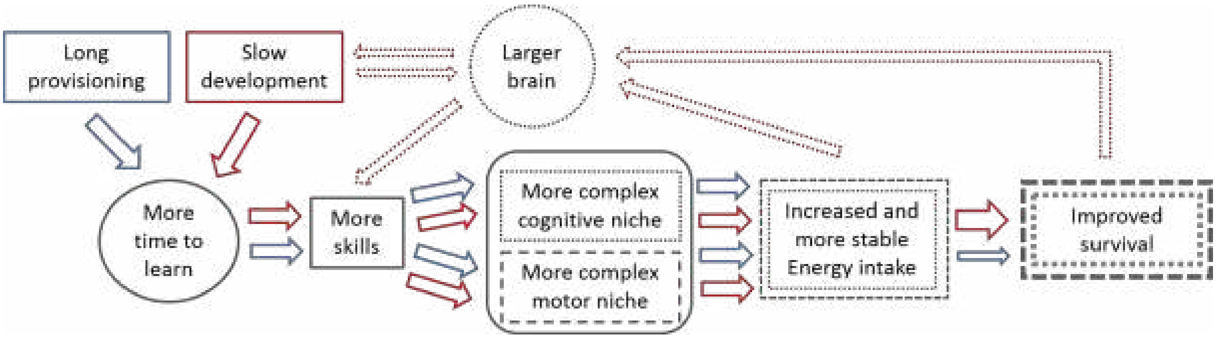

Figure 7.1. The niche complexity life history framework. Red represents the common primate- and blue the carnivore pathway.

Interestingly, different taxa seem to consistently follow distinct pathways on how to evolve into complex niches, with only a few exceptions choosing the other path. The general mammal pattern is to slow down the entire development, which leads to a relative increase in the developmental period and extended time for skill acquisition before weaning. Primates exemplify the classic mammal pathway, with a slow conservative development being consistently correlated with complex niches. However, in certain mammal taxa, some forms of post-weaning provisioning could nonetheless evolve: in carnivores, several species show post-weaning provisioning whereby the relative length of it is correlated with niche complexity. Similarly, only in primates but not in carnivores, complex knowledge niches are correlated with brain size. Thus, complex niches do not necessarily depend on larger brains but can also be reached by sufficient availability of time to learn and practice skills. Since brain growth is dependent on high and constant energy flow to the brain and physical growth is only completed after brains are fully developed, large brains go inevitably hand in hand with slow development. Our results indicate that in carnivores it might be difficult to slow down development even though it would be favorable for cognitive evolution. This suggests that in carnivores, the improvement in adult survival is insufficient, most likely caused by unavoidable mortality (e.g. diseases acquired from kills). Both examples are likely cases of constrained evolution where a species' preexisting life history characteristics make evolution in a certain direction less likely or even impossible [198, 199].

Even though in most primate species provisioning ends at weaning, certain species adopted post-weaning provisioning in the form of cooperative breeding. Cooperative breeding in primates includes provisioning of the infants by alloparents but often also extensive food sharing of adults with weaned immatures [424]. Cooperatively breeding primate species mainly show enhanced cognitive abilities in the socio-cognitive context but not always a higher cognitive performance in the ecological domain [425] relative to other species with similar brain size. In general, a species' ecological niche determines how well it can respond to selection pressures on enhanced cognition with an actual increase in brain size: being small bodied, most cooperatively breeding species have a high external mortality and thus enhanced cognition would not lead to an increased survival and thus lifetime fitness [426]. However, in our hominin ancestors, large body size and the availability of effective weapons supported the evolution of enhanced general cognition. Also, when our ancestor adopted cooperative breeding, an ape-like level of cognition was already in place. The extreme case of human cognitive evolution shows that adding extensive provisioning to an already sophisticated cognitive system, combined with a reduced extrinsic mortality, can lead to a whole cascade of events resulting in the emergence of unique levels of cognition [425, 427].

Humans combine all factors of our *niche complexity/ life history framework*: From our great ape ancestor we have inherited a slow conservative development, on top of which systematic provisioning of immatures and adults was added [26]. First of all, extensive provisioning allowed our ancestors to expand the period during which skills could be acquired and to systematically rely on skills for which peak performance is only reached well after the onset of reproduction. Second, these more complex skills gave access to a variety of new resources: human foragers have broad diets composed of food items that require detailed knowledge and intensive processing, including tool use and cooperative hunting [25]. Thus, around 2.5 my years ago, 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. Also, big-game hunting coincides with enhanced technology and thus most likely further favored the evolution of prolonged periods of provisioning and food sharing among group members in general. In sum, our findings strongly suggests that during human evolution an increased time span to acquire skills, which had been made possible through carnivore-like systematic provisioning, was added to a great ape level of cognition and a great ape-like life history which ultimately allowed for the evolution into a niche of unmatched complexity.

Outlook Part 1: Ecological- versus social challenges as main drivers of bran size evolution

All in all, our results also provide strong support for the importance of ecological factors in the evolution of life history and brain size. We do not rule out the effects of social factors and it is even very likely that some of the remaining variance in our data can be explained by social variables. Social challenges proposed as drivers of brain size evolution range from the size and complexity of the social group [5, 6, 428] to specific elements of group living, such as social bonds (Dunbar and Schultz 2007). A plausible scenario would be one of correlated evolution of life history, brain size, ecological- and social challenges. However, since larger brains are extremely costly, they necessitate a higher net energy intake – a fact that has been neglected by theories focusing on social drivers of brain size evolution.

Complex niches provide species access to an increased and more stable energy intake, which supported an increase in brain size. If we can a assume a form of general intelligence as opposed to a completely modular mind [2, 429, 430], it is plausible that increased cognitive abilities will not only be used in the domain they originally evolved for but also in other areas. Thus, if ecological challenges originally drove brain size evolution, the cognitive abilities thus gained could then have been applied in the social domain and led to an increase in social complexity in some species. Once a certain level of social complexity is reached, it is unlikely that the underlying capacities will be lost again, even in the absence of direct selection pressures: individuals with enhanced social skills will always have advantages over conspecifics because they will be able to reach a higher rank or maintain social bonds better[431]. As a next step, in order to disentangle the effects of ecological and social pressures on brain size evolution one would have to use a comparative approach across different lineages and look at the effects of different social and ecological variables simultaneously (Graber et al. submitted).

Part 2: Social learning and the evolution of cognition

The aim of the second part of this dissertation was to test the predictions of the cultural intelligence hypothesis. The cultural intelligence hypothesis states that on the developmental level, opportunities for social learning positively impact the number of skills an individual will have acquired as an adult as well as the current learning ability. On the evolutionary level, the cultural intelligence hypothesis states that species with more opportunities for social learning will evolve a better innate learning ability [32, 66]. To test these predictions, two populations of wild orangutans that differ in their level of sociability and thus the opportunities for social learning: a highly sociable population of Sumatran orangutans at Suaq Balimbing to a less sociable population of Bornean orangutans at Tuanan.

Testing the preconditions of the cultural intelligence hypothesis

The first precondition for being able to test the cultural intelligence hypothesis is that the study system must show skills that are acquired through learning rather than genetically fixed. To test this precondition, in chapter 4 we looked at developmental trajectories of foraging skills in immatures at both populations. We distinguished between (i) food detection competence, assessed through diet repertoires, (ii) food processing competence, evaluated by measuring feeding rates, and (iii) food locating competence, assessed by the directness of their travel routes. We found ample evidence that orangutan foraging skills are learned rather than intrinsic: first, it takes immatures more than ten years to reach adult like feeding rates and diet repertoire size. Second, more complex skills are reached later in development than simpler ones, with the most complex skills, such as tool use, reached the latest. However, the vast majority of all subsistence skills are in place well before the age of first reproduction, which makes it unlikely that skill acquisition is limiting on orangutan development.

The results of chapter 4 are in line with the findings of the first part of this thesis. Orangutans live in a complex foraging niche and on top of that are dependent on their own knowledge and skills as soon as they reach juvenility. Accordingly, most of their foraging skills are in place around the age of weaning or shortly thereafter and they thus cannot be a limiting factors on age at first reproduction. For the development of large brains, energy shortages during periods of learning would be devastating. Accordingly, as predicted by our *niche complexity/ life history framework*, orangutans develop very slowly: after weaning immature orangutans take another 6-7 years before they start reproducing and adult body size is only reached around the age at first reproduction. Thus, like most other primates, orangutans chose the pathway of slow and conservative development to be able to reach a higher skill complexity and ultimately evolve into a complex foraging niche. They indeed exemplify the most extreme case of the primate pathway of slow development: they show the latest age at first reproduction of all non-human and the latest age of weaning of all primate species. Their late weaning age is most likely explained by the time needed to acquire sufficient competence in complex foraging skills they need to master to successfully compete in the adult niche. The difference in weaning age between the two populations coincides with a difference in the overall complexity of the diet, which is further in line with this argument.

The second precondition of the CIH is that at least to some extent, skills must be socially learned as opposed to individually learned. To test this, in chapter 5 we looked at indicators of social- and independent learning during immature skill acquisition. As an indicator for social learning we used peering (attentive close range watching of a conspecifics' actions) and for independent learning different types of explorative behavior. Our results were in line with all predictions under the assumption of social learning through peering: peering was most frequent in skill intense contexts where learning is likely, namely feeding and nest building. In the feeding context, peering rates increased with increasing rarity and complexity of the food item. We also found that peering in the feeding and nest-building context was followed by increased exploration of the same items using the same techniques as the demonstrator. This suggests that selective practice of an observed behavior is an important element in the orangutan skill acquisition process. We also found that whereas young infants show almost exclusive interest in their mothers, with increasing age, the interest in role models other than the mother increases. These other role models were mainly males but also juvenile animals and other mothers. Thus, young orangutans seem to acquire their foraging and nest-building skills through social learning and socially induced practice. Their role models are the mother as well as other adult and juvenile conspecifics.

In sum, the results of chapter 4 and 5 showed that immature orangutans take several years to learn their complex foraging skills. They acquire their foraging and nest-building skills through social learning combined with socially induced practice. As role models they use their mothers but also other individuals. Thus, orangutans fulfill all the necessary preconditions to test the predictions of CIH. Due to the substantial difference in sociability levels between the populations, immatures are to varying degrees exposed to those role models other than the mother. This makes orangutans the ideal species to test the predictions on the effects of varying opportunities for social learning on skill acquisition.

Testing the predictions of the cultural intelligence hypothesis

When testing the actual predictions of the CIH We found that immatures as well as adults at the more sociable population at Suaq show higher rates of independent exploration than their peers at the less sociable population at Tuanan. While searching for the underlying mechanisms, we found on the one hand that associations have direct positive effects on exploration rates. This finding is somewhat counter-intuitive because one could think that when being in associations, individuals might be busy with social interactions and thus too distracted to explore. So far, the studies that have looked for effects of associations on exploration have produced mixed results [406, 408, 409, 432]. Positive effects of associations on exploration rates could be explained by a vigilance effect, where shared vigilance among association partners reduces the overall cognitive load and allows for increased exploration rates. To our knowledge, this is the first study to show that exploration in the wild is socially facilitated. This factor may have played an important role in the evolution of the high innovation tendency in humans [66]. More studies on a greater range of taxa would be needed to draw better-founded conclusions.

On the other hand, we also found two lines of evidence suggesting long-lasting developmental effects of increased levels of sociability on exploration. First, we found that individuals at Suaq are more exploratory even if direct effects of the higher association times are accounted for. This finding is in line with developmental effects of higher sociability levels on exploration rates but also with intrinsic differences in exploratory tendency. Second, we found that within a population, the mother's level of sociability is correlated with her own exploratory tendency as well as with her offspring's. The effect on the offspring's exploratory tendency was even stronger when taking the mother's sociability level during the time of the offspring's infancy as a predictor variable as opposed to her overall sociability level. Our sample size allowed only for testing the effects of the mother's sociability level on the offspring's exploratory tendency during its immaturity: for each offspring we only had 1-3 data points on exploratory tendency during infancy and juvenility available. It would be interesting to see if these effects also last into adulthood, and also what stage of development the experienced sociability has the greatest effect on the exploratory tendency once independent. It is possible that there are specific developmental windows during which the experienced exposure has the most determining effect on later life. To test these questions, more long-term data is needed.

We also found that immatures at the more sociable population at Suaq peer more frequently than the same-aged immatures at Tuanan. This is in line with a higher dietary complexity at Suaq. However, higher dietary complexity cannot explain the big difference in peering rates, especially not the one in the nest-building context, where skill complexity is very similar. It therefore seems as if Suaq individuals show a higher intrinsic motivation to peer than those at Tuanan. In the second orangutan study conducted for this thesis (chapter 5), we showed that peering directly leads to practice by increased exploration rates with the same food item for peering in the feeding context or nest practice for peering in the nest-building context. In sum, a higher level of sociability leads to higher exploration rates at Suaq and thus indirectly presumably to an increased innovation probability. Especially in combination with the greater probability of social transmission and thus retention in the more sociable population, this will lead to more diverse and more complex repertoires. Those will then again be harder to learn and increase the pay-off of an enhanced motivation to peer. It thus seems as if higher levels of sociability trigger a social learning cascade, where a higher attentiveness to conspecifics' activities leads to an increased exploratory tendency and ultimately a higher probability of innovation to occur and then spread in a population (figure 7.2).

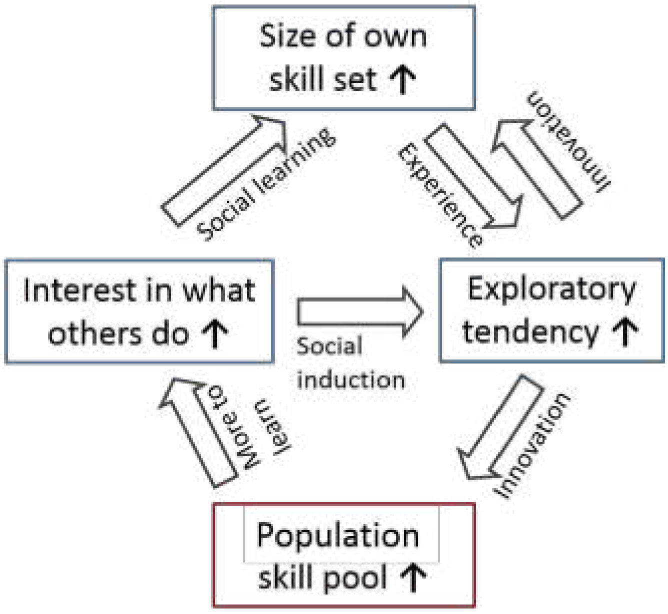

Figure 7.2. The social learning cascade: an increased interest in what others do leads to increased social as well as independent learning which ultimately leads to a higher probability of innovations to be made, spread and maintained in a population. With each loop of this circle the pay-off of an increased motivation to peer increases.

To sum up, the results of chapter 6 provided first evidence for direct effects of associations on exploration rates as well as strong support for long lasting developmental effects of increased opportunities for social learning on exploratory tendency. The latter is in line with the developmental prediction of the CIH. However, what we cannot disentangle at this point is whether the observed differences are all on the developmental level or whether there is concurrently an intrinsic species difference in exploratory tendency between the two populations.

Outlook Part 2: The next steps in testing the cultural intelligence hypothesis

Although our results support the developmental prediction of the CIH, further work is needed to gain more conclusive insight. The next steps are (i) experimental field studies to strengthen this conclusion, (ii) to test the evolutionary predictions of the framework and (iii) comparative studies across species.

One critical weakness of our approach was that we equated the exploratory tendency with current learning ability. Experimental testing would provide more accurate measures of the cognitive performance and allow us to distinguish between different domains of cognition as well as to show to what extent cognitive performance across different domains can be explained by one factor (i.e. general intelligence). During the course of this dissertation, such field experiments have been successfully piloted at the Suaq study population and will be continued in future. The experiments are based on a test battery on cognitive performance conducted with captive orangutans in zoos and rehabilitation stations as part of two simultaneous dissertations [433, 434]. It will be highly insightful to directly compare the performance of wild individuals to that of captive individuals (figure 7.3). Under the developmental prediction of the CIH, animals with the lowest level of enculturation (i.e. the wild ones) will show the lowest cognitive performance, whereas with increasing level of enculturation, the performance will increase. Under the evolutionary predictions of the CIH there will be a consistent difference between the two species on all levels of enculturation. However, depending on the strength of the developmental effects and their potential to dilute intrinsic differences, this difference might decrease with increasing level of enculturation.

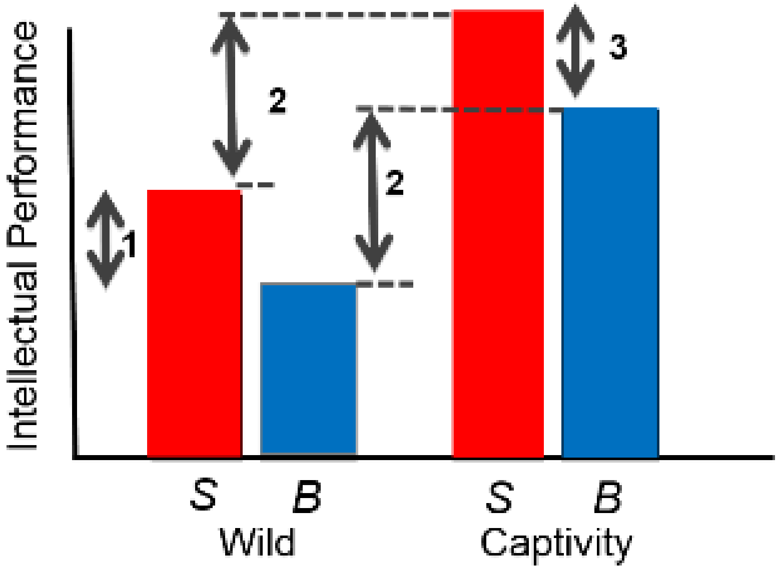

Figure 7.3. Predictions of the cultural intelligence hypothesis (CIH): If difference 1 is larger than difference 3, the developmental version of the CIH is confirmed. If difference 2 is bigger than zero, there is a captivity effect, which is also highly in line with the developmental version of the CIH. If difference 3 is bigger than zero, the evolutionary version of the CIH is confirmed. Comparing difference 1 and 3, will elucidate how well developmental effects can dilute intrinsic differences.

Another step that has not yet been included in this dissertation is to test the evolutionary prediction of the CIH, namely that increased opportunities for social learning also lead to an increase of a species' innate learning ability. To most accurately test for intrinsic differences between the two study populations one would have to do cross-fostering experiments by switching newborn infants between populations at birth. If there are intrinsic differences, the infants will show levels of exploratory tendencies according to their genetic background rather than their foster population. However, such experiments cannot be justified from an ethical point of view. The other, more realistic option is to compare cognitive performance of Sumatran and Bornean orangutans in the captive setting. This was successfully done by two fellow PhD candidates who ran an elaborate test battery on a variety of measures of cognitive performance orangutans kept in rehabilitation centers and zoos respectively. The results produced in captivity demonstrated that rearing and housing conditions have the an effect on cognitive performance in terms of attention structure, exploration style, and curiosity, which is in line with the developmental predictions of the CIH [435, 436]. The results obtained from zoos showed an overall higher cognitive performance of Sumatran orangutans compared to Bornean's suggesting that the difference in sociability levels between the two species has led to intrinsic differences in their cognitive performance, supporting the evolutionary prediction of the CIH [437].

To further evaluate the CIH and draw more solid conclusions, one would have to test its predictions across a broader range of species. One possibility would be to test correlations between different measures for opportunities for social learning (e.g. length of the mother offspring association) with a species' cognitive performance in a standardized test battery using a comparative approach.

General conclusion

By investigating the developmental link between cognitive ability and skills, the results of this dissertation have provided important insight into the evolution of cognitive abilities: first, across species we could show that life history, skill acquisition time and niche complexity are all tightly linked. Only if a species can either slow down its life history or adopt extensive post-weaning provisioning can it eventually evolve into a complex foraging niche. In primates, complex foraging niches are correlated with enhanced cognition, which suggests that their slow life history pathway allows for the evolution into complex foraging niches through increased behavioral flexibility. No species is born intelligent. It only has the potential to be so, but acquiring the skills and realize its potential learning ability takes time.

Second, by comparing two orangutan populations with varying levels of sociability, we found convincing evidence that increased opportunities for social learning lead to larger skill sets and an increased current learning ability, as predicted by the CIH. The two findings of the two parts of this thesis are complementary and add up to a more detailed picture of cognitive evolution: both of the life-history pathways described above, in combination with extended skill acquisition periods and higher niche complexity, are likely to provide immatures with increased opportunities for social learning or at least a form of supported- or protected learning [438]: a slower development implies a longer infancy with intense contact to the mother and in most primate species also to other group members. Extended periods of provisioning automatically go hand in hand with ample opportunities for social learning [102]. Thus, whereas we first showed that ecological niche of a species must fulfill certain preconditions to allow for expanded skill acquisition, social learning might be an important mechanism for how those skills are actually acquired.

The findings of both parts of the dissertation provided novel insights into the extreme case of human cognitive evolution. First, humans show two life-history features that allow for extended periods of skill acquisition and the evolution into complex foraging niches: both slow development and long-term provisioning. Also, for skill acquisition, humans rely heavily on high fidelity forms of social learning and teaching. When our hominin ancestors changed their social system from a great ape level of sociability to cooperative breeding, extensive allomaternal care was added on top of an already rather sophisticated great ape level of cognition. The change in social system implied a major increase in opportunities for social learning, which promoted the development of enhanced cognitive abilities leading to larger skill pools and thus increased ecological performance of the species as such (figure 4). Archeological evidence is in line with this theory: around the time that cooperative breeding was likely to be adopted for the first time in in the human ancestry, the complexity in stone technology increased drastically [414]. Also around that time, our hominin ancestors became top carnivores and started to become reliant on cooperative and skill intense big game hunting [23]. Cooperative hunting favored more effective forms of social learning such as teaching. Both changes coincided with a significant increase in brain size, likely made possible by the increased energy intake through meat consumption and systematic food sharing [25-27] and the improved survival due to the avoidance of both starvation and predation. Thus, the coevolution of life-history features that allowed for extended learning periods with a shift to a social system with increased opportunities for social learning most likely played a crucial role in the evolution of human cognition.

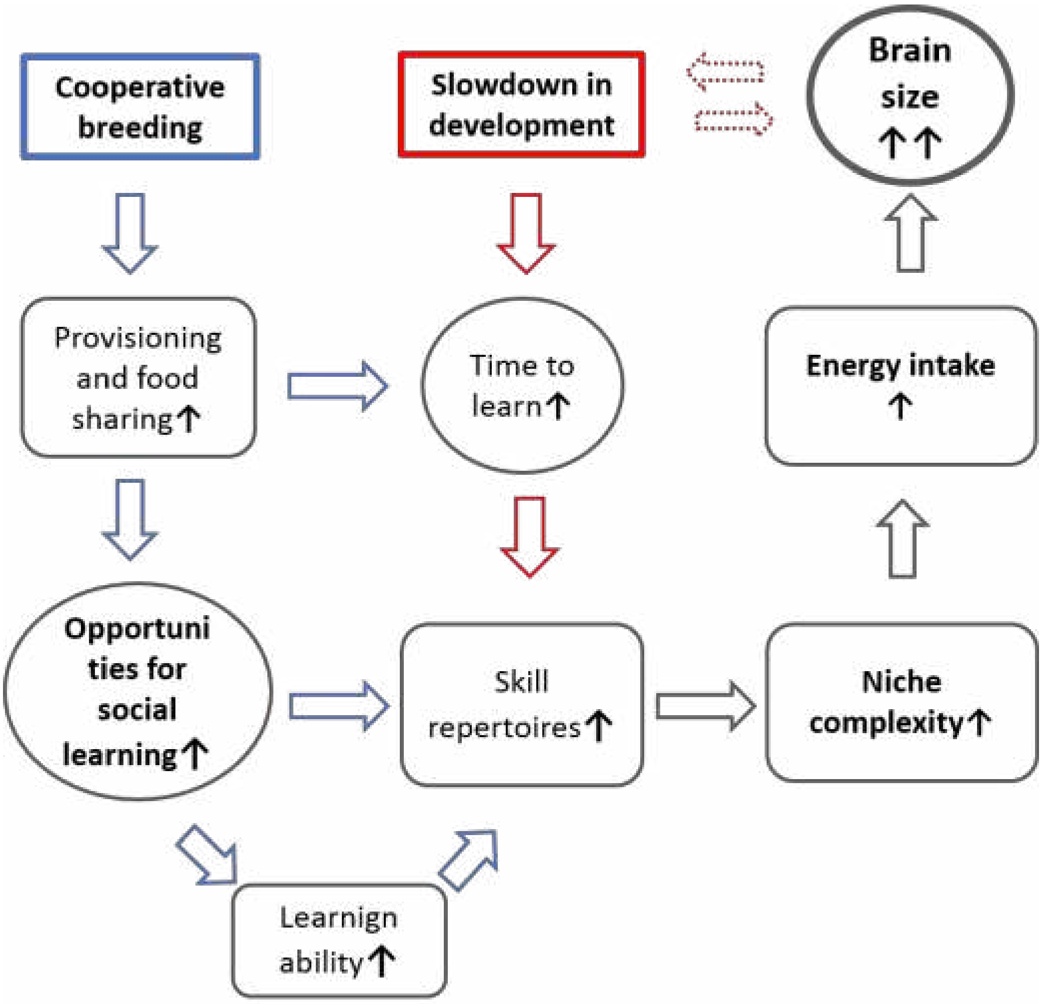

Figure 7.4. Human evolution: The findings of this thesis suggest that the evolution of the unmatched human brain size and level of cognition was made possible by combining a slow development with cooperative breeding which lead to extended skill acquisition periods and increased opportunities for social learning. The emanating larger skill repertoires then enabled the evolution into a highly complex foraging niche which provided the necessary energy for brain size expansion.

References

1. Kolata, S., K. Light, and L.D. Matzel, *General and domain-specific cognitive abilities in heterogeneous stock mice.* Intelligence, 2008. **36**: p. 619-629.
2. Deaner, R.O., C.P. Van Schaik, and V. Johnson, *Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies.* Evolutionary Psychology, 2006.
3. Reader, S.M., Y. Hager, and K.N. Laland, *The evolution of primate general and cultural intelligence.* Philosophical Transactions of the Royal Society B, 2011. **366**(1567): p. 1017-1027.
4. Deaner, R.O., et al., *Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates.* Brain, Behavior and Evolution, 2007. **70**(2): p. 115-124.
5. Byrne, R.W., Whiten, A. , *Machiavellian Intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans*. 1988, Oxford: Calderon Press.
6. Dunbar, R.I.M., *The social brain hypothesis.* Evolutionary Anthropology, 1998. **6**: p. 178-190.
7. Dunbar, R.I.M. and S. Shultz, *Evolution in the social brain.* Science, 2007. **317**(5843): p. 1344-1347.
8. Milton, K., *Foraging behaviour and the evolution of primate intelligence*, in *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*, R.W. Byrne and A. Whiten, Editors. 1988, Clarendon Press: Oxford. p. 285-305.
9. Clutton-Brock, T.H., S.D. Albon, and P.H. Harvey, *Antlers, body size and breeding group size in the Cervidae.* Nature, 1980. **285**: p. 565-567.
10. Parker, S.T. and K.R. Gibson, *Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes.* Journal of Human Evolution, 1977. **6**(7): p. 623-641.
11. Byrne, R.W., *The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence?*, in *Machiavellian intelligence II: extensions and evaluations.*, A. Whiten and R.W. Byrne, Editors. 1997, Cambridge University Presss: Cambridge. p. 289-311.
12. Povinelli, D.J. and J.G.H. Cant, *Arboreal clambering and the evolution of self-conception.* Q. Rev. Biol., 1995. **70**: p. 393-XXX.
13. Rolfe, D.F.S. and G.C. Brown, *Cellular energy utilization and molecular origin of standard metabolic rate in mammals.* Physiol. Rev., 1997. **77**(3): p. 731-758.
14. Bauernfeind, A.L., et al., *Aerobic glycolysis in the primate brain: reconsidering the implications for growth and maintenance.* Brain Structure and Function, 2014. **219**(4): p. 1149-1167.
15. Holliday, M.A., *Body composition and energy needs during growth*, in *Postnatal Growth Neurobiology*. 1986, Springer. p. 101-117.
16. van Schaik, C.P., K. Isler, and J.M. Burkart, *Explaining brain size variation: from social to cultural brain.* Trends in Cognitive Science, 2012. **16**(5): p. 277-284.
17. Isler, K. and C.P. van Schaik, *The Expensive Brain: A framework for explaining evolutionary changes in brain size.* J. Hum. Evol, 2009. **57**(4): p. 392-400.
18. Burkart, J.M., S.B. Hrdy, and C.P. Van Schaik, *Cooperative Breeding and Human Cognitive Evolution.* Evolutionary Anthropology, 2009. **18**(5): p. 175-186.
19. Hrdy, S.B., *Meet the Alloparents.* Natural History, 2009. **118**(3): p. 24-29.

20. van Schaik, C.P. and J.M. Burkart, *Mind the gap: Cooperative breeding and the evolution of our unique features*, in *Mind the Gap: Tracing the origins of Human Universals*, P.M. Kappeler and J. Silk, Editors. 2010, Springer: Berlin. p. 477-496.
21. Isler, K. and C.P. van Schaik, *Allomaternal care, life history and brain size evolution in mammals.* Journal of Human Evolution, 2012. **63**(1): p. 52-63.
22. Pobiner, B.L., et al., *New evidence for hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya.* Journal of Human Evolution, 2008. **55**(1): p. 103-130.
23. Ferraro, J.V., et al., *Earliest Archaeological Evidence of Persistent Hominin Carnivory.* PLoS One, 2013. **8**(4): p. e62174.
24. Stanford, C.B., *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. 1999, Princeton: Princeton University Press.
25. Kaplan, H., et al., *A theory of human life history evolution: Diet, intelligence, and longevity.* Evolutionary Anthropology, 2000. **9**(4): p. 156-185.
26. Gurven, M., H. Kaplan, and M. Gutierrez, *How long does it take to become a proficient hunter? Implications for the evolution of extended development and long life span.* Journal of Human Evolution, 2006. **51**(5): p. 454-470.
27. Milton, K., *A hypothesis to explain the role of meat-eating in human evolution.* Evolutionary Anthropology, 1999. **8**: p. 11-21.
28. Schoenemann, P.T., *Evolution of the size and functional areas of the human brain.* Annu. Rev. Anthropol., 2006. **35**: p. 379-406.
29. Marlowe, F.W., *Hunter-gatherers and human evolution.* Evolutionary Anthropology, 2005. **14**: p. 54-67.
30. Shea, J.J., *The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe.* Journal of Archaeological Science, 2006. **33**: p. 823-846.
31. Dean, M.C. and V.S. Lucas, *Dental and skeletal growth in early fossil hominins.* Annals of Human Biology, 2009. **36**(5): p. 545-561.
32. van Schaik, C.P. and J.M. Burkart, *Social learning and evolution: the cultural intelligence hypothesis.* Royal Society Philosophical Transactions Biological Sciences, 2011. **366**(1567): p. 1008-1016.
33. Gibson, K., *Cognition, brain size and the extraction of embedded food resources.* Primate ontogeny, cognition and social behaviour, 1986. **3**: p. 93-104.
34. Leonard, W.R. and M.L. Robertson, *Comparative primate energetics and hominid evolution.* American Journal of Physical Anthropology, 1997. **102**(2): p. 265-281.
35. Berbesque, J.C., et al., *Hunter-gatherers have less famine than agriculturalists.* Biology Letters, 2014. **10**(1): p. 4.
36. Hill, K. and H. Kaplan, *Life history traits in humans: theory and empirical studies.* Annual Review of Anthropology, 1999. **28**: p. 397-430.
37. Kaplan, H.S., et al., *The evolution of diet, brain and life history among primates and humans*, in *Guts and Brains: An Interative Approach to the Hominin Record*, W. Roebroeks, Editor. 2007, Leiden University Press: Leiden, NL. p. 47-81.
38. Charnov, E.L., *Evolution of mammal life histories.* Evolutionary Ecology Research, 2001. **3**: p. 521-535.
39. Janson, C.H., and Carel P. van Schaik, *Ecological Risk Aversion in Juvenile Primates: Slow and Steady Wins the Race*, in *Juvenile Primates. Life History, Development, and Behavior.*, M.E.P.a.L.A. Fairbanks, Editor. 1993, Oxford University Press: New York. p. 57-74.
40. Ross, C. and K.E. Jones, *Socioecology and the evolution of primate reproductive rates.* Cambridge Studies in Biological Anthropology, 1999. **22**: p. 73-110.
41. Kaplan, H.S. and J. Lancaster, *An evolutionary and ecological analysis of human fertility, mating patterns and parental investment*, in *Offspring: Human Fertility Behavior in*

Biodemographic Perspective, K. Wachter and R.A. Bulatao, Editors. 2003, National Academy Press: Washington, DC. p. 170-220.
42. Barrickman, N.L., et al., *Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild.* Journal of Human Evolution, 2008. **54**(5): p. 568-590.
43. Isler, K. and C.P. van Schaik, *The Expensive Brain: A framework for explaining evolutionary changes in brain size.* Journal of Human Evolution, 2009. **57**(4): p. 392-400.
44. Navarrete, A., C.P. van Schaik, and K. Isler, *Energetics and the evolution of human brain size.* Nature, 2011. **480**(7375): p. 91-94.
45. Tanner, J.M., *Normal growth and techniques of growth assessment.* Clinics in Endocrinology and Metabolism, 1986. **15**(3): p. 411-451.
46. Sacher, G.A. and E.F. Staffeldt, *Relation of gestation time to brain weight in placental mammals: implications for the theory of vertebrate growth.* American Naturalist, 1974. **108**: p. 593-615.
47. Leigh, S.R., *Evolution of human growth.* Evolutionary Anthropology, 2001. **10**: p. 223-236.
48. Leigh, S.R., *Brain growth, life history, and cognition in primate and human evolution.* American Journal of Primatology, 2004. **62**: p. 139-164.
49. Deaner, R.O., R.A. Barton, and C.P. Van Schaik, *Primate Brains and Life Histories: Renewing the Connection*. Primate life histories and socioecology, ed. P.M. Kappeler and M.E. Pereira. 2003, Chicago: The University of Chicago Press. 233-265.
50. Kuzawa, C.W., et al., *Metabolic costs and evolutionary implications of human brain development.* Proceedings National Academy of Sciences USA, 2014. **111**: p. 13010-13015.
51. Boyd, R., P.J. Richerson, and J. Henrich, *The cultural niche: Why social learning is essential for human adaptation.* Proceedings of the National Academy of Sciences of the United States of America, 2011. **108**: p. 10918-10925.
52. Heyes, C., *What's Social About Social Learning?* Journal of Comparative Psychology, 2012. **126**(2): p. 193-202.
53. Horner, V. and A. Whiten, *Causal knowledge and imitation/emulation switching in chimpanzees (Pan trogiodytes) and children (Homo sapiens).* Animal Cognition, 2005. **8**(3): p. 164-181.
54. McGuigan, N., et al., *Imitation of causally opaque versus causally transparent tool use by 3- and 5-year-old children.* Cognitive Development, 2007. **22**(3): p. 353-364.
55. Custance, D.M., A. Whiten, and T. Fredman, *Social learning and primate reintroduction.* International Journal of Primatology, 2002. **23**(3): p. 479-499.
56. Caldwell, C. and A. Whiten, *Social learning in monkeys and apes: Cultural animals?*, in *Primates in Perspective*, C.J. Campbell, et al., Editors. 2007, Oxford University Press: Oxford. p. 652-664.
57. Gardner, B.T. and R.A. Gardner, *Prelinguistic development of children and chimpanzees.* Human Evolution, 1989. **4**: p. 433-460.
58. Bard, K.A. and K.H. Gardner, *Influences on development in infant chimpanzees: Enculturation, temperament, and cognition*, in *Reaching into Thougth: The Mind of Great Apes*, A. Russon, K. Bard, and S.T. Parker, Editors. 1996, Cambridge University Press: Cambridge. p. 235-255.
59. Galef, B.G., *Why behaviour patterns that animals learn socially are locally adaptive.* Animal Behaviour, 1995. **49**: p. 1325-1334.
60. Heyes, C., *What's social about social learning?* Journal of Comparative Psychology, 2012. **126**(2): p. 193.
61. Heyes, C., *Social learning in animals: categories and mechanisms.* Biological Reviews, 1994. **69**: p. 702-731.
62. Jaeggi, A.V., et al., *Social Learning of Diet and Foraging Skills by Wild Immature Bornean Orangutans: Implications for Culture.* American Journal of Primatology, 2010. **72**(1): p. 62-71.

63. Galef, B.G., *Laboratory studies of imitation/field studies of tradition: Towards a synthesis in animal social learning.* Behavioural Processes, 2015. **112**: p. 114-119.
64. Whiten, A., *Experimental studies illuminate the cultural transmission of percussive technologies in Homo and Pan.* Royal Society Philosophical Transactions Biological Sciences, 2015. **370**(1682): p. 20140359-20140359.
65. Whiten, A., et al., *Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee.* Philosophical transactions of the Royal Society of London, 2009. **364**: p. 2417-2428.
66. van Schaik, C.P., et al., *The reluctant innovator: orangutans and the phylogeny of creativity.* Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 2016. **371**(1690).
67. Zeanah, C.H., A.T. Smyke, and L.D. Settles, *Orphanages as a developmental context for early childhood.* Blackwell handbook of early childhood development, 2006: p. 424-454.
68. Nelson, C.A., et al., *Cognitive recovery in socially deprived young children: The Bucharest Early Intervention Project.* Science, 2007. **318**(5858): p. 1937-1940.
69. Chugani, H.T., et al., *Local brain functional activity following early deprivation: a study of postinstitutionalized Romanian orphans.* Neuroimage, 2001. **14**(6): p. 1290-1301.
70. Eluvathingal, T.J., et al., *Abnormal brain connectivity in children after early severe socioemotional deprivation: a diffusion tensor imaging study.* Pediatrics, 2006. **117**(6): p. 2093-2100.
71. Tomasello, M., *The Cultural Origins of Human Cognition*. 1999, Cambridge MA: Harvard University Press.
72. Herrmann, E., et al., *Humans have evolved specialized skills of social cognition: The Cultural Intelligence Hypothesis.* Science, 2007. **317**: p. 1360-1366.
73. Moll, H. and M. Tomasello, *Cooperation and human cognition: the Vygotskian intelligence hypothesis.* Philosophical Transactions of the Royal Society B: Biological Sciences, 2007. **362**(1480): p. 639-648.
74. Mason, W.A., R.K. Davenport, and E.W. Menzel, *Early experinece and the social development of rhesus monkeys and chimpanzees*, in *Early Experience and Behavior: The Psychological and Physiological Effects of Early Environmental Variaton*, G. Newton and S. Levine, Editors. 1968, Charles C. Thomas: Springfield, Illinois. p. 440-480.
75. Sanchez, M.M., et al., *Differential rearing affects corpus callosum size and cognitive function of rhesus monkeys.* Brain Research, 1998. **812**: p. 38-49.
76. Schrijver, N.C.A., et al., *Double dissociation of social and environmental stimulation on spatial learning and reversal learning in rats.* Behavioural Brain Research, 2004. **152**(2): p. 307-314.
77. Call, J. and M. Tomasello, *The effect of humans on the cognitive development of apes*, in *Reaching into Thought: The Minds of the Great Apes*, A.E. Russon, K.A. Bard, and S.T. Parker, Editors. 1996, Cambridge University Press: Cambridge. p. 371-403.
78. Tomasello, M. and J. Call, *The role of humans in the cognitive development of apes revisited.* Animal Cognition, 2004. **7**(4): p. 213-215.
79. Whiten, A. and C.P. van Schaik, *The evolution of animal 'cultures' and social intelligence.* Philosophical Transactions of the Royal Society B-Biological Sciences, 2007. **362**(1480): p. 603-620.
80. Vygotsky, L., *Interaction between learning and development.* Readings on the development of children, 1978. **23**(3): p. 34-41.
81. Nisbett, R.E., *Intelligence and How to Get it: Why Schools and Cultures Count*. 2009, New York: W.W. Norton & Company.
82. Hobolth, A., et al., *Incomplete lineage sorting patterns among human, chimpanzee, and orangutan suggest recent orangutan speciation and widespread selection.* Genome research, 2011. **21**(3): p. 349-356.

83. Prado-Martinez, J., et al., *Great ape genetic diversity and population history.* Nature, 2013. **499**(7459): p. 471-475.
84. Goossens, B., et al., *Taxonomy, geographic variation and population genetics of Bornean and Sumatran orangutans*, in *Orangutans: Geographic variation in behavioral ecology and conservation, SA Wich, SS Utami Atmoko, T. Mitra Setia, and CP van Schaik (eds.). Oxford University Press, Oxford, UK*, S.A. Wich, et al., Editors. 2009. p. 1-14.
85. Taylor, A.B. and C.P. van Schaik, *Variation in brain size and ecology in Pongo.* Journal of Human Evolution, 2007. **52**(1): p. 59-71.
86. van Schaik, C.P., A.J. Marshall, and S.A. Wich, *Geographic variation in orangutan behavior and biology: its functional interpretation and its mechanistic basis*. Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.], ed. S.A. Wich, et al. 2009. 351-361.
87. van Schaik, C.P., *The socioecology of fission-fusion sociality in orangutans.* Primates, 1999. **40**: p. 73-90.
88. Mitra Setia, T., et al., *Social organization and male-female relationships*, in *Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.]*, S.A. Wich, et al., Editors. 2009. p. 245-253.
89. van Noordwijk, M.A., *From maternal investment to lifetime maternal care*, in *The Evolution of Primate Societies*, J.C. Mitani, et al., Editors. 2012, The University of Chicago Press: Chicago. p. 321-342.
90. Van Noordwijk, M.A., et al., *Development of independence: Sumatran and Bornean orangutans compared*, in *Orangutans Compared: Geographic Variation in Behavioral Ecology and Conservation*, S.A. Wich, et al., Editors. 2009, Oxford University Press: Oxford. p. 189-203.
91. Wich, S.A., et al., *Life history of wild Sumatran orangutans (Pongo abelii).* Journal of Human Evolution, 2004. **47**: p. 385-398.
92. Wich, S.A., et al., *Orangutan Life history variation*, in *Orangutans Geographic Variation in Behavioral Ecology and Conservation*, S.A. Wich, et al., Editors. 2009, Oxford University Press: New York.
93. van Noordwijk, M.A. and C.P. van Schaik, *Development of ecological competence in Sumatran orangutans.* American Journal of Physical Anthropology, 2005. **127**(1): p. 79-94.
94. Galdikas, B.M.F., *Subadult male orangutan sociality and reproductive behavior at Tanjung Puting.* International Journal of Primatology, 1985. **8**: p. 87-99.
95. Knott, C.D., M. Emery Thompson, and S.A. Wich, *The ecology of female reproduction in wild orangutans*, in *Orangutans: Geographic Variation in Behavioral Ecology and Conservation*, S.A. Wich, et al., Editors. 2009, Oxford University Press: New York. p. 171-188.
96. Marshall, A.J., et al., *The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans.* Orangutans: geographic variation in behavioral ecology and conservation. Oxford: Oxford University Press. p, 2009: p. 97-117.
97. Van Schaik, C.P. and C.D. Knott, *Geographic variation in tool use on Neesia fruits in orangutans.* American Journal of Physical Anthropology, 2001. **114**(4): p. 331-342.
98. Meulman, E.J.M. and C.P. van Schaik, *Orangutan tool use and the evolution of technology.* Tool Use in Animals: Cognition and Ecology, 2013: p. 176-202.
99. Prasetyo, D., et al., *Nest building in orangutans*, in *Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.]*, S.A. Wich, et al., Editors. 2009. p. 269-277.
100. Russon, A.E., *Acquisition of complex foraging skills in juvenile and adolescent orangutans (Pongo pygmaeus): Developmental influences.* Aquatic Mammals, 2006. **32**(4): p. 500-510.
101. Russon, A.E., et al., *Orangutan leaf-carrying for nest-building: Toward unraveling cultural processes.* Animal Cognition, 2007. **10**(2): p. 189-202.

102. Jaeggi, A.V., M.A. van Noordwijk, and C.P. van Schaik, *Begging for information: Mother-offspring food sharing among wild Bornean orangutans.* American Journal of Primatology, 2008. **70**: p. 533-541.
103. van Schaik, C.P., et al., *Orangutan cultures and the evolution of material culture.* Science, 2003. **299**(5603): p. 102-105.
104. Kruetzen, M., E.P. Willems, and C.P. van Schaik, *Culture and Geographic Variation in Orangutan Behavior.* Current Biology, 2011. **21**(21): p. 1808-1812.
105. Forss, S.I.F., et al., *Contrasting Responses to Novelty by Wild and Captive Orangutans.* American Journal of Primatology, 2015. **77**(10): p. 1109-1121.
106. Singleton, I., et al., *Ranging behavior of orangutan females and social organization*, in *Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.]*, S.A. Wich, et al., Editors. 2009. p. 205-213.
107. Husson, S.J., et al., *Orangutan distribution, density, abundance and impacts of disturbance*, in *Orangutans Geographic variation in Behavioral Ecology and Conservation*, S.A. Wich, et al., Editors. 2009, Oxford University Press: New York.
108. Blurton Jones, N. and F.W. Marlowe, *Selection for delayed maturity. Does it take 20 years to learn to hunt and gather?* Human Nature, 2002. **13**: p. 199-238.
109. Stephens, D.W. and J.R. Krebs, *Foraging Theory*. 1986, Princeton, NJ: Princeton University Press. xiv+ 247 pp.
110. Silk, J.B., *Why are infants so attractive to others? The form and function of infant handling in bonnet macaques.* Animal Behaviour, 1999. **57**(5): p. 1021-1032.
111. Ricklefs, R.E., *Patterns of growth in birds.* Ibis, 1968. **110**(4): p. 419-451.
112. Guo, H., et al., *Parental care, development of foraging skills, and transition to independence in the red-footed booby.* The Condor, 2010. **112**(1): p. 38-47.
113. Lack, D., *Ecological Adaptations for Breeding in Birds*. 1968, London, UK: Methuen.
114. Morrison, M.L., R.D. Slack, and E. Shanley Jr, *Age and foraging ability relationships of Olivaceous Cormorants.* The Wilson Bulletin, 1978: p. 414-422.
115. Ashmole, N.P. and H. Tovar, *Prolonged parental care in Royal Terns and other birds.* The Auk, 1968: p. 90-100.
116. Marchetti, K. and T. Price, *Differences in the foraging of juvenile and adult birds: the importance of developmental constraints.* Bio. Rev., 1989. **64**: p. 51-70.
117. Johnson, S.E. and J. Bock, *Trade-offs in skill acquisition and time allocation among juvenile chacma baboons.* Human Nature-an Interdisciplinary Biosocial Perspective, 2004. **15**(1): p. 45-62.
118. Gunst, N., S. Boinski, and D.M. Fragaszy, *Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (Cebus apella apella).* J. Comp. Psychol., 2010. **124**(2): p. 194-204.
119. Stone, A.I., *Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (Saimiri sciureus).* Ethology, 2006. **112**(2): p. 105-115.
120. Clutton-Brock, T.H., *Structure and function in mammalian societies.* Philosophical Transactions of the Royal Society of London, 2009. **364**: p. 3229-3242.
121. R Development Core Team, *A language and environment for statistical computing*. 2011, R foundation for statistical computing: Vienna, Austria.
122. Orme, D., *The caper package: comparative analysis of phylogenetics and evolution in R*. 2011.
123. Pagel, M., *Inferring evolutionary processes from phylogenies.* Zoologica Scripta, 1997. **26**(4): p. 331-348.
124. Nunn, C.L., *The Comparative Approach in Evolutionary Anthropology and Biology*. 2011, Chicago and London: The University of Chicago Press.
125. Lee, P.C., *The meanings of weaning: growth, lactatioin, and life history.* Evol. Anthro., 1996. **5**: p. 87-96.

126. Schuppli, C., *Skill learning in immature Sumatran orangutans (Pongo abelii): When and how do immatures reach adult levels of skill competence?* , in *Department of Anthropology*. 2012, University of Zürich: Zürich.
127. Hrdy, S.B., *Mothers & Others: The Evolutionary Origins of Mutual Understanding*. 2009, Cambridge: Harvard University Press.
128. Isler, K. and C.P. van Schaik, *How our ancestors broke through the gray ceiling comparative evidence for cooperative breeding in early Homo.* Curr. Anthropol., 2012. **53**: p. S453-S465.
129. Kaplan, H.S. and A.J. Robson, *The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers.* Proceedings of the National Academy of Sciences, 2002. **99**(15): p. 10221-10226.
130. Isler, K. and C.P. Van Schaik, *Why are there so few smart mammals (but so many smart birds)?* Biol. Lett., 2009. **5**(1): p. 125-129.
131. Robson, S.L., K. Hawkes, and C.P. van Schaik, *The derived features of human life history*, in *The Evolution of Human Life History*, K. Hawkes and R.L. Paine, Editors. 2006, School of American Research Press: Santa Fe. p. 17-44.
132. Koga, T. and Y. Ono, *Sexual differences in foraging behavior of sika deer, Cervus nippon.* Journal of mammalogy, 1994: p. 129-135.
133. Ciofolo, I. and Y. Le Pendu, *The feeding behaviour of giraffe in Niger.* Mammalia, 2002. **66**(2): p. 183-194.
134. Gillingham, M.P., K.L. Parker, and T.A. Hanley, *Forage intake by black-tailed deer in a natural environment: bout dynamics.* Canadian Journal of Zoology, 1997. **75**(7): p. 1118-1128.
135. Oakes, E., R. Harmsen, and C. Eberl, *Sex, age, and seasonal differences in the diets and activity budgets of muskoxen (Ovibos moschatus).* Canadian Journal of Zoology, 1992. **70**(3): p. 605-616.
136. Forchhammer, M.C., *Sex, age, and seasonal variation in the foraging dynamics of muskoxen, Ovibos moschatus, in Greenland.* Canadian journal of zoology, 1995. **73**(7): p. 1344-1361.
137. Ruckstuhl, K., M. Festa-Bianchet, and J. Jorgenson, *Bite rates in Rocky Mountain bighorn sheep (Ovis canadensis): effects of season, age, sex and reproductive status.* Behavioral Ecology and Sociobiology, 2003. **54**(2): p. 167-173.
138. Sargeant, B.L., et al., *Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (Tursiops sp.).* Canadian Journal of Zoology-Revue Canadienne De Zoologie, 2005. **83**(11): p. 1400-1410.
139. Eaton, R.L., *Hunting behavior of the cheetah.* The Journal of Wildlife Management, 1970: p. 56-67.
140. MacNulty, D.R., et al., *Predatory senescence in ageing wolves.* Ecology letters, 2009. **12**(12): p. 1347-1356.
141. MacNulty, D.R., et al., *Body size and predatory performance in wolves: is bigger better?* Journal of Animal Ecology, 2009. **78**(3): p. 532-539.
142. Sand, H., et al., *Effects of hunting group size, snow depth and age on the success of wolves hunting moose.* Animal Behaviour, 2006. **72**: p. 781-789.
143. Holekamp, K.E., et al., *Hunting rates and hunting success in the spotted hyena (Crocuta crocuta).* Journal of Zoology, 1997. **242**: p. 1-15.
144. Payne, S.F. and R.J. Jameson, *Early behavioral development of the sea otter, Enhydra lutris.* Journal of Mammalogy, 1984: p. 527-531.
145. Rasa, A.O.E., *Aspects of social organization in captive dwarf mongooses.* J. Mammol., 1972. **53**: p. 181-185.
146. Heggberget, T.M. and K.E. Moseid, *Prey selection in coastal Eurasian otters Lutra lutra.* Ecography, 1994. **17**(4): p. 331-338.
147. Malcolm, J.R. and K. Marten, *Natural selection and the communal rearing of pups in African wild dogs (Lycaon pictus).* Behavioral Ecology and Sociobiology, 1982. **10**(1): p. 1-13.

148. Maehr, D.S. and J.R. Brady, *Food habits of bobcats in Florida.* Journal of Mammalogy, 1986. **67**(1): p. 133-138.
149. McLEAN, M.L., T.S. McCAY, and M.J. Lovallo, *Influence of age, sex and time of year on diet of the bobcat (Lynx rufus) in Pennsylvania.* The American midland naturalist, 2005. **153**(2): p. 450-453.
150. Fritts, S.H. and J.A. Sealander, *Diets of bobcats in Arkansas with special reference to age and sex differences.* The Journal of Wildlife Management, 1978: p. 533-539.
151. Roper, T. and P. Lüps, *Diet of badgers (Meles meles) in central Switzerland: an analysis of stomach contents.* Zeitschrift für Säugetierkunde, 1995. **60**(1): p. 9-19.
152. Field, I.C., et al., *Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche.* Marine Biology, 2007. **150**(6): p. 1441-1452.
153. Seidensticker, J. and C. McDougal. *Tiger predatory behaviour, ecology and conservation*. in *Symposia of the Zoological Society of London*. 1993.
154. Schaller, G., *The deer and the tiger: a study ofwildlife in India*. 1967, Univ. Chicago Press, Chicago, IL.
155. Clutton-Brock, T.H., *Cooperative breeding in mammals*, in *Cooperation in Primates and Humans. Mechanisms and Evolution*, P.M. Kappeler and C.P. van Schaik, Editors. 2006, Springer: Berlin. p. 173-190.
156. Thornton, A., *Early body condition, time budgets and the acquisition of foraging skills in meerkats.* Animal Behaviour, 2008. **75**(3): p. 951-962.
157. Stirling, I. and P.B. Latour, *Comparative hunting abilities of polar bear cubs of different ages.* Canadian Journal of Zoology, 1978. **56**(8): p. 1768-1772.
158. Kunz, T.H., *Feeding ecology of a temperate insectivorous bat (Myotis velifer).* Ecology, 1974: p. 693-711.
159. Swift, S.M., *Foraging, colonial and maternal behaviour of bats in north-east Scotland*. 1981, University of Aberdeen.
160. Schiel, N., et al., *Hunting strategies in wild common marmosets are prey and age dependent.* American journal of primatology, 2010. **72**(12): p. 1039-1046.
161. Gunst, N., S. Boinski, and D.M. Fragaszy, *Acquisition of foraging competence in wild brown capuchins (Cebus apella), with special reference to conspecifics' foraging artefacts as an indirect social influence.* Behaviour, 2008. **145**: p. 195-229.
162. O'Malley, R.C. and L. Fedigan, *Variability in food-processing behavior among white-faced capuchins (Cebus capucinus) in Santa Rosa National Park, Costa Rica.* American Journal of Physical Anthropology, 2005. **128**: p. 63-73.
163. Fragaszy, D.M. and S. Boinski, *Patterns of individual diet choice and efficiency of foraging in wedge-capped capuchin monkeys (Cebus olivaceus).* Journal of Comparative Psychology, 1995. **109**(4): p. 339.
164. Watts, D.P., *Observations on the ontogeny of feeding-behavior in Mountain Gorillas (Gorilla Gorilla Beringei)).* American Journal of Primatology, 1985. **8**(1): p. 1-10.
165. Watts, D.P., *Environmental influences on mountain gorilla time budgets.* Am. J. Primatol., 1988. **15**.
166. Nowell, A.A. and A.W. Fletcher, *Development of independence from the mother in Gorilla gorilla gorilla.* International Journal of Primatology, 2007. **28**(2): p. 441-455.
167. Hanya, G., *Age differences in food intake and dietary selection of wild male Japanese macaques.* Primates, 2003. **44**(4): p. 333-339.
168. Nakayama, Y., S. Matsuoka, and Y. Watanuki, *Feeding rates and energy deficits of juvenile and adult Japanese monkeys in a cool temperate area with snow coverage.* Ecological Research, 1999. **14**(3): p. 291-301.

169. Post, D.G., G. Hausfater, and S.A. McCuskey, *Feeding behavior of yellow baboons (Papio cynocephalus): relationship to age, gender and dominance rank.* Folia Primatologica 34, 1980: p. 170-195.
170. Byrne, R.W., et al., *Nutritional constraints on mountain baboons (Papio Ursinus) - Implications for baboon socioecology.* Behavioral Ecology and Sociobiology, 1993. **33**(4): p. 233-246.
171. Dunkel, L.P., *Developmnt of ecological competence in Bornean orangutans (Pongo pygmaeus): with special reference to difficult-to-process food items.*, in *Anthropological Institute and Museum*. 2006, University of Zürich: Zürich.
172. Schuppli, C., K. Isler, and C.P. van Schaik, *How to explain the unusually late age at skill competence among humans.* Journal of Human Evolution, 2012. **63**(6): p. 843-850.
173. Barton, R.A. and I. Capellini, *Maternal investment, life histories, and the costs of brain growth in mammals.* Proceedings of the National Academy of Sciences, 2011. **108**(15): p. 6169-6174.
174. Gonzalez-Lagos, C., D. Sol, and S.M. Reader, *Large-brained mammals live longer.* J. Evol. Biol., 2010. **23**(5): p. 1064-1074.
175. Fish, J.L. and C.A. Lockwood, *Dietary constraints on encephalization in primates.* American Journal of Physical Anthropology, 2003. **120**: p. 171-181.
176. Reader, S.M. and K.N. Laland, *Social intelligence, innovation, and enhanced brain size in primates.* Proceedings of the National Academy of Sciences, 2002. **99**(7): p. 4436-4441.
177. Barton, R.A., *Embodied cognitive evolution and the cerebellum.* Philosophical transactions of the Royal society B: Biological Sciences, 2012. **367**(1599): p. 2097-2107.
178. Van Woerden, J.T., C.P. Van Schaik, and K. Isler, *Effects of seasonality on brain size evolution: evidence from strepsirrhine primates.* The American Naturalist, 2010. **176**(6): p. 758-767.
179. Van Woerden, J.T., et al., *Large brains buffer energetic effects of seasonal habitats in catarrhine primates.* Evolution, 2012. **66**(1): p. 191-199.
180. Van Woerden, J.T., C.P. Schaik, and K. Isler, *Seasonality of diet composition is related to brain size in New World Monkeys.* American Journal of Physical Anthropology, 2014.
181. Anton, S.C., R. Potts, and L.C. Aiello, *Evolution of early Homo: An integrated biological perspective.* Science, 2014. **345**(6192).
182. Milton, K., *Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development.* American Anthropologist, 1981. **83**(3): p. 534-548.
183. Walker, R., et al., *Evolution of brain size and juvenile periods in primates.* Journal of Human Evolution, 2006. **51**(5): p. 480-489.
184. Dittus, W., *The social regulation of population density and age-sex distribution in the toque monkey.* Behaviour, 1977. **63**: p. 281-322.
185. Lonsdorf, E., *What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (Pan troglodytes schweinfurthii)?* Animal Cognition, 2006. **9**(1): p. 36-46.
186. Lefebvre, L., S.M. Reader, and D. Sol, *Brains, innovations and evolution in birds and primates.* Brain, behavior and evolution, 2004. **63**(4): p. 233-246.
187. Matthews, L.J., et al., *Primate extinction risk and historical patterns of speciation and extinction in relation to body mass.* Proceedings of the Royal Society B: Biological Sciences, 2010: p. rspb20101489.
188. Ho, L.S.T., C. Ane, and M.L.S.T. Ho, *Package 'phylolm'.* 2014.
189. Pagel, M., *The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies.* Systematic biology, 1999: p. 612-622.
190. Ives, A.R. and T. Garland, *Phylogenetic logistic regression for binary dependent variables.* Systematic Biology, 2010. **59**(1): p. 9-26.
191. Bininda-Emonds, O.R.P., et al., *The delayed rise of present-day mammals (vol 446, pg 507, 2007).* Nature, 2008. **456**(7219): p. 274-274.

192. Perelman, P., et al., *A molecular phylogeny of living primates.* PLoS Gen., 2011. **7**(3): p. e1001342.
193. Watt, J., *Ontogeny of hunting behavior of otters (Lutra Lutra) in a marine environment*, in *Mammals as Predators*, N. Dunstone and M.L. Gorman, Editors. 1993. p. 87-104.
194. Meulman, E., A. Seed, and J. Mann, *If at first you don't succeed… Studies of ontogeny shed light on the cognitive demands of habitual tool use.* Phil. Trans. R. Soc. B, 2013. **368**(1630): p. 20130050.
195. Boesch, C., *Cooperative hunting roles among taï chimpanzees.* Human Nature, 2002. **13**(1): p. 27-46.
196. Harvey, P.H. and Clutton-Brock, *Life history variation in primates.* Evolution, 1985. **39**(3): p. 559-581.
197. Swanson, E.M., et al., *Multiple Determinants of Whole and Regional Brain Volume among Terrestrial Carnivorans.* Plos One, 2012. **7**(6): p. 11.
198. McKitrick, M.C., *Phylogenetic constraint in evolutionary theory: has it any explanatory power?* Annual Review of Ecology and Systematics, 1993: p. 307-330.
199. Futuyama, D.J., *Evolutionary Biology*. 3rd ed. 1997, Sunderland, MA: Sinauer Associates Inc.
200. Dominguez-Rodrigo, M., T.R. Pickering, and H.T. Bunn, *Configurational approach to identifying the earliest hominin butchers.* Proceedings of the National Academy of Sciences of the United States of America, 2010. **107**(49): p. 20929-20934.
201. Myers, P., et al. *The animal diversity web*. 1995.
202. Jaeggi, A.V. and C.P. Van Schaik, *The evolution of food sharing in primates.* Behavioral Ecology and Sociobiology, 2011. **65**(11): p. 2125-2140.
203. Bentley-Condit, V.K. and E. Smith, *Animal tool use: current definitions and an updated comprehensive catalog.* Behaviour, 2010. **147**(2): p. 185.
204. Smith, J.E., et al., *Evolution of cooperation among mammalian carnivores and its relevance to hominin evolution.* Current Anthropology, 2012. **53**(S6): p. S436-S452.
205. Caro, T.M., *Cheetahs of the Serengeti Plains: group living in an asocial species*. 1994: University of Chicago Press.
206. Wei, F., et al., *Feeding strategy and resource partitioning between giant and red pandas.* Mammalia, 1999. **63**(4): p. 417-430.
207. Hersteinsson, P. and D. Macdonald, *Diet of arctic foxes (Alopex lagopus) in Iceland.* Journal of Zoology, 1996. **240**(3): p. 457-474.
208. Kitchen, A.M., E.M. Gese, and E.R. Schauster, *Resource partitioning between coyotes and swift foxes: space, time, and diet.* Canadian Journal of Zoology, 1999. **77**(10): p. 1645-1656.
209. Hovens, J. and K. Tungalaktuja, *Seasonal fluctuations of the wolf diet in the Hustai National Park (Mongolia).* Mammalian Biology-Zeitschrift für Säugetierkunde, 2005. **70**(4): p. 210-217.
210. Bothma, J.d.P., J. Nel, and A. Macdonald, *Food niche separation between four sympatric Namib Desert carnivores.* Journal of Zoology, 1984. **202**(3): p. 327-340.
211. Sunquist, M. and F. Sunquist, *Wild cats of the world*. 2002: University of Chicago Press.
212. Rodrigues, F.H., et al., *Feeding habits of the maned wolf (Chrysocyon brachyurus) in the Brazilian Cerrado.* Mastozoología Neotropical, 2007. **14**(1): p. 37-51.
213. Wilson, D.E. and R.A. Mittermeier, *The Handbook of the Mammals of the World, Volume 1: Carnivores*. 2009, Barcelona: Lynx Ediciones.
214. Silvestre, I., O. Novelli, and G. Bogliani, *Feeding habits of the spotted hyaena in the Niokolo Koba National Park, Senegal.* African Journal of Ecology, 2000. **38**(2): p. 102-107.
215. Nowak, R.M., *Walker's Mammals of the World*. Vol. 1. 1999: JHU Press.
216. Skinner, J. and R. Smithers, *The mammals of the southern African subregion, 1990.* University of Pretoria, Pretoria: p. 234-244.
217. Bisbal, F., *Food habits of some neotropical carnivores in Venezuela (Mammalia, Carnivora).* Mammalia, 1986. **50**(3): p. 329-339.

218. Cohn, J.P., *Understanding sea otters.* BioScience, 1998: p. 151-155.
219. Mukherjee, S., et al., *The importance of rodents in the diet of jungle cat (Felis chaus), caracal (Caracal caracal) and golden jackal (Canis aureus) in Sariska Tiger Reserve, Rajasthan, India.* Journal of Zoology, 2004. **262**(04): p. 405-411.
220. Rosalino, L. and M. Santos-Reis, *Feeding habits of the common genet Genetta genetta (Carnivora: Viverridae) in a semi-natural landscape of central Portugal.* Mammalia, 2002. **66**(2): p. 195-206.
221. Lofroth, E.C., et al., *Food habits of wolverine Gulo gulo in montane ecosystems of British Columbia, Canada.* Wildlife Biology, 2007. **13**(sp2): p. 31-37.
222. Bowland, J.M. and M. Perrin, *Diet of serval Felis serval in a highland region of Natal.* African Zoology, 2012. **28**(3).
223. Schmidt, K., et al., *Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland.* Ecological research, 2009. **24**(1): p. 207-214.
224. Neale, J.C. and B.N. Sacks, *Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats.* Canadian Journal of Zoology, 2001. **79**(10): p. 1794-1800.
225. Slauson, K.M., J.M. Higley, and S.M. Matthews, *Fisher (Martes pennanti) Conservation on the Hoopa Valley Reservation, California: Fall-Winter Diet of Fishers on the Hoopa Valley Indian Reservation.* 2011.
226. Sidorovich, V.E., I.I. Rotenko, and D.A. Krasko. *Badger Meles meles spatial structure and diet in an area of low earthworm biomass and high predation risk*. in *Annales Zoologici Fennici*. 2011. BioOne.
227. Joshi, A.R., D.L. Garshelis, and J.L. Smith, *Seasonal and habitat-related diets of sloth bears in Nepal.* Journal of Mammalogy, 1997: p. 584-597.
228. Tapper, S., *The effect of fluctuating vole numbers (Microtus agrestis) on a population of weasels (Mustela nivalis) on farmland.* The Journal of Animal Ecology, 1979: p. 603-617.
229. Sidorovich, V.E., et al., *Seasonal and annual variation in the diet of the raccoon dogNyctereutes procyonoides in northern Belarus: the role of habitat type and family group.* Acta Theriologica, 2008. **53**(1): p. 27-38.
230. Klare, U., J.F. Kamler, and D.W. Macdonald, *The bat-eared fox: A dietary specialist?* Mammalian Biology-Zeitschrift für Säugetierkunde, 2011. **76**(5): p. 646-650.
231. Hayward, M., et al., *Prey preferences of the leopard (Panthera pardus).* Journal of Zoology, 2006. **270**(2): p. 298-313.
232. Maude, G., *The Comparative Ecology of the Brown Hyaena (Hyaena brunnea) in Makgadikgadi National Park and a Neighbouring Community Cattle Area in Botswana*. 2005, University of Pretoria.
233. Kays, R.W., *Food preferences of kinkajous (Potos flavus): a frugivorous carnivore.* Journal of mammalogy, 1999: p. 589-599.
234. Matsebula, S.N., et al., *The diet of the aardwolf, Proteles cristatus at Malolotja Nature Reserve, western Swaziland.* African Journal of Ecology, 2009. **47**(3): p. 448-451.
235. Carter, S. and F.C. ROSAS, *Biology and conservation of the giant otter Pteronura brasiliensis.* Mammal Review, 1997. **27**(1): p. 1-26.
236. Doolan, S. and D. Macdonald, *Diet and foraging behaviour of group-living meerkats, Suricata suricatta, in the southern Kalahari.* Journal of Zoology, 1996. **239**(4): p. 697-716.
237. Garcelon, D.K., et al., *Food provisioning by island foxes, Urocyon littoralis, to conspecifics caught in traps.* The Southwestern naturalist, 1999: p. 83-86.
238. Beeman, L.E. and M.R. Pelton, *Seasonal foods and feeding ecology of black bears in the Smoky Mountains.* Bears: Their Biology and Management, 1980: p. 141-147.
239. Munro, R.H.M., et al., *Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta.* Journal of Mammalogy, 2006. **87**(6): p. 1112-1121.

240. Stirling, I. and E.H. McEwan, *The caloric value of whole ringed seals (Phoca hispida) in relation to polar bear (Ursus maritimus) ecology and hunting behavior.* Canadian Journal of Zoology, 1975. **53**(8): p. 1021-1027.
241. Chuang, S.A. and L.L. Lee, *Food habits of three carnivore species (Viverricula indica, Herpestes urva, and Melogale moschata) in Fushan Forest, northern Taiwan.* Journal of Zoology, 1997. **243**(1): p. 71-79.
242. Ben-David, M., S.M. Pellis, and V.C. Pellis, *Feeding habits and predatory behaviour in the marbled polecat (Vormela peregusna syriaca): I. Killing methods in relation to prey size and prey behaviour.* Behaviour, 1991: p. 127-143.
243. Nel, J., *Behavioural ecology of canids in the south-western Kalahari.* Koedoe, 1984. **27**(2): p. 229-235.
244. Andersen, D.E., et al., *Aspects of swift fox ecology in southeastern Colorado.* The swift fox: ecology and conservation of swift foxes in a changing world. Canadian Plains Research Center, University of Regina, Regina Saskatchewan, Canada, 2003: p. 139-148.
245. Johnson, W.J., *Food habits of the red fox in Isle Royale National Park, Lake Superior.* American Midland Naturalist, 1970: p. 568-572.
246. Di Fiore, A. and C.J. Campbell, *The atelines: variation in ecology, behavior, and social organization.* Primates in perspective, 2007: p. 155-185.
247. Charles-Dominique, P., *Ecology and feeding behaviour of five sympatric lorisids in Gabon*. 1974: Duckworth.
248. Harcourt, A., *Sperm competition and the evolution of nonfertilizing sperm in mammals.* Evol, 1991. **45**: p. 314-328.
249. Norconk, M.A., *Sakis, uakaris, and titi monkeys.* Behav. Ecol, Sociobiol, 2007. **41**: p. 291-309.
250. Porter, L.M., *Dietary differences among sympatric Callitrichinae in northern Bolivia: Callimico goeldii, Saguinus fuscicollis and S. labiatus.* International Journal of Primatology, 2001. **22**(6): p. 961-992.
251. Digby, L.J., S.F. Ferrari, and W. Saltzman, *Callitrichines: The role of competition in cooperatively breeding species*, in *Primates in Perspective*, C.J. Campbell, et al., Editors. 2007, Oxford University Press: New York. p. 85-105.
252. Defler, T.R., *On the ecology and behavior ofCebus albifrons in eastern Colombia: I. Ecology.* Primates, 1979. **20**(4): p. 475-490.
253. Mittermeier, R.A. and M. Van Roosmalen, *Preliminary observations on habitat utilization and diet in eight Surinam monkeys.* Folia Primatologica, 1981. **36**(1-2): p. 1-39.
254. Rose, L.M., *Sex differences in diet and foraging behavior in white-faced capuchins (Cebus capucinus).* International Journal of Primatology, 1994. **15**(1): p. 95-114.
255. Izar, P., *Female social relationships of Cebus apella nigritus in a southeastern Atlantic forest: an analysis through ecological models of primate social evolution.* Behaviour, 2004. **141**(1): p. 71-99.
256. Miller, L.E., *Socioecology of the Wedge-capped Capuchin Monkey (Cebus Olivaceus)*. 1992, University of California, Davis.
257. Rutte, C., *Strategien der Nahrungssuche bei der Rauchgrauen Mangabe (Cercocebus torquatus atys)*. 1998, Thesis, University of Erlangen-Nürnberg.
258. Enstam, K.L. and L.A. Isbell, *The guenons (genus Cercopithecus) and their allies: behavioral ecology of polyspecific associations.* Primates in perspective, 2007: p. 252-274.
259. Galat, G. and A. Galat-Luong, *Démographie et régime alimentaire d'une troupe de Cercopithecus aethiops sabaeus en habitat marginal au nord Sénégal.* La Terre et la Vie: Revue d'Ecologie Appliquée, 1977. **31**: p. 557-577.
260. Fashing, P.J., *African colobine monkeys: patterns of between-group interaction.* Primates in perspective, 2007: p. 201-224.

261. Fashing, P.J., E.S. Dierenfeld, and C.B. Mowry, *Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of Colobus guereza in Kakamega Forest, Kenya.* International Journal of Primatology, 2007. **28**(3): p. 673-703.
262. Dasilva, G.L., *The ecology of the Western Black and White Colobus (Colobus polykomos polykomos Zimmerman 1780) on a riverine island in South-Eastern Sierra Leone*. 1989, University of Oxford.
263. Sterling, E.J., *Evidence for nonseasonal reproduction in wild aye-ayes (Daubentonia madagascariensis).* Folia Primatologica, 1994. **62**(1-3): p. 46-53.
264. Rasmussen, M.A., *Ecological influences on activity cycle in two cathemeral primates, the mongoose lemur (Eulemur mongoz) and the common brown lemur (Eulemur fulvus fulvus)*. 1999, Duke University.
265. Birkinshaw, C., *Fruit Characteristics of Species Dispersed by the Black Lemur (Eulemur macaco) in the Lokobe Forest, Madagascar1.* Biotropica, 2001. **33**(3): p. 478-486.
266. Harcourt, C.S., *Seasonal variation in the diet of South African galagos.* International Journal of Primatology 7, 1986: p. 491-506.
267. Remis, M., et al., *Nutritional aspects of western lowland gorilla (Gorilla gorilla gorilla) diet during seasons of fruit scarcity at Bai Hokou, Central African Republic.* International Journal of Primatology, 2001. **22**(5): p. 807-836.
268. Overdorff, D.J., S.G. Strait, and A. Telo, *Seasonal variation in activity and diet in a small-bodied folivorous primate, Hapalemur griseus, in southeastern Madagascar.* American journal of primatology, 1997. **43**(3): p. 211-223.
269. Kelley, E., *Lemur catta in the region of Cap Sainte-Marie, Madagascar: introduced cacti, xerophytic Didiereaceae-Euphorbia bush, and tombs.* 2011.
270. Miller, K.E. and J.M. Dietz, *Effects of individual and group characteristics on feeding behaviors in wild Leontopithecus rosalia.* International journal of primatology, 2006. **27**(3): p. 911-939.
271. Thalmann, U., *Food resource characteristics in two nocturnal lemurs with different social behavior: Avahi occidentalis and Lepilemur edwardsi.* International Journal of Primatology, 2001. **22**(2): p. 287-324.
272. Poulsen, J.R., C.J. Clark, and T.B. Smith, *Seasonal variation in the feeding ecology of the grey-cheeked mangabey (Lophocebus albigena) in Cameroon.* American Journal of Primatology, 2001. **54**(2): p. 91-105.
273. Nekaris, K. and D.T. Rasmussen, *Diet and feeding behavior of Mysore slender lorises.* International Journal of Primatology, 2003. **24**(1): p. 33-46.
274. Thierry, B., *The macaques: a double-layered social organization.* Primates in perspective, 2007: p. 224-239.
275. Goldstein, S. and A. Richard, *Ecology of rhesus macaques (Macaca mulatta) in northwest Pakistan.* International Journal of Primatology, 1989. **10**(6): p. 531-567.
276. Caldecott, J.O., *Mating patterns, societies and the ecogeography of macaques.* Animal Behaviour, 1986. **34**: p. 208-220.
277. O'Brien, T.G. and M.F. Kinnaird, *Behavior, Diet, and movement of the Sulawesi crested black macaque (Macaca nigra).* Int. J. Primatol., 1997. **18**: p. 321-351.
278. Krishnamani, R., *Diet composition of the bonnet macaque (Macaca radiata) in a tropical dry evergreen forest of southern India.* Tropical Biodiversity, 1994. **2**(2): p. 285-302.
279. Kumar, A., *The ecology and population dynamics of the lion-tailed macaque (Macaca silenus) in South India*. 1987, University of Cambridge.
280. Hoshino, J., *Feeding ecology of mandrills (Mandrillus sphinx) in Campo animal reserve, Cameroon.* Primates, 1985. **26**(3): p. 248-273.
281. Génin, F., *Gumnivory in mouse lemurs during the dry season in Madagascar.* Folia Primatol, 2001. **72**: p. 119-120.

282. Kirkpatrick, R.C., *The Asian colobines: diversity among leaf-eating monkeys.* Primates in perspective, 2007. **2**: p. 189-201.
283. Wiens, F., A. Zitzmann, and N.A. Hussein, *Fast food for slow lorises: is low metabolism related to secondary compounds in high-energy plant diet?* Journal of Mammalogy, 2006. **87**(4): p. 790-798.
284. Crompton, R., *Foraging, habitat structure, and locomotion in two species of Galago.* 1984.
285. Harcourt, C., *Seasonal variation in the diet of South African galagos.* International journal of primatology, 1986. **7**(5): p. 491-506.
286. Stumpf, R., *Chimpanzees and bonobos: diversity within and between species.* Primates in perspective, 2007: p. 321-344.
287. Hill, R. and R. Dunbar, *Climatic determinants of diet and foraging behaviour in baboons.* Evolutionary Ecology, 2002. **16**(6): p. 579-593.
288. Soini, P., *A synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru.* Primate Conservation, 1986. **7**: p. 63-71.
289. Norconk, M.A., *Sakis, Uakaris, and Titi Monkeys. Behaviroal diversity in a radiation of primate seed predators*, in *Primates in Perspective*, C.J. Campbell, et al., Editors. 2007, Oxford University Press: New York.
290. Morrogh-Bernard, H.C., et al., *Orangutan activity budgets and diet: a comparison between species, populations and habitats*. Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.], ed. S.A. Wich, et al. 2009. 119-133.
291. Sterck, E.H.M., *Females, foods and fights: a socioecological comparison of the sympatric Thomas langur and long-tailed macaque*. 1995.
292. Irwin, M.T., *Feeding ecology of Propithecus diadema in forest fragments and continuous forest.* International Journal of Primatology, 2008. **29**(1): p. 95-115.
293. Arrigo-Nelson, S.J., *The impact of habitat disturbance on the feeding ecology of the Milne-Edwards' sifaka (Propithecus edwardsi) in Ranomafana National Park, Madagascar*. 2006, Stony Brook University.
294. Lippold, L.K., *Natural history of douc langurs.* The natural history of the doucs and snub-nosed monkeys, 1998: p. 191-206.
295. Garber, P.A., *Seasonal patterns of diet and ranging in two species of tamarin monkeys: stability versus variability.* International Journal of Primatology, 1993. **14**(1): p. 145-166.
296. Garber, P.A., *Locomotor behavior and feeding ecology of the Panamanian tamarin (Saguinus oedipus geoffroyi, Callitrichidae, Primates).* International Journal of Primatology 1980. **1**: p. 185-201.
297. Peres, C., *Diet and feeding ecology of saddle-back (Saguinus fuscicollis) and moustached (S. mystax) tamarins in an Amazonian terra firme forest.* Journal of Zoology, 1993. **230**(4): p. 567-592.
298. Lima, E.M. and S.F. Ferrari, *Diet of a free-ranging group of squirrel monkeys (Saimiri sciureus) in eastern Brazilian Amazonia.* Folia Primatologica, 2003. **74**(3): p. 150-158.
299. Gursky, S.L., *The response of spectral tarsiers toward avian and terrestrial predators*, in *Primate anti-predator strategies*. 2007, Springer. p. 241-252.
300. Hunter, C.P., *Ecological determinants of gelada ranging patterns (Theropithecus gelada)*. 2001, University of Liverpool.
301. Morland, H.S., *Social organization and ecology of black and white ruffed lemurs (Varecia variegata variegata) in lowland rain forest, Nosy Mangabe, Madagascar*. 1991, Yale University.
302. Read, A.F. and P.H. Harvey, *Life history differences among the eutherian radiations.* J. Zool. (Lond.), 1989. **219**: p. 329-353.
303. Charnov, E.L., *Life History Invariants: some explorations of symmetry in evolutionary ecology*. 1993, Oxford: Oxford University Press.

304. van Schaik, C.P., et al., *Primate life histories and the role of brains*, in *The Evolution of Human Life History*, K. Hawkes and R.R. Paine, Editors. 2006, School of American Research Press: Santa Fe. p. 127-154.
305. Charnov, E.L., *The optimal balance between growth rate and survival in mammals.* Evol Ecol Res, 2004. **6**: p. 307-313.
306. Kirkwood, T.B.L., *Evolution of ageing.* Mechanisms of Ageing and Development, 2002. **123**: p. 737-745.
307. Tarnaud, L., *Ontogeny of feeding behavior of Eulemur fulvus in the dry forest of Mayotte.* International Journal of Primatology, 2004. **25**(4): p. 803-824.
308. van Noordwijk, M.A., et al., *Female philopatry and its social benefits among Bornean orangutans.* Behavioral Ecology and Sociobiology, 2012. **66**: p. 823-834.
309. van Schaik, C.P., E.A. Fox, and A.F. Sitompul, *Manufacture and use of tools in wild Sumatran orangutans.* Naturw., 1996. **83**: p. 186-188.
310. Rapaport, L.G. and G.R. Brown, *Social influences on foraging behavior in young nonhuman primates: Learning what, where, and how to eat.* Evolutionary Anthropology, 2008. **17**(4): p. 189-201.
311. Schuppli, C., et al., *Observational social learning and socially induced practice of routine skills in wild immature orang-utans.* Animal Behaiour, 2016. **In press**.
312. van Schaik, C.P., M.A. van Noordwijk, and E.R. Vogel, *Ecological sex differences in wild orangutans*. Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.], ed. S.A. Wich, et al. 2009. 255-268.
313. ESRI, *Arc GIS Desktop: Release 10*. 2011: Redlands, CA: Environmental Systems Research Institute.
314. Beyer, H.L., *Hawth's Analysis Tools for ArcGIS*. 2004.
315. Rothman, J.M., et al., *Measuring physical traits of primates remotely: the use of parallel lasers.* American Journal of Primatology, 2008. **70**(12): p. 1191-1195.
316. Chappell, J., et al., *The Ontogeny of gap crossing behaviour in Bornean orangutans (Pongo pygmaeus wurmbii).* PloS one, 2015. **10**(7): p. e0130291.
317. Bates, D., et al., *lme4: Linear mixed-effects models using Eigen and S4.* R package version, 2014. **1**(7).
318. Hothorn, T., Bretz, F., Westfall P., *Simultaneous Inference in General Parametric Models.* Biometrical Journal 2008. **50**(3): p. 346-363.
319. Borchers, H.W., *Practical Numerical Math Functions*. 2015.
320. Vogel, E.R., et al., *The mechanical properties of foods consumed by wild Orangutans (Pongo pygmaeus wurmbii) in Central Kalimantan, Indonesia.* Journal of Morphology, 2007. **268**(12): p. 1146-1146.
321. Basabose, A.K., *Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo.* American Journal of Primatology, 2002. **58**(1): p. 1-21.
322. Wrangham, R., et al., *The significance of fibrous foods for Kibale Forest chimpanzees [and discussion].* Philosophical Transactions of the Royal Society of London B: Biological Sciences, 1991. **334**(1270): p. 171-178.
323. van Schaik, C.P. and M.A. van Noordwijk, *The hidden costs of sociality: intra-group variation in feeding strategies in sumatran long-tailed macaques (Macaca fascicularis).* Behav, 1986. **99**: p. 296-315.
324. Durston, S., et al., *Anatomical MRI of the developing human brain: what have we learned?* Journal of the American Academy of Child & Adolescent Psychiatry, 2001. **40**(9): p. 1012-1020.
325. Giedd, J.N., et al., *Brain development during childhood and adolescence: a longitudinal MRI study.* Nature Neuroscience, 1999. **2**: p. 861-863.

326. Paus, T., *Mapping brain maturation and cognitive development during adolescence.* Trends in cognitive sciences, 2005. **9**(2): p. 60-68.
327. Crews, F., J. He, and C. Hodge, *Adolescent cortical development: a critical period of vulnerability for addiction.* Pharmacology Biochemistry and Behavior, 2007. **86**(2): p. 189-199.
328. Casey, B., R.M. Jones, and T.A. Hare, *The adolescent brain.* Annals of the New York Academy of Sciences, 2008. **1124**(1): p. 111-126.
329. Nowicki, S., S. Peters, and J. Podos, *Song learning, early nutrition and sexual selection in songbirds.* Amer. Zool., 1998. **38**: p. 179-190.
330. Levitsky, D.A. and B.J. Strupp, *Malnutrition and the brain: changing concepts, changing concerns.* Journal of Nutrition, 1995. **125**: p. S2212-2220.
331. Hiraiwa-Hasegawa, M., *The ontogeny of feeding*, in *The Chimpanzees of the Mahale Mountains. Sexual and Life History Strategies.*, T. Nishida, Editor. 1990b, University of Tokyo Press: Tokyo. p. 277-283.
332. Agostini, I. and E. Visalberghi, *Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (Capucinus nigritus).* American Journal of Primatology, 2005. **65**: p. 335-351.
333. O'Mara, M.T. and C.M. Hickey, *Social influences on the development of ringtailed lemur feeding ecology.* Animal Behaviour, 2012. **84**(6): p. 1547-1555.
334. Gautier-Hion, A., *Seasonal variations of diet related to species and sex in a community of Cercopithecus monkeys.* J. Anim. Ecol., 1980. **49**: p. 237-269.
335. Fragaszy, D.M. and E. Visalberghi, *Social processes affecting the appearance of innovative behaviors in capuchin monkeys.* Folia Primatol., 1990. **54**: p. 155-165.
336. Lonsdorf, E.V., *Sex differences in the development of termite-fishing skills in the wild chimpanzees, Pan troglodytes schweinfurthii, of Gombe National Park, Tanzania.* Animal Behaviour, 2005. **70**: p. 673-83.
337. Utami Atmoko, S.S., et al., *Orangutan mating behavior and strategies*. Orangutans: geographic variation in behavioral ecology and conservation. [Oxford Biology.], ed. S.A. Wich, et al. 2009. 235-244.
338. van Noordwijk, M.A., et al., *Multi-year lactation and its consequences in Bornean orangutans (Pongo pygmaeus wurmbii).* Behavioral Ecology and Sociobiology, 2013. **67**: p. 805-814.
339. van Noordwijk, M.A., et al., *Spatial position and behavioral sex differences in juvenile long-tailed macaques*, in *Juvenile primates. Life History, Development, and Behavior*, M.E. Pereira and L.A. Fairbanks, Editors. 1993, Oxford University Press: New York. p. 77-85.
340. Clutton-Brock, T.H., *Some aspects of intraspecific variation in feeding and ranging behaviour in primates*, in *Primate Ecology*, T.H. Clutton-Brock, Editor. 1977, Academic Press: London. p. 539-556.
341. Schuppli, C., et al., *Life history, cognition and the evolution of complex foraging niches.* Journal of human evolution, 2016. **92**: p. 91-100.
342. Whiten, A., et al., *Cultures in chimpanzees.* Nature, 1999. **399**(6737): p. 682-685.
343. Galef, B.G. and K.N. Laland, *Social learning in animals: Empirical studies and theoretical models.* Bioscience, 2005. **55**(6): p. 489-499.
344. Reader, S.M. and D. Biro, *Experimental identification of social learning in wild animals.* Learning & Behavior, 2010. **38**(3): p. 265-283.
345. van Schaik, C.P., *Social learning and culture in animals*. Animal Behaviour: Evolution and Mechanisms, ed. P. Kappeler. 2010. 623-653.
346. Hoppitt, W., et al., *Identification of Learning Mechanisms in a Wild Meerkat Population.* Plos One, 2012. **7**(8).
347. Tomasello, M., *The question of chimpanzee culture*, in *Chimpanzee Cultures*, R.W. Wrangham, et al., Editors. 1994, Harvard University Press. p. 301-318.

348. Byrne, R.W. and A.E. Russon, *Learning by imitation: A hierarchical approach.* Behavioral and Brain Sciences, 1998. **21**(5): p. 667-+.

349. Fragaszy, D.M. and S. Perry, *Towards a biology of traditions.* The biology of traditions: Models and evidence, 2003: p. 1-32.

350. Galef, B.G., *Approaches to the study of traditional behaviors of free-living animals.* Learning & Behavior, 2004. **32**(1): p. 53-61.

351. Whiten, A., *Social learning, traditions, and culture*. The evolution of primate societies., ed. J.C. Mitani, et al. 2012. 682-700.

352. van de Waal, E., et al., *Similarity in Food Cleaning Techniques within Matrilines in Wild Vervet Monkeys.* Plos One, 2012. **7**(4).

353. Hobaiter, C., et al., *Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees.* Plos Biology, 2014. **12**(9).

354. van Schaik, C.P., *Orangutan cultures and the comparative study of culture.* American Journal of Physical Anthropology, 2003: p. 214-214.

355. Whiten, A. and A. Mesoudi, *Establishing an experimental science of culture: animal social diffusion experiments.* Philosophical Transactions of the Royal Society B-Biological Sciences, 2008. **363**(1509): p. 3477-3488.

356. Matthews, L.J., *Cluster analysis and social network theory applied to the study of socially learned traditions in primates.* American Journal of Physical Anthropology, 2009: p. 186-187.

357. Perry, S., *Socia influence and the development of food processing techniques in wil White-faced Cauchin Monkeys (Cebus Capucinus) at Lomas Barbudal, Costa Rica.* American Journal of Primatology, 2009. **71**: p. 99-99.

358. Thornton, A. and A. Malapert, *Experimental evidence for social transmission of food acquisition techniques in wild meerkats.* Animal Behaviour, 2009. **78**(2): p. 255-264.

359. Dawson, B.V. and B.M. Foss, *Observational learning in budgerigars.* Animal Behaviour, 1965. **13**(4): p. 470-&.

360. Whiten, A. and D. Custance, *Studies of imitation in chimpanzees and children*. Social learning in animals: The roots of culture, ed. C.M. Heyes and B.G. Galef, Jr. 1996. 291-318.

361. Hopper, L.M., et al., *Experimental studies of traditions and underlying transmission processes in chimpanzees.* Animal Behaviour, 2007. **73**: p. 1021-1032.

362. Whiten, A., et al., *Transmission of multiple traditions within and between chimpanzee groups.* Current Biology, 2007. **17**(12): p. 1038-1043.

363. Stoinski, T.S., et al., *Imitative learning by captive western lowland gorillas (Gorilla gorilla gorilla) in a simulated food-processing task.* J. Comp. Psych., 2001/2.

364. Russon, A.E. and B.M. Galdikas, *Imitation in free-ranging rehabilitant orangutans (Pongo pygmaeus).* Journal of Comparative Psychology, 1993. **107**(2): p. 147.

365. Stoinski, T. and A. Whiten, *Social learning by orangutans (Pongo abelii and Pongo pygmaeus) in a simulated food processing task.* J. Comp. Psych., 2003. **117**: p. 272-282.

366. Dindo, M., T. Stoinski, and A. Whiten, *Observational learning in orangutan cultural transmission chains.* Biology Letters, 2011. **7**(2): p. 181-183.

367. Zentall, T.R., *Social learning mechanisms Implications for a cognitive theory of imitation.* Interaction Studies, 2011. **12**(2): p. 233-261.

368. Kummer, H. and J. Goodall, *Conditions of innovative behavior in primates.* Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 1985. **308**(1135): p. 203-214.

369. Benson-Amram, S., M.L. Weldele, and K.E. Holekamp, *A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, Crocuta crocuta.* Animal Behaviour, 2013. **85**(2): p. 349-356.

370. Gajdon, G.K., N. Fijn, and L. Huber, *Testing social learning in a wild mountain parrot, the kea (Nestor notabilis).* Learning & Behavior, 2004. **32**(1): p. 62-71.

371. Gajdon, G.K., N. Fijn, and L. Huber, *Limited spread of innovation in a wild parrot, the kea (Nestor notabilis).* Animal Cognition, 2006. **9**(3): p. 173-181.
372. Galef, B.G., Jr. and L.-A. Giraldeau, *Social influences on foraging in vertebrates: causal mechanisms and adaptive functions.* Anim. Behav., 2001. **61**: p. 3-15.
373. Tarnaud, L. and J. Yamagiwa, *Age-Dependent Patterns of Intensive Observation on Elders by Free-Ranging Juvenile Japanese Macaques (Macaca fuscata yakui) within Foraging Context on Yakushima.* American Journal of Primatology, 2008. **70**(12): p. 1103-1113.
374. Whitehead, J.M., *Development of feeding selectivity in mantled howling monkeys, Alouatta palliata*. Primate ontogeny, cognition and social behaviour., ed. J.G. Else and P.C. Lee. 1986. 105-117.
375. Mann, J. and B. Sargeant, *Like mother, like calf: the ontogeny of foraging traditions in wild Indian ocean bottlenose dolphins (Tursiops sp.)*. The biology of traditions: models and evidence., ed. D.M. Fragaszy and S. Perry. 2003. 236-266.
376. Matsuzawa, T., et al., *Emergence of culture in wild chimpanzees: Education by master-apprenticeship.* Primate Origins of Human Cognition and Behavior, 2001: p. 557-574.
377. Lonsdorf, E.V., L.E. Eberly, and A.E. Pusey, *Sex differences in learning in chimpanzees.* Nature, 2004. **428**: p. 715-716.
378. Humle, T., C.T. Snowdon, and T. Matsuzawa, *Social influences on ant-dipping acquisition in the wild chimpanzees (Pan troglodytes verus) of Bossou, Guinea, West Africa.* Animal Cognition, 2009. **12**: p. S37-S48.
379. Biro, D., et al., *Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments.* Animal Cognition, 2003. **6**(4): p. 213-223.
380. Coelho, C.G., et al., *Social learning strategies for nut-cracking by tufted capuchin monkeys (Sapajus spp.).* Animal Cognition, 2015. **18**(4): p. 911-919.
381. Ottoni, E.B., B.D. de Resende, and P. Izar, *Watching the best nutcrackers: what capuchin monkeys (Cebus apella) know about others' tool-using skills.* Animal Cognition, 2005. **8**(4): p. 215-219.
382. Laland, K.N., *Social learning strategies.* Learning & Behavior, 2004. **32**(1): p. 4-14.
383. van Schaik, C.P., et al., *A simple alternative to line transects of nests for estimating orangutan densities.* Primates, 2005. **46**(4): p. 249-254.
384. Bretz, F., T. Hothorn, and P. Westfall, *Multiple comparisons using R*. 2016: CRC Press.
385. van Schaik, C.P., E.A. Fox, and L.T. Fechtman, *Individual variation in the rate of use of tree-hole tools among wild orang-utans: implications for hominin evolution.* Journal of Human Evolution, 2003. **44**(1): p. 11-23.
386. Meulman, E., *Flexible tool use and its acquisition in wild Sumatran orangutans, Pongo abelii*, in *Anthropological Institute and Museum*. 2014, University of Zürich: Zürich.
387. Schuppli, C., et al., *Development of foraging skills in two orangutan populations: needing to learn or needing to grow?* Frontiers in Zoology, 2016. **13**(1): p. 43.
388. InoueNakamura, N. and T. Matsuzawa, *Development of stone tool use by wild chimpanzees (Pan troglodytes).* Journal of Comparative Psychology, 1997. **111**(2): p. 159-173.
389. Stoinski, T.S. and A. Whiten, *Social learning by orangutans (Pongo abelii and Pongo pygmaeus) in a simulated food-processing task.* Journal of Comparative Psychology, 2003. **117**(3): p. 272-282.
390. Griesser, M. and T.N. Suzuki, *Kinship modulates the attention of naive individuals to the mobbing behaviour of role models.* Animal Behaviour, 2016. **112**: p. 83-91.
391. Feinman, S., *Social referencing in infancy.* Merrill-Palmer Quarterly-Journal of Developmental Psychology, 1982. **28**(4): p. 445-470.
392. Harlow, H.F., Dodswort.Ro, and M.K. Harlow, *Total social isolation in monkeys.* Proceedings of the National Academy of Sciences of the United States of America, 1965. **54**(1): p. 90-&.

393. Brent, L., M.A. Bloomsmith, and S.D. Fisher, *Factor determining tool-using ability in 2 captive chimpanzee (Pan troglodytes) colonies.* Primates, 1995. **36**(2): p. 265-274.
394. Bastian, M.L., et al., *Diet Traditions in Wild Orangutans.* American Journal of Physical Anthropology, 2010. **143**(2): p. 175-187.
395. Wich, S.A., et al., *Call Cultures in Orang-Utans?* PLoS One, 2012. **7**(5): p. e36180.
396. van Schaik, C.P. and G.R. Pradhan, *A model for tool-use traditions in primates: implications for the coevolution of culture and cognition.* Journal of Human Evolution, 2003. **44**(6): p. 645-664.
397. Kline, M.A., *How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals.* Behavioral and Brain Sciences, 2015. **38**: p. null-null.
398. Maggi, S., et al., *The social determinants of early child development: An overview.* Journal of Paediatrics and Child Health, 2010. **46**(11): p. 627-635.
399. Broberg, A.G., et al., *Effects of day care on the development of cognitive abilities in 8-year-olds: A longitudinal study.* Developmental Psychology, 1997. **33**(1): p. 62-69.
400. Landry, S.H., et al., *Does early responsive parenting have a special importance for children's development or is consistency across early childhood necessary?* Developmental Psychology, 2001. **37**(3): p. 387-403.
401. Landry, S.H., et al., *An experimental study evaluating professional development activities within a state funded pre-kindergarten program.* Reading and Writing, 2011. **24**(8): p. 971-1010.
402. RStudio, T., *RStudio: Integrated Development for R.* 2015: Boston, MA
403. Krause, J. and G.D. Ruxton, *Living in groups*. 2002: Oxford University Press.
404. Stöwe, M., et al., *Effetcs of group size on approach to novel objects in ravens (Corvus corax).* Ethology, 2006. **112**: p. 1079-1088.
405. Overington, S.E., et al., *Technical innovations drive the relationship between innovativeness and residual brain size in birds.* Animal Behaviour, 2009. **78**: p. 1001-1010.
406. Mainwaring, M.C., J.L. Beal, and I.R. Hartley, *Zebra finches are bolder in an asocial, rather than social, context.* Behavioural processes, 2011. **87**(2): p. 171-175.
407. Greenberg, R., *Feeding Neophobia and Ecological Plasticity - A Test of the hypothesis with captive sparrows.* Animal Behaviour, 1990. **39**: p. 375-379.
408. Moretti, L., et al., *The influence of relationships on neophobia and exploration in wolves and dogs.* Animal Behaviour, 2015. **107**: p. 159-173.
409. Visalberghi, E. and E. Addess, *Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys.* Animal Behaviour, 2000. **60**: p. 69-76.
410. Roberts, G., *Why individual vigilance declines as group size increases.* Animal Behaviour, 1996. **51**: p. 1077-1086.
411. Dukas, R., *Evolutionary biology of limited attention*, in *Cognitive Biology: Evolutionary and developmental perspectives on mind, brains and behavior*, L. Tomassi, M.A. Peterson, and Nadel.L., Editors. 2009, MIT Press: Cambridge, MA. p. 147-162.
412. Lehner, S.R., J.M. Burkart, and C.P. van Schaik, *An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans.* Primates, 2010. **51**: p. 101-118.
413. Haslam, M., *'Captivity bias' in animal tool use and its implications for the evolution of hominin technology.* Philosophical Transactions of the Royal Society of London, 2013. **368**: p. 20120421.
414. Ambrose, S.H., *Paleolithic technology and human evolution.* Science, 2001. **291**: p. 1748-1753.
415. Richerson, P.J. and R. Boyd, *Not by Genes Alone: How Culture Transformed Human Evolution*. 2005, Chicago: University of Chicago Press.

416. Russon, A.E., et al., *How orangutans (Pongo pygmaeus) innovate for water.* Journal of Comparative Psychology, 2010. **124**: p. 14-28.
417. Lenneberg, E.H., *Biological foundations of language*. Biological foundations of language. 1967. xvi+489p. Illus.-xvi+489p. Illus.
418. Scott, J.P., *Critical periods in behavioral development - critical periods determine direction of social, intellectual and emotional development* Science, 1962. **138**(3544): p. 949-&.
419. De Villiers, J.G. and P.A. De Villiers, *Language acquisition*. 1978: Harvard University Press.
420. Brainard, M.S. and A.J. Doupe, *What songbirds teach us about learning.* Nature, 2002. **417**(6886): p. 351-358.
421. Bruner, J.S., *From Communication to Language - Psychological Perspective.* Cognition, 1975. **3**(3): p. 255-287.
422. Rovee-Collier, C., *Time windows in cognitive development.* Developmental Psychology, 1995. **31**(2): p. 147.
423. Koops, K., E. Visalberghi, and C.P. van Schaik, *The ecology of primate material culture.* Biology Letters, 2014. **10**: p. 20140508.
424. Hrdy, S.B., *Evolutionary context of human development: The cooperative breeding model.* Family relationships: An evolutionary perspective, 2007: p. 39-68.
425. Burkart, J.M. and C.P. van Schaik, *Cognitive consequences of cooperative breeding in primates.* Animal Cognition, 2010. **13**: p. 1-19.
426. van Schaik, C.P. and K. Isler, *Life-history evolution*, in *The Evolution of Primate Societies*, J.C. Mitani, et al., Editors. 2012, The University of Chicago Press: Chicago. p. 220-244.
427. Tomasello, M. and M. Carpenter, *The emergence of social cognition in three young chimpanzees*. Monographs of the Society for Research in Child Development. Vol. 70. 2007, Boston: Blackwell. 160.
428. Barton, R.A., *Embodied cognitive evolution and the cerebellum.* Phil. Trans. R. Soc. B, 2012. **367**(1599): p. 2097-2107.
429. Geary, D.C., *The Origin of Mind: Evolution of Brain, Cognition, and General Intelligence.* 2005, Washington: American Psychological Association.
430. Banerjee, K., et al., *General intelligence in another primate: individual differences across cognitive task performance in a New World monkey (Saguinus oedipus).* PLoS One, 2009. **4**(6): p. e5883.
431. Silk, J.B., et al., *The benefits of social capital: close social bonds among female baboons enhance offspring survival.* Proceedings Royal Society, B, 2009. **276**: p. 3099-3104.
432. McCowan, L.S., et al., *Personality in the wild zebra finch: exploration, sociality, and reproduction.* Behavioral Ecology, 2015: p. aru239.
433. Forss, S.I.F., *Testing the Cultural Intelligence Hypothesis in Orangutans: Variation in Novelty Response, Exploration and Intelligence*, in *Department of Anthropology*. 2016, University of Zürich: Zürich.
434. Damerius, L.A., *What Makes Orangutans Intelligent? The Role of Experience and Learning in the Development of Problem Solving Abilities in Orangutans*, in *Department of Anthropology*. 2017, University of Zürich: Zürich.
435. Damerius, L.A., et al., *Orientation toward humans predicts cognitive performance in orang-utans.* Scientific Reports, 2017. **7**: p. 40052.
436. Damerius, L.A., et al., *Determinants of Variation in Cognitive Performance in Rehabilitation Station-living Orangutans.* In preparation.
437. Forss, S.I., et al., *Cognitive differences between orang-utan species: a test of the cultural intelligence hypothesis.* Scientific Reports, 2016. **6**.
438. van Schaik, C., et al., *The ecology of social learning in animals and its link with intelligence.* The Spanish Journal of Psychology, 2017. **19**.

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In Review:

Schuppli, C., Forss, S., Meulman, E. J. M., Utami Atmoko, S. S., van Noordwijk, M. A., & van Schaik, C. P. (In review). Sociability positively affects exploratory tendency and innovation repertoires in wild orang-utans.

Graber, S., Schuppli, C., Heldstab, S., Isler, K., & van Schaik, C. (In review). Ecology is the Main Driver of Primate Brain Size Evolution.

Haslam, M. R., Hernandez-Aguilar, A., Proffitt, T., Arroyo, A., Falótico, T., Fragaszy, D., Gumert, M., Harris, J.W.K., Huffman, M., Kalan, A., Malaivijitnond, S., Matsuzawa, T., McGrew, W., Ottoni, E.B., Pascual-Garrido, A., Piel, A., Pruetz, J., Schuppli, C., Stewart, F., Tan, A., Visalberghi, E., Luncz L.V. (Submitted). Primate archaeology evolves.

2017:

van Schaik, C., Graber, S., Schuppli, C., & Burkart, J. (2017). The ecology of social learning in animals and its link with intelligence. *The Spanish Journal of Psychology, 19*.

Schuppli, C., Koops, K., & van Schaik, C. (2017). Cultural behavior. In A. Fuentes (Ed.), *The International Encyclopedia of Primatology*: Wiley Online Library.

2016:

Marzec, A. M., Kunz, J. A., Falkner, S., Atmoko, S. S. U., Alavi, S. E., Moldawer, A. M., . . . van Noordwijk, M. A. (2016). The dark side of the red ape: male-mediated lethal female competition in Bornean orangutans. *Behavioral Ecology and Sociobiology, 70*(4), 459-466.

Schuppli, C., Forss, S. I., Meulman, E. J., Zweifel, N., Lee, K. C., Rukmana, E., . . . van Schaik, C. P. (2016). Development of foraging skills in two orangutan populations: needing to learn or needing to grow? *Frontiers in Zoology, 13*(1), 43.

Schuppli, C., Graber, S. M., Isler, K., & van Schaik, C. P. (2016). Life history, cognition and the evolution of complex foraging niches. *Journal of Human Evolutio n, 92*, 91-100.

Schuppli, C., Meulman, E., Forss, S. I. F., Aprilinayati, F., Van Noordwijk, M. A., & Van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in wild immature orang-utans. *Animal Behaiour, 119*, 87-98.

van Schaik, C. P., Burkart, J., Damerius, L., Forss, S. I. F., Koops, K., van Noordwijk, M. A., & Schuppli, C. (2016). The reluctant innovator: orangutans and the phylogeny of creativity. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 371*(1690). doi:10.1098/rstb.2015.0183

2015:

Forss, S. I. F., Schuppli, C., Haiden, D., Zweifel, N., & Van Schaik, C. P. (2015). Contrasting Responses to Novelty by Wild and Captive Orangutans. *American Journal of Primatology, 77*(10), 1109-1121. doi:10.1002/ajp.22445

2012:

Schuppli, C., Isler, K., & van Schaik, C. P. (2012). How to explain the unusually late age at skill competence among humans. *Journal of Human Evolution, 63*(6), 843-850. doi:10.1016/j.jhevol.2012.08.009