# Cooperative Breeding and the Evolution of Brain Size in Birds


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A comparative study investigating the effect of help on brain size in cooperatively breeding bird species.

Master's Thesis

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# Contents

# Abstract

Great apes have relatively larger brains than monkeys and crows have relatively larger brains than pheasants. Brain size variation runs across a vast number of different taxa and still seems to be an unsolved and controversial phenomenon. Many different approaches and comparative methods have been used to understand and explain brain size variation. Either adaptive benefits of enhanced cognitive abilities or energetic aspects of enlarged brains were part of several theories in recent years. However, why certain species have bigger brains than others seems to stay an evolutionary puzzle. Bennett and Owens (2002, p.74) implied in their book of Evolutionary Ecology of birds: „A study is required that uses modern comparative methods to investigate a range of potential correlates of variation in relative brain size across a wide range of bird species. Only then can the relative importance of ecological and behavioural complexity, developmental and energetic constraints, or sexual selection, be unravelled“. In this regard, this study helps to understand this still unclear variation in brain size by using an energy balance perspective. Others suggest that more energy-rich and cognitively demanding foods might have been important preconditions in the evolution of large brains (Aiello and Wheeler 1995). This research project looked at the framework between cooperative breeding, energetic resources and brain size in birds.

As in mammals, avian species without allomaternal care show a strong trade-off between reproduction and relative brain size, whereas species with allomaternal care show no such negative relationship. I predicted more helpers at the nest to positively affect either relative brain size or reproduction, leading to an alleviated reproduction trade-off. However, my results suggest that more helpers at the nest do not result in higher total energetic resources during breeding, larger brains or higher reproduction but rathers act as a energetic load-lightening for the breeding pair. The energetic load-lightening increases adult survival which in the end allows cooperatively breeding species to evade the trade-off between reproduction and relative brain size. Contrarily to my initial prediction, it is not brain size or reproduction which is positively affected by additional helpers during breeding, but rather survival which allows to maintain a relativley large brains besides the energetically demanding reproduction process.

Moreover, variation in total energetic resources cannot be explained by differences in breeding systems, but rather by other, yet uknown factors (e.g. ecology). However, variation in energetic resources during breeding positively correlate with variation in relative brain size.

In sum, with this study I have demonstrated that energy plays a crucial role in the framework of allomaternal care and relative brain size. The framework as a whole enlightens important aspects of cooperative breeding and brain size evolution in birds. These findings are important for the further study of brain size evolution in mammals, especially in the lineage of *Homo*.

# 1 Introduction

## 1.1 Brain size variation - a puzzling phenomenon

A puzzling and controversial phenomenon is the continuous increase of relative brain size (corrected for body size) over evolutionary time - in mammals, birds, and other taxa (Marsh's rule) (Jerison 1970, 1973, 2000, Dunbar and Shultz 2007, Finarelli 2008). Noticeable is the large relative brain size of us humans compared to our closest relatives, the great apes. Further, relative brain size shows a huge variation across species which is not observed in other organs (Jerison 1973, Bennett and Owens 2002). Figure 1.1 illustrates the differences in variation between organs such as brain and heart in relation to body mass for a range of avian species.

How can we explain this variation, and the enlargement of the brain observed over time? What made the evolution of enlarged brains even possible ? Why have some species larger brains than others? What are the benefits and costs of large brains ? Two different approaches exist to explain the variation in brain size: on one hand, the investigation of selective benefits of enlarged brains and on the other hand, the metabolic and developmental constraints on large brains. To understand the underlying evolutionary processes, it is mandatory to consider both, costs and benefits. Whereas the adaptive benefits of bigger brains and enhanced cognitive abilities may explain the overall trend towards larger brains, considering developmental and energetic costs is imperative in order to explain why an increase in brain size was possible for some lineages or species but not for others. In order for large brains to evolve, the benefits need to overcome the costs of growth and maintenance (Mink et al. 1981, Dunbar 1998, Kaufman et al. 2003). Vertebrate species spend on average 2-8% of their resting metabolism for the central nervous system (Mink et al. 1981). In primates, these percentages are even higher (13-20%), especially in humans, where the brain accounts for only 2% of the total body mass and is responsible for 20% of the total resting metabolic rate (figure 1.2) (Mink et al. 1981, Aiello and Wheeler 1995, Rolfe and Brown 1997). Human brains need in average eight to ten times more energy than skeletal muscle (Dunbar and Shultz 2007). Immature animals have relatively large brains and thus spend extremely high amounts of energy to brain growth and maintenance (over 60% of BMR in human neonates). Malnutrition in such an early stage of development can have harmful long-term effects on brain functions and cognitive behaviour (Levitsky and Strupp 1995, Nowicki et al. 1998). In times where energy resources are scarce, the energy flow to the brain is preferred over other expensive organs, which also emphasises its importance and its susceptibility to energy scarcity (Lukas and Campbell 2000). The costs for maintaining and growing large brains become even higher, as vertebrate taxa show an increase in encephalization over evolutionary time (Jerison 1970, 2000, Dunbar and Shultz 2007). Thus, energetic constraints most probably have its impact on brain size evolution.

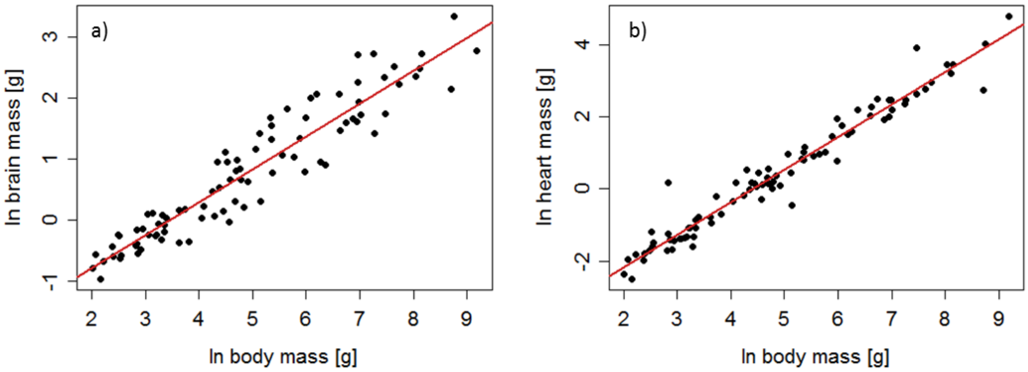


Figure 1.1: **Brain and heart mass vs. body mass.** Least-square regressions of (a) ln brain mass ($r^2 = 0.94$), (b) ln heart mass ($r^2 = 0.98$) on ln body mass for 87 bird species, showing that variation in brain size is bigger than in other organs ($mean \pm SD$ of residuals: residuals ln brain mass: $2.87e - 09 \pm 0.35$; residuals ln heart mass: $3.79e - 09 \pm 0.37$).

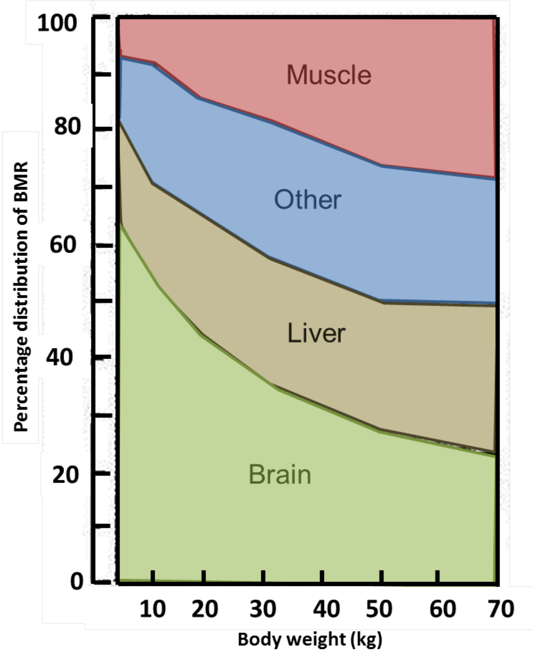


Figure 1.2: **Allocation of BMR to different organs.** Percentage of BMR for brain, liver, muscle and other organs for different body mass in humans. The brain is especially expensive during childhood (according to Holliday 1986).

## 1.2 Hypotheses explaining variation in relative brain size

In recent years, a variety of comparative analyses have tried to explain this huge variation in relative brain size in birds as well as in other taxa, especially in primates, using either adaptive benefit or energetic and developmental constraint approaches. Many hypotheses are still under consideration. These partly overlapping theories are summarized in table 1.1. The theories including ecological and social system traits mainly focus on the advantages of large brains (indicated with B). Looking at life histories, development patterns and metabolic costs, the focus is rather directed to energetic and time constraints (indicated with C).

Table 1.1: **Hypotheses explaining brain size variation.** Either using an adaptive benefit (B) or a constraint (C) approach.

| **Hypothesis** | **Description** | **C or B** | **Supported in** | **Source** |
|---|---|---|---|---|
| **Ecological Hypotheses** | | | | |
| 1)Technical Intelligence Hypothesis | Technical skills and innovations like tool use are only possible with larger brains, thus they confer a fitness benefit. | B | primates, birds | Byrne and Whiten 1997 |
| 2)Extractive Foraging Hypothesis | Complex cognitive and sensorimotor foraging techniques drive the evolution of enhanced cognitive abilities and bigger brains. | B | mammals (especially primates), birds | Gibson 1986 |
| 3) Diet Hypothesis | Frugivores profit from enhanced cognitive abilities in terms of spatial and temporal memory (higher foraging demands) compared to folivores. | B | mammals (especially primates), rodents, bats | Eisenberg and Wilson 1978 |
| 4) Home Range and Navigation Hypotheses | In large home range sizes, higher cognitive abilities in form of complex information processing and storage about food sources are a selective advantage. | B | primates | Clutton-Brock 1980 |
| **Social Brain/Complexity Hypothesis (Machiavellian Intelligence Hypothesis)** | Higher social complexity drives the evolution of larger brains. Group living requires good cognitive skills in terms of dealing with other individuals and recognizing other group member‘s sex, rank etc. | B | primates, birds | Byrne and Whiten 1988,1997 |

(to be continued)

|  |  |  |  |  |
|---|---|---|---|---|
| **Life history Hypotheses** |  |  |  |  |
| 1) Cognitive Buffer Hypothesis | Large-brained species have longer lifespan and higher survival rates (which again correlates with many other life history traits), as they are better in adapting to environmental fluctuations by shifting to alternative food resources. Only long-lived species can benefit from having a large brain. | B | Mammals including primates, birds | Allman et al. 1993; Sol et al. 2007 |
| 2)Needing-to-learn Hypothesis | Maturing or learning periods for large-brained species are longer, as they have to acquire cognitively demanding adult skills. A correlation between juvenile period and brain size is expected. | C | primates | Ross and Jones 1999 |
| 3)Maturational Constraint Hypothesis | To develop complex behaviour, a mature nervous system is required. Large brains elongate behavioural and brain development periods. | C | primates | Deaner et al. 2003 |
| 4)Juvenile Risk Hypothesis (Brain Malnutrition Risk Hypothesis) | Large brains demand slow development periods (adult brain size at the age at weaning) in order to prevent brain growth to be too fast which could be harmful due to energy deficit (brain growth as a constraint) and could therefore improve the survival to maturity. | C | primates | Janson and van Schaik 1993 |
| **Epiphenomenal Hypothesis** | Enlarged brains or brain structures are byproducts of enlarged body sizes, and not the result of selection pressures. | - | primates | Gould 1975 |

(to be continued)

| | | | | |
|---|---|---|---|---|
| **Metabolic Constraint Hypothesis** | Total energy turnover (BMR) acts as a constraint on fetal brain growth respectively on brain maintenance in general. To pay for large brains, the total energy turnover has to be increased. | C | mammals | Armstrong 1983, Hofmann 1983 |
| **Maternal Energy Hypothesis** | Brain size is either constrained by the mother‘s energy budget and the amount she is able to invest into the offspring or by the length of gestation and postnatal growth, or a combination of the two. | C | mammals, reptiles, birds | Martin 1981 |
| **Development Hypothesis** | Developmental pattern (either linked to differences in energetic supply or developmental lengths) as a strong correlate of brain size. | C | birds | Bennett and Harvey 1985, Iwaniuk and Nelson 2003 |
| **Expensive Tissue Hypothesis** | The costs of large brains can be met by investing less in other expensive organs, such as gut or liver. | C | primates, bats, birds | Aiello and Wheeler 1995 |
| **Expensive Brain Framework** | Costs of large brains can either be paid by increasing the total energy turnover, by reducing allocation of resources to locomotion and growth and reproduction, or by a combination of these strategies. | C | some mammals (including bats, marsupials and placentals), birds (details are described in the text) | Isler and van Schaik 2009, Navarrete et al. 2011 |

### 1.2.1 Adaptive benefits of large brains

Life history, social organisation, ecological and cognitive traits were used as explanations for the phenomenon of brain size variation, many studies of which were carried out in primates including *Homo sapiens* and birds. As relative brain size is known to reflect intellectual abilities at least in primates (Deaner et al. 2007, Reader et al. 2011), cognitive theories have become quite popular. The proposed hypotheses concerning positive selection on larger brains in terms of higher cognitive abilities are summarized in table 1.1 (noted with B). In context with foraging, navigation and behavioural flexibility, the **ecological theories** suggest that complex cognitive abilities and skills drive encephalization. Gibson (1986), for example, found evidence suggesting a coherence between neocortex size and complex cognitive and sensorimotor foraging techniques in non-human primates. Several similar studies demonstrated adaptive benefits of large brains in birds: they found relationships between relative brain size and tool use (Lefebvre et al. 2002), innovation rates (Sol et al. 2002, Lefebvre et al. 2004, Sol et al. 2005b, Overington et al. 2009), handling with novel environments (Jerison 1973, Sol et al. 2005a) and population trends (Shultz et al. 2005). However, flightlessness and endocranial volume are not related (Iwaniuk et al. 2004). Other associations between brain structures and cognitive functions have been found in birds, as for example, the correlation between the size of a higher vocal centre and repertoire size in singing behaviour (Szekely et al. 1996) or the complexity of bowers and relative brain size (Madden 2001). However, some of the ecological hypotheses in primates and birds are still highly disputed (Bennett and Harvey 1985b, Dunbar 1998).

The **social complexity hypothesis**, known as well as the **Machiavellian intelligence hypothesis**, posits that higher social complexity acts as an evolutionary force towards larger brains (Byrne and Whiten 1988, 1997). Group living requires good cognitive skills, assuming that conspecific‘s sex, rank, competitive and deceptive behaviours have to be recognised. Some evidence has been found in primates and birds, where positive correlations between neocortex size and social structures such as group size were detected (Sawaguchi and Kudo 1990, Emery et al. 2007, Shultz and Dunbar 2010). However, in general, social mammal systems other than group size effects seem to correlate with brain size, as correlations with group size were only found in primates (Shultz and Dunbar 2007). As in mammals, no group size effect was found in birds (Beauchamp and Fernandez 2004). Furthermore, Iwaniuk and Arnold (2004) did not find evidence that cooperative breeding, with all its complex cognitive demands (group displays (Arnold 2000), coalition formation (Arnold 2000), stable queues for breeding status (Wiley and Rabenold 1984) etc.), has a significant positive effect on corvid relative brain size. In fact, non-cooperatively breeding Corvida species have as large brains as cooperatively breeding Corvida species (Iwaniuk and Arnold 2004).

The best known life history hypothesis concerning adaptive benefits of encephalization is the **cognitive buffer hypothesis** (e.g. Allman et al. 1993; Sol et al. 2007), which claims that large-brained animals show higher behavioural flexibility and thus, have higher survival rates and longer lifespans, correlating with many other life history traits (Charnov 1993). Only long-lived species can thus fully benefit from large brains. Allman et al. (1993) found a positive correlation between relative brain size and life span in haplorhine primate species. Further evidence was found in several other vertebrate species, including primates and birds (Vertebrates in general: Sacher (1978); Charnov (1993); Mammals in general: Isler and van Schaik 2009b, Gonzalez-Lagos et al. 2010; Primates: Allman et al. (1993); Deaner et al. (2003); van Schaik et al. (2006); Barrickman et al. (2008); Birds: Sol et al. (2007)). A recent study based on data from wild primate populations demonstrated a significant association between encephalization and elongation in developmental life history stages (Barrickman et al. 2008). All developmental stages as well as reproductive lifespan (except lactational period) are positively correlated with brain size. These results however do not differentiate between the costs of enlarged brains and their beneficial effects. The cognitive buffer hypothesis nicely explains why large-brained species live longer, but as many long-lived species are not very large-brained (e.g. turtles) it does not convincingly explain variation in relative brain size.

### 1.2.2 Energy and time constraints on brain size

Complementary to the benefits approach of enhanced cognitive abilities, it is important to look at the costs, as time and energetic constraints are essential for understanding evolutionary processes. The brain is the most expensive organ, thus time and energetic resources might limit brain growth and maintenance. One can look at the costs of brains from two perspectives: the perspective of offspring growing large brains and the perspective of adults maintaining large brains. These two perspectives have to be kept in mind while looking at the constraint point of view.

Life history traits like skill learning and brain growth periods might be essential for explaining the constraints of brain size evolution. These explanations are known as the needing-to-learn, maturational constraint and juvenile risk hypotheses and were mainly investigated in primates. Large-brained species need longer learning periods (time constraint), as they have to acquire cognitively demanding adult skills, which is known as the **needing-to-learn hypothesis** (Janson and van Schaik 1993, Joffe 1997, Ross and Jones 1999, Kaplan et al. 2000, Deaner et al. 2003, van Schaik et al. 2006). Similarly, the **maturational constraint hypothesis** claims that a mature nervous system is needed in order to develop complex adult behaviour, which then results in elongated maturing periods (Deaner et al. 2003, van Schaik et al. 2006). It seems that bigger brains and more complex nervous systems need longer to develop and mature. The **juvenile risk hypothesis** proposes that slow brain growth rates avoid malnourishment during brain development and thus combine energetic and time constraints (Janson and van Schaik 1993, Deaner et al. 2003, van Schaik et al. 2006). This hypothesis has recently found support, by the finding that large-brained mammals invest much more in each individual before birth in contrast to smaller brained species, emphasizing the brain malnutrition risk (Isler and van Schaik 2009a). Brain growth and maintenance are very expensive especially during childhood (Aiello 1992).

Energy shortages during this critical time can have harmful consequences (Levitsky and Strupp 1995, Nowicki et al. 1998). Thus, slow growth rates and prolonged juvenile periods might avoid energy shortages and increase the probability of surviving to adulthood (van Schaik et al. 2006).
These three hypotheses (needing-to-learn, maturational constraint and juvenile risk hypothesis) explain variation in life history rather than variation in relative brain size. In fact, they try to clarify why large brains entail a prolonged development period to adulthood. However, to explain variation in brain size through these maturational constraints, one would need to invoke external factors such as socio-ecological conditions or extrinsic mortality rates which influence the likelihood of prolonging development periods in some species, which would then in turn allow for the evolution of relatively large brains only in some species or lineages, but not in others.

The **metabolic constraint hypothesis** (more details are discussed in the paragraph 'expensive brain framework´) focuses on energetic constraints such as basal metabolic rates (BMR) and suggests that large brains can be afforded by increasing the total energy turnover (Armstrong 1983, Hofman 1983a, Armstrong 1985, Dunbar 1989, Dunbar 1998, Isler and van Schaik 2006b, Weisbecker and Goswami 2010, Isler 2011). Various studies found positive correlations between adult brain size and BMR across mammalian species, including marsupials and placentals. Within orders, only primates show significant results (Armstrong 1983, Isler and van Schaik 2006b, Isler 2011). For birds, no supporting evidence has been found so far for a link between BMR and relative brain size (Isler and van Schaik 2006a).
Martin (1981) suggested the mother's metabolic turnover to be the most important link to relative brain size in terrestrial vertebrates (mammals, reptiles and birds). In 1996, he proposed the **maternal energy hypothesis** (Martin 1981, Hofman 1983b, Keverne et al. 1996, Martin 1996, Jones and MacLarnon 2004, Isler et al. 2008, Weisbecker and Goswami 2010) which suggests that brain size is constrained either by the mother's energy budget and the amount she is able to invest into the offspring or by the length of gestation and postnatal growth, or a combination of both. This assumption implies that large-brained species or lineages with low BMRs should have longer maternal investment periods. Therefore, this theory represents a combination of the ideas from the metabolic constraint and development hypothesis (see below), as maternal investments are strongly linked to development patterns. Martin (1996) claims that, as brain growth is completed very early during development, the resources received during these periods (gestation/incubation and postnatal growth up to weaning) decide about the adult size of the brain. This was supported by a study of Isler et al. (2008), which shows both BMR and gestation period to be correlated with brain size in primates. According to a further study of Isler (2011), maternal investments seem to play a role concerning brain growth, both in placental and marsupial mammals. The maternal energy hypothesis was partly supported in bats as well, where a relationship between gestation length and adult brain size was found (Jones and MacLarnon 2004). Furthermore, Hofman (1983b) argued that maternal energy metabolism acts as a constraint on the length of the gestation period and thus, indirectly on the growth

of the fetal‘s body and brain. Nevertheless, the maternal energy hypothesis is only considering the maternal investment while the energetic and time investment by other caretakers (male and helpers) is not taken into account. Moreover, it is rather a mechanistic than an ultimate explanation as it does not explain why some mothers invest more than others.

Closely related to the maternal energy hypothesis, other studies claim that differences in development modes (either linked to differences in energetic supply (Bennett and Harvey 1985a,b) or developmental lengths (Iwaniuk and Nelson 2003)) explain variation in relative brain size (**development hypothesis**). Precocial avian and mammalian species have larger neonatal brain sizes than altricial ones (Portmann 1947, Pagel and Harvey 1988), but in the adult state, altricial species have larger brains only in birds. In mammals, altricial and precocial adults have similar relative brain sizes (Bennett and Harvey 1985a). Bennett and Harvey (1985a) use differences in energetic contraints linked to variation in parental investment (which in the end is based on developmental differences) to explain variation in relative brain size. Altricial avian hatchlings are provisioned and protected by parents and sometimes helpers after birth. This stands in contrast to precocial species, where hatchlings are provisioned and protected to a smaller degree, thus altricial hatchlings are provisioned with more energy to invest in brain growth and maintenance. Young precocial and altricial mammals are both fed continuously (but restricted) after birth which would explain the equal adult relative brain sizes.

A study of Iwaniuk and Nelson (2003) support the development hypothesis linked to differences in developmental lengths as they found different developmental traits (incubation period, time of fledging, period of postfledging parental care and the total duration of parental care) to be correlated with relative brain size in birds.

After all, the differences in developmental modes are not sufficiently and ultimately explaining the variation in relative brain size. Why do precocial bird species not provision their offspring after hatching to grow larger brains as well but precocial mammals do ? The development hypothesis rather represents a mechanical than an ultimate explanation. Moreover, the developmental differences do not explain brain size variation in mammals (e.g. marsupials are highly altricial but are not very large-brained (Isler, personal communication)).

In summary, there are various non-exclusive alternatives explaining how high encephalization can be reached. The two main possibilities are: slow down life history and/or increase total metabolic costs. Both of these aspects are included in the expensive brain framework by Navarrete et al. (2011) (original framework proposed by Isler and van Schaik (2009a)), which encompasses aspects of various earlier hypotheses. This framework illustrates energy allocations between brains and other functions, looking at the constraint perspective of brain growth and maintenance.

### Expensive brain framework

Energy is a limited resource and has to be allocated proportionally to different functions. Species only evolve larger brains if associated changes in their energy budget are feasible. The expensive brain framework (Isler and van Schaik 2009a, Navarrete

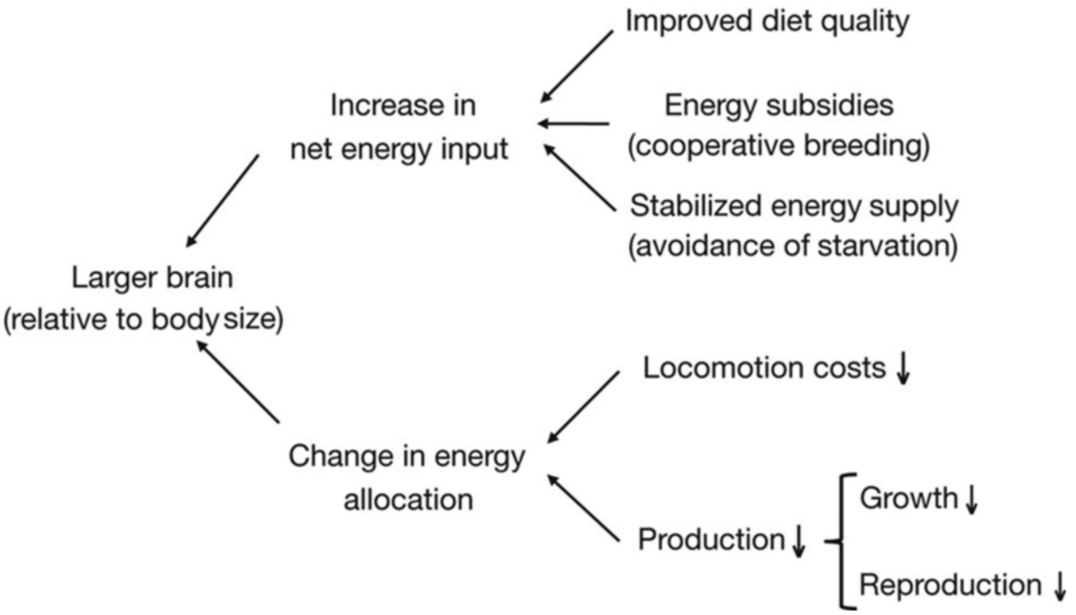


Figure 1.3: **Expensive brain framework.** Diagram of the expensive brain framework according to Navarrete et al. (2011). Enlarged brains can either be afforded by increasing the total energy turnover or by allocating energetic resource with locomotion or production.

et al. 2011) illustrates these energy allocations and links brain size to different life history traits. First, it posits that the costs of relatively large brains can be paid by increasing the total energy turnover (**metabolic constraint hypothesis**). This can be achieved by an improvement in diet quality (Aiello and Wells 2002, Wells 2009, Wrangham 2009), by energy subsidies in form of allomaternal care (Isler and van Schaik 2009a, Isler 2011) or by stabilizing the energy supply by buffering habitat seasonality (van Woerden et al. 2010). Second, larger brains can be evolved by reducing allocation of resources to locomotion or growth and reproduction (**production trade-off hypothesis**), or any combination of these (figure 1.3). Reducing growth and reproduction would mean a slower life history resulting in reduced fertility, longer developmental periods and elongated lifespan.

In the original version of the expensive brain framework, proposed by Isler and van Schaik (2009a), the **expensive tissue hypothesis** has been included for partly explaining the variation in relative brain size. The expensive tissue hypothesis, proposed by Aiello and Wheeler (1995), claims an energetic trade-off between relative brain size and another expensive tissue, the digestive tract. Aiello and Wheeler (1995) found support from a negative correlation between relative brain size and relative gut mass in anthropoid primates. In accordance with that, Fish and Lockwood (2003) found a positive correlation between brain size and diet quality in primates, as enhanced diet quality would allow for a reduction in the digestive tract. But enhanced cognitive abilities in terms of spatial and temporal memory, referred to as the diet hypothesis, may favour larger brains concerning high quality food as well (e.g. Eisenberg and Wilson

1978).
Contradicting the expensive tissue hypothesis, a positive relationship between brain and gut mass was found in bats (Jones and MacLarnon 2004). In concordance with this results, Isler and van Schaik (2006a) found no evidence for the trade-off between brains and gut length in avian species. However, a negative correlation between brain mass and pectoral muscle mass was detected. Pectoral muscles might reflect the locomotor costs (Isler and van Schaik 2006a), which are highly expensive, especially in birds (Butler 1991).
Until a recent study by Navarrete et al. (2011) using proper statistical methods and a broad range of mammalian species, the debate about the expensive tissue hypothesis seemed not to be settled. Navarrete et al. (2011) came to the final conclusion of refuting the expensive tissue hypothesis. They found no negative relationship between the relative size of brain and any other expensive tissue. Rather than expensive tissue they found adipose depots to correlate negatively with relative brain size and linked that to locomotor efficiency. To sum up, the expensive tissue hypothesis has recently been rejected and thus, is not part of the expensive brain framework anymore.

So far, comparative studies find support for the new expensive brain framework proposed by Navarrete et al. (2011). Evidence for the **metabolic constraint hypothesis** has been found across marsupial (Isler 2011) and placental mammals (Isler and van Schaik 2006b, Navarrete et al. 2011), showing a positive correlation between relative brain mass and basal metabolic rate (BMR). Within orders, this relationship could only be detected in primates (Jones and MacLarnon 2004, Isler and van Schaik 2006a) and rodents (Sobrero et al. 2011). However in birds, no correlation between BMR and relative brain size has been found so far (Isler and van Schaik 2006a).
Support for an increase in net energy intake in form of improved diet quality and energy subsidies comes from early *Homo*. Aiello and Wheeler (1995) and Aiello and Wells (2002) suggest that the early representatives of the genus *Homo*, (*Homo ergaster*, *Homo erectus*) showed a shift towards a higher diet quality in form of animal and vegetable foods and tool-based foraging behaviour. Furthermore, in *Homo erectus*, cooperative breeding allowing for energy subsidies might have evolved due to a change in environment and thus, a change in diet (O'Connell et al. 1999). In form of comparative analyses in extant mammals, two recent studies (Isler and van Schaik 2009a, Isler 2011) demonstrated that cooperative breeding is related to energy subsidies and allows for an increase in relative brain size. Details are discussed in the following section.
Stabilized energy supply is considered as a third possibility to reach a higher metabolic turnover. The finding of a negative relationship between relative brain size and experienced seasonality in Strepsirrhine primates suggests that variation in dietary intake acts as an energetic constraint on relative brain size (van Woerden et al. 2010).

Besides increasing the total energy turnover, larger brains can be afforded by compensating the high costs with the decrease of other functions. As already mentioned, reducing the costs of locomotion by bipedalism in early *Homo* lineages might have allowed for reallocation of the energy resources and thus for an increase in relative brain size in humans (Navarrete et al. 2011, Isler and van Schaik 2006a).

The second change in energy allocation is reproduction. Especially the reproduction process, including egg production, gestation or incubation and the offspring rearing period, is energetically challenging. Thus, the main focus of this research project lies on the **production trade-off hypothesis** in order to investigate the relationship between energy expenditures during breeding and brain sizes. We must consider that relatively large-brained animals not only have to maintain their own big brains, but need to sufficiently provide energy for the offspring to enable them to grow big brains as well. Therefore, assuming a trade-off between reproduction and brain size is straightforward. The energy reduced allocation to reproduction may either entail longer development periods, including longer birth intervals, or reduce clutch or litter size. As the developmental states of neonates strongly differ, precocial and altricial species are probably affected differently by the energy allocation to reproduction. In precocial, monotokous animals, a positive correlation between brain size and development periods is predicted, as they do not have the possibility to reduce litter size as they produce only a single offspring per litter. Large-brained altricial, polytokous species on the other hand are expected to have smaller litters (Isler and van Schaik 2009a, Isler and van Schaik in prep.). These predictions were well supported by Isler and van Schaik (2009a). A negative correlation between brain mass and litter size was detected in altricial polytokous mammals, whereas in precocial ones, having mostly only a single offspring, bigger brains were paid by lower birth rates resulting in a slower development (longer gestation, lactation, immature periods and longer lifespan) (Isler and van Schaik 2009a). However in altricial birds, although durations of incubation and dependency periods positively correlate with brain size (Iwaniuk and Nelson 2003), fertility rates are not negatively correlated with relative brain mass (Isler and van Schaik 2006a). This might not be expected considering the production trade-off hypothesis, but might be explained by higher direct provisioning of offspring in large-brained species (Isler and van Schaik 2006a). Large-brained neonates are known to be bigger, which also fits into the expensive brain framework as it might act preventive on malnourishment or starvation concerning brain growth and maintenance (Isler and van Schaik 2009a).

When the costs of enlarged brains are paid by reduced fertility and delayed life history, elongated reproductive lifespan and reduced mortality rates are required to result in nonetheless evolutionary stable populations. This has been shown in several studies including mammalian and avian species (Sacher 1978, Deaner et al. 2003, Isler and van Schaik 2009a, b). Sol et al. (2007) demonstrated that large-brained bird species show higher adult survival. This should not be confused with the cognitive buffer hypothesis, as Isler and van Schaik (2009a) could show that large brains in carnivores are not necessarily correlated with prolonged reproductive lifespan. In sum, large-brained mammals reduce fertility or birth rates and elongate reproductive lifespan (figure 1.4 a), b)).

Furthermore, Isler and van Schaik (2009b) found big-brained precocial avian and mammalian species to have lower maximum rates of population increase ($r_{max}$: calculated from (max. lifespan-AFR) and average annual fertility), which actually results in a so called „grey ceiling“ (maximum viable brain size) for each lineage (figure 1.4 c)).

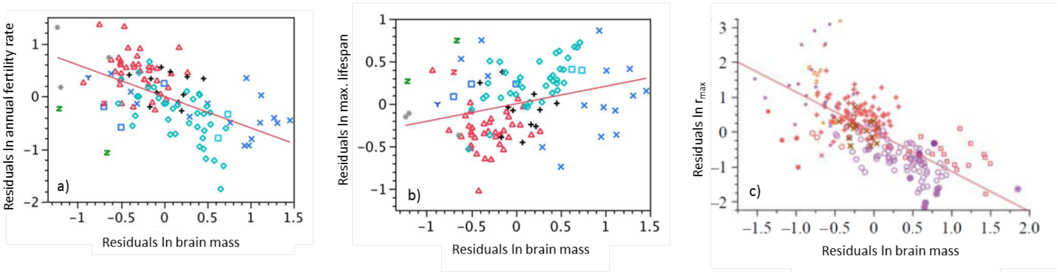


Figure 1.4: **Reproduction trade-off in precocial mammals.** Least-squares regressions of relative brain mass and (a) residuals of annual fertility rate (IC $p = 0.002$), (b) residuals of maximum lifespan (IC $p = 0.049$), (c) residuals of $\mathrm{r}_{max}$ (IC $p < 0.0001$) for precocial mammalian species according to Isler and van Schaik (2009a) (IC=independent contrasts).

This means, that compensation by prolonged longevity and reduced mortality rates is incomplete. Species can not evolve too large brains, otherwise they might not be able to recover from population collapses which makes them much more vulnerable to extinction. Great apes are supposed to be very close to the primate „grey ceiling“. To sum up, Isler and van Schaik (2009b) suggest that large-brained species show higher vulnerability during mass extinctions, and the only way to increase both brain size and reproduction rate would be through a massive change in lifestyle.

Such a possible change in lifestyle to evade this trade-off between brain size and reproduction (fertility or $\mathrm{r}_{max}$) would most likely be found in the breeding system, as the load of the adults is highest during the breeding period. Especially feeding the offspring is energetically very costly (cited in Clutton-Brock (1991a)). Isler and van Schaik (2009a,b, in prep.) suggested that cooperative breeding or any other kind of allomaternal care during the breeding period provides additional energy and may act as energy relief for breeding individuals. The energy subsidies during breeding may allow for maintaining and growing bigger brains and/or increased reproduction and would alleviate or even eliminate the energy allocation problem between brains and fertility. Thus, energetic resources may not apply as strong constraints for big brains any longer, only a slight reduction in fertility may be required and therefore compensation by elongated lifespan and reduction in $\mathrm{r}_{max}$ are expected to be smaller. In this regard, after taking phylogenetic relationships into account, encouraging results have been found. Isler and van Schaik (in prep.) found a strong link between the amount of help and encephalization in altricial mammals. This correlation has not been found in precocial species, as there help is very rare during gestation in terms of courtship feeding. Further, a negative correlation between $\mathrm{r}_{max}$ and brain mass was alleviated or even absent in altricial species (figure 1.5 a), c)). This would fit the notion that species with cooperative breeding systems, especially altricial species, are less restricted in terms of energy for brain and reproduction. In earlier works of Isler and van Schaik (2009a,b), they found that cooperatively breeding carnivores neither show a negative relationship between brain size and fertility nor a positive correlation between brain size and reproductive lifespan and no trade-off between relative brain size and $\mathrm{r}_{max}$ (figure 1.6). Further, Isler (2011) has shown that extra energy inputs, in form of allomaternal care, are important concerning the relation between brain size and offspring

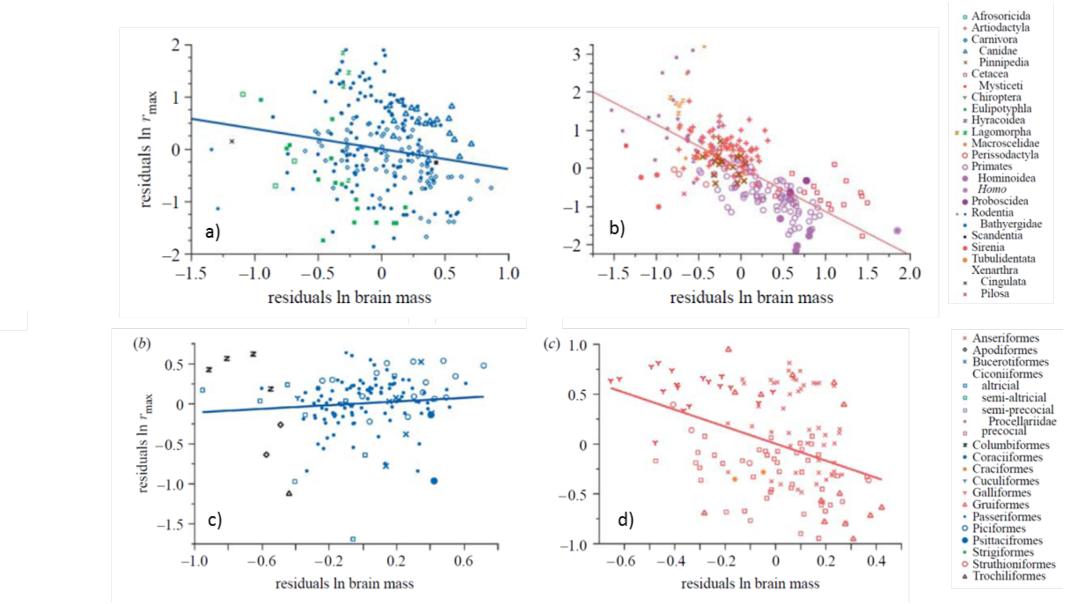


Figure 1.5: **Reproduction trade-off in precocial and altricial species.** Least-squares regressions of relative brain mass and maximum rates of population increases ($r_{max}$) for (a) altricial (IC $p = 0.032$), (b) precocial mammalian species (IC $p < 0.0001$) and (c) altricial (IC $p = 0.216$), (d) precocial (IC $p = 0.0002$) avian species according to Isler and van Schaik (2009b) (IC=independent contrasts).

production in marsupials. She found strong negative correlations between brain size and reproduction in placentals and marsupials. To sum up, this definitively implies the importance of energy allocation problem in general and the effect of extra energy inputs during breeding, so far particularly in mammals. But before going into more detail and to refer these hypotheses and analyses on avian species, it is necessary to discuss what kind of breeding patterns exist and in which terms helpers mean additional energy inputs, especially in the study group of birds.

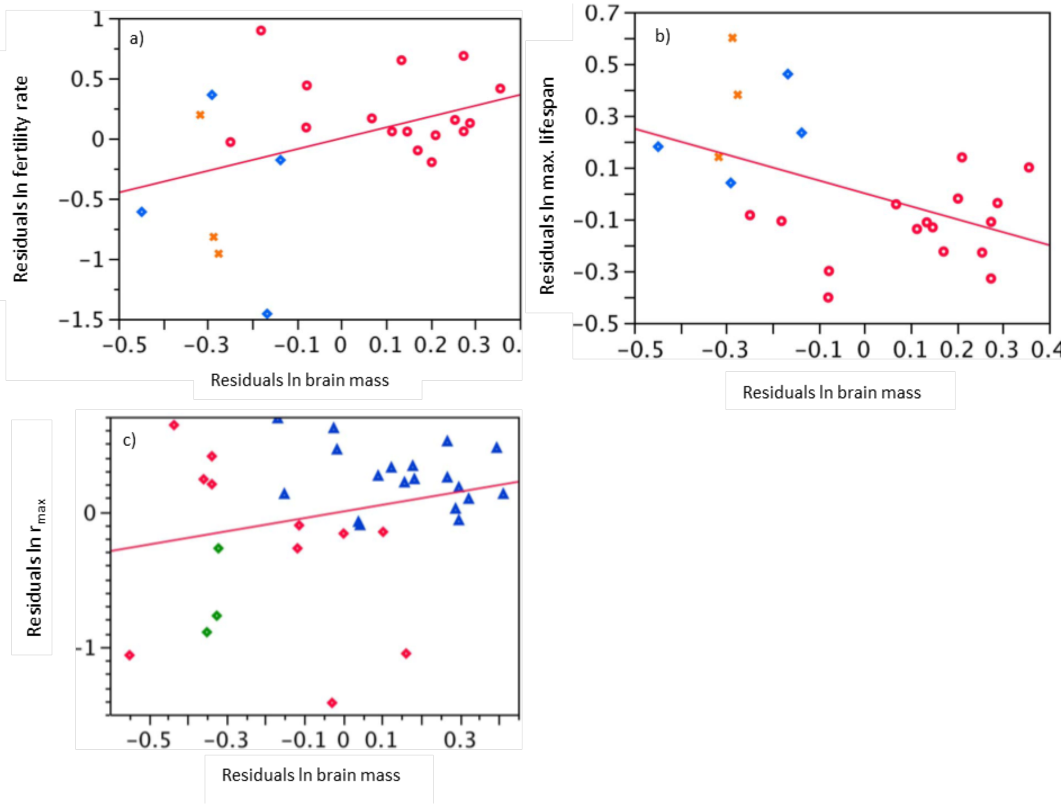


Figure 1.6: **Alleviated reproduction trade-off in carnivores.** Least-squares regressions of relative brain mass and (a) residuals of fertility rate (IC $p = 0.843(-)$), (b) residuals of maximum lifespan (IC $p = 0.705(-)$), (c) residuals of $r_{max}$ (IC p-value missing) in carnivore families with cooperative breeding in some species (*Canidae*, *Hyaenidae*, *Herpestidae*) (according to Isler and van Schiak (2009a) (IC=independent contrasts).

## 1.3 Parental care and breeding types

Birds show a huge variety of different breeding types and therefore represent a perfect group for a comparative study investigating the modes of parental care and its effects on brain size.

Very few avian taxa groups, such as the geothermal breeders and brood parasites, escape the effort of rearing young and show no parental care at all (Cockburn 2006). However, all other birds show a huge variety of how caring for offspring. The post hatching care mainly consists of feeding and protecting young and varies among species in form of duration or number and identity of caretakers. Post fledging care shows as well high variability. In some species offspring are actively fed after they have left the nest, in other species the food is only shown to offspring but not directly fed and in others again the offspring are only guarded (Clutton-Brock 1991b).

Among birds one can distinguish between six different breeding types based on the number of individuals caring for young (classification according to Cockburn 2006): (1) geothermal breeders; (2) brood parasites; (3) single breeders; (4) pair breeders; (5) occasional cooperative breeders; (6) cooperative breeders. Among mammalian species one distinguishes among the breeding types (3) to (6). As already mentioned, **geothermal breeders and brood parasites** such as cuckoos and megapodes escape the effort of rearing young using geothermal heat or laying the own eggs in foreign nests (Cockburn 2006). **Uniparental care by males or females** is rather rare among birds (male care: 1%; female care: 8%). Uniparental care by males including incubation, chick feeding and guarding occurs in bird families such as tinamous (*Tinamidae*) or sandpipers (*Scolopacidae*). Typical avian species showing uniparental female care belong to the families of the ducks, geese and swans (*Anatidae*) and the hummingbirds (*Trochilidae*). Most singly breeding species are precocial (figure 1.7). In contrast to birds, in most mammals females alone care for the offspring but uniparental care by males does not occur (Clutton-Brock 1991b).

The most common form of parental care in birds is **pair breeding** including more than 90% of all species (Cockburn 2006). Amongst others, many seabirds, raptors and parrots belong to that breeding category and most of them have altricial young (figure 1.7). Parental care can be shared equally between the parents, however, in some species males and females are responsible for different task during the breeding season. For example, in many parrots the females are incubating eggs while the males provide them with food. Interestingly, in mammals less than 5% of all species show biparental care including mainly primates and carnivores (Clutton-Brock 1991b).

**Cooperative breeding** occurs in 8 or 9% of all avian species and is much more common than in mammals (Cockburn 2006). Iwaniuk and Arnold (2004)(p. 204) define cooperatively breeding bird species as follows: „...species in which individuals in addition to the parents participate in parent-like behaviour towards young of a single brood“. Usually, the alloparents (individuals other than the parents = helpers) attending the nest in the current season are offspring from previous breeding seasons (del Hoyo et al. 1992-2011). Typical representatives of cooperatively breeding birds are parrots (*Psittacidae*), rails, gallinules and coots (*Rallidae*), and fairy-wrens (*Maluridae*). It has been shown that certain complex social behaviours such as group mobbing and maintenance of social relationships are more common in cooperatively

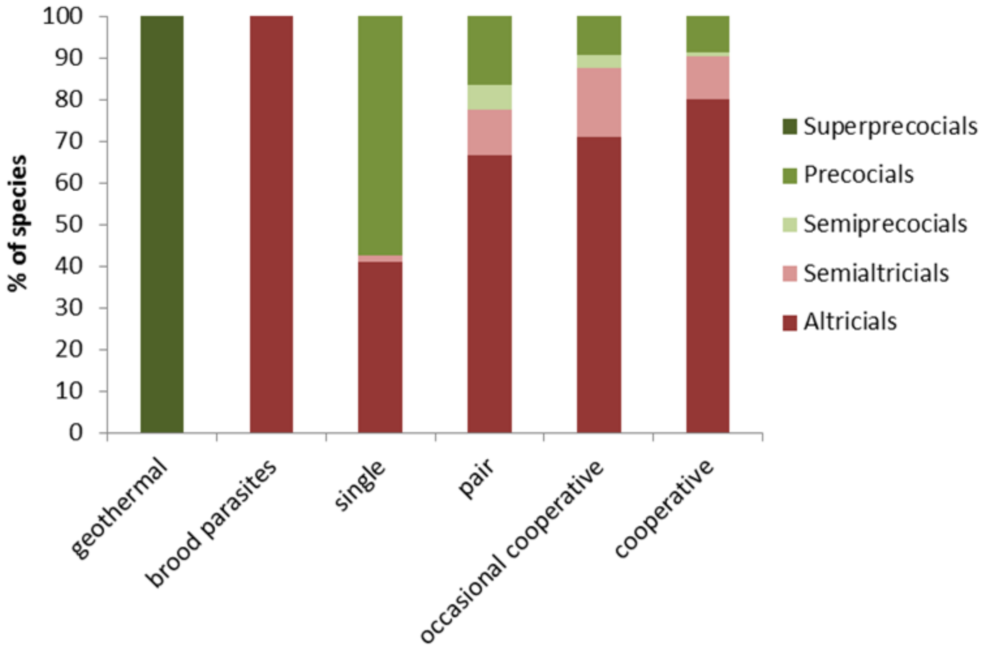


Figure 1.7: **Breeding type and development mode.** Percentages of species for the different development modes (superprecocial, precocial, semiprecocial, semialtricial, altricial) within breeding types (geothermal breeders ($n = 3$; superprecocial: 100%, precocial: 0%, semiprecocial: 0%, semialtricial: 0%, altricial: 0%), brood parasites ($n = 12$; superprecocial: 0%, precocial: 0%, semiprecocial: 0%, semialtricial: 0%, altricial: 100%), single breeders ($n = 170$; superprecocial: 0%, precocial: 57.3%, semiprecocial: 0%, semialtricial: 1.8%, altricial: 40.9%), pair breeders ($n = 1080$; superprecocial: 0%, precocial: 16.5%, semiprecocial: 6%, semialtricial: 11.1%, altricial: 66.5%), occasional cooperative breeders ($n = 152$; superprecocial: 0%, precocial: 9.3%, semiprecocial: 3.3%, semialtricial: 16.6%, altricial: 70.9%), cooperative breeders ($n = 109$; superprecocial: 0%, precocial: 8.6%, semiprecocial: 1%, semialtricial: 10.5%, altricial: 80%)).

than in non-cooperatively breeding species (reviewed in Iwaniuk and Arnold 2004). Most of the species showing cooperation during breeding have altricial young (figure 1.7). More details about cooperative breeding especially in the context of energy supply are discussed in the following section.

## 1.4 Energetic aspects of allomaternal helpers

In cooperatively breeding species, helpers support the parents during the breeding period through territory defence, nest construction, incubation, food provisioning and protection of mothers and offspring and in some mammalian taxa, carrying of young belongs as well to the range of functions of helpers (Stacey and Koenig 1990, Burkart and van Schaik 2010). More precisely, for birds, Skutch (1961, p. 198) defined a helper as „a bird which assists in the nesting of an individual other than its mate, or feed or otherwise attends a bird of whatever age which is neither its mate nor its dependent offspring. Helpers may be of almost any age; they may be breeding or non-breeding individuals; they may aid other birds of the most diverse relationship to themselves, including those of distinct species; and they may assist in various ways". Having helpers aside often provides additional amount of energy and alleviates the load of the parents. The term of „helpers lighten the load of the parents" was firstly used by Brown (1978), meaning that additional helpers reduce risks and costs of breeding parents. Later on, a broader definition was made by Russel et al. (2007, p. 943), namely „Load lightening describes lower overall levels of investment in the presence of helpers". But a load-lightening effect for the parents is not always necessarily the case. Thus, Hatchwell (1999) made the distinction between two strategies of helping behaviour. First, if helpers provide additional energy in form of higher feeding rates or protection and parents do not compensate by working less, no load-lightening occurs, but the total energy amount received by nestlings increases. Second, if there is an actual load-lightening for the breeding pair and the helper‘s energy input is compensated by parents investing less in breeding, the total energy amount received by offspring stays the same. A study of Russel et al. (2007) nicely demonstrated the actual load-lightening in a communally breeding species, the superb fairy-wren (*Malurus cyaneus*). They found that mothers in presence of helpers produce smaller eggs (resulting in lighter hatchlings) than mothers without helpers. This premature state of a hatchling is compensated by the support of helpers later in development and the smaller eggs increase the survival rates of the mothers. This supports the idea that in the presence of helpers, mothers are load-lightened by laying smaller eggs resulting in higher survival rates. Hatchwell (1999) even found evidence that both strategies (load-lightening and no load-lightening in presence of helpers) can occur within the same species. His results concerning the load-lightening strategy are graphically illustrated in figure 1.8: the more helpers, the lower the feeding rates of the parents. A wealth of other empirical evidence in birds as well as other taxa supports the idea that helpers convey benefits for parents and offspring, as correlations between the presence of helpers and general parental load-lightening (Brown et al. 1978, Scantlebury et al. 2002), higher survival rates of offspring and parents (Reyer 1984, Hodge 2005, Cockburn et al. 2008), higher feeding and nestling growth rates (Langen and Vehrencamp 1999, Clutton-Brock et al. 2001, Hodge 2005) and increased reproductive and fledging success (Austad and Rabenold 1985, Mumme 1992, Jennions and Macdonald 1994, Langen and Vehrencamp 1999) have been found. Thus, allomaternal care certainly does have an influence on the energy resources of breeding parents, and some species may even be evolutionary forced to become cooperative breeders because of energetic limitations (Creel and Creel 1991). The extra energy inputs in cooperative breeding species may not only allow for better survival or higher reproductive success, but as well for maintaining and growing bigger brains, as shown for marsupials (Isler 2011). To have an effect on brain size and because brain growth is known to be a time of high vulnerability (Dobbing 1974), the time of helpers assisting the breeding pair has to overlap with the main period of brain growth (figure 1.11). Therefore, in precocials, where brain growth mostly occurs before birth, help is expected to be mostly effective during the prenatal period and to act indirectly via the mother (e.g courtship feeding). For altricial species, on the other hand, support during the postnatal period would be most effective. However, cooperative breeding or any other kinds of allomaternal care are expected to be much more common in altricial species, as help is more effective by acting directly on offspring. Descriptive statistical

results support this assumption in birds (figure 1.9).
More than 90% of altricial species are either breeding in pairs or cooperatively, whereas precocial species breed in 32% of the cases alone. It already has been shown that the association between brain size and help is stronger in altricial than precocial mammals and that primates with more help are more altricial (Isler and van Schaik in prep.).

However, for example mate/courtship feeding is a frequent phenomenon in birds and mostly occurs during pair-formation, egg production, egg laying and incubation (Lack 1940, Avery et al. 1988, Hatupka 1994). Therefore, this kind of support also makes sense in precocial species and may significantly contribute to the total energy budget. Courtship feeding (also known as mate feeding) is defined as mates feeding their female partners and has been suggested to mainly strengthen pair bonds (Lack 1940). But several studies showed that feeding the female contributes a fair proportion of her daily energy intake (Nisbet 1973, Tasker and Mills 1981, Avery et al. 1988, Donazar et al. 1992, Hatupka 1994). Pearse et al. (2004) found that females being supported by their mates show higher nest attentiveness, a trend towards shorter incubation periods, and that additional food leads to greater hatching success. Nisbet (1973) found evidence that courtship feeding is associated with higher clutch and egg sizes and even higher hatching and fledging success. Courtship feeding definitely has its impact on a female‘s energy metabolism during reproduction and has to be taken into account regarding energetic subsidies during breeding. As mate feeding during incubation overlaps with the main period of offspring‘s brain growth in precocial species (figure 1.11), this may have enabled relatively large brains in some species.
After regarding the beneficial perspective of cooperatively breeding parents, one might wonder about the benefits for alloparents. In fact, alloparents mostly do not reproduce themselves while helping at nests of others, and therefore, makes the evolution of such altruistic behaviour interesting. Several hypotheses have been proposed trying to explain the evolution of breeding helpers. First, there are immediate and delayed direct benefits for alloparents in form of higher survival due to reduced predation and increased foraging efficiency (Jennions and Macdonald 1994) and better and more frequent breeding opportunities. Second, they might profit from indirect fitness benefits in form of supporting the reproduction of close relatives (cited in Wiley and Rabenold (1984)).

## 1.5 The continuum of precocial and altricial species

Due to the strong network between social mating systems, help behaviour, brain growth periods and development patterns, it is crucial to look at the differences between precocial and altricial species in more detail.
Precocials have rather long gestation or incubation periods, neonates which are quite mature and well developed, and in mammals they often have a single offspring per litter (monotokous). On the other hand, altricial species showing only short gestation or incubation periods, are quite helpless right after birth or hatching, and in mammals they are polytokous, i.e. they have several young per litter (Portmann 1939). In contrast to mammals, avian species can be classified in several additional development stages going beyond altricial and precocial, including superprecocial, semiprecocial

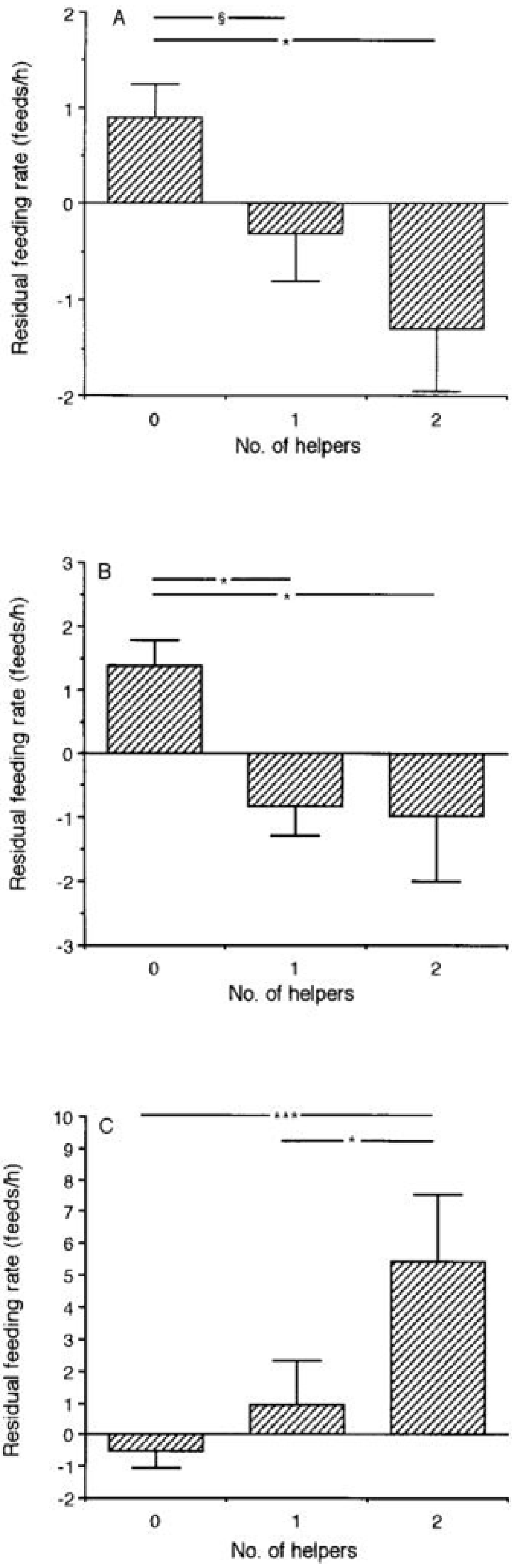


Figure 1.8: **Load-lightening.** The relationship between number of helpers and feeding rates for A) breeding females, B) breeding males and C) total provisioning to offspring, illustrating load-lightening for parents in long tailed tits (*Aegithalos caudatus*) (according to Hatchwell, 1999).

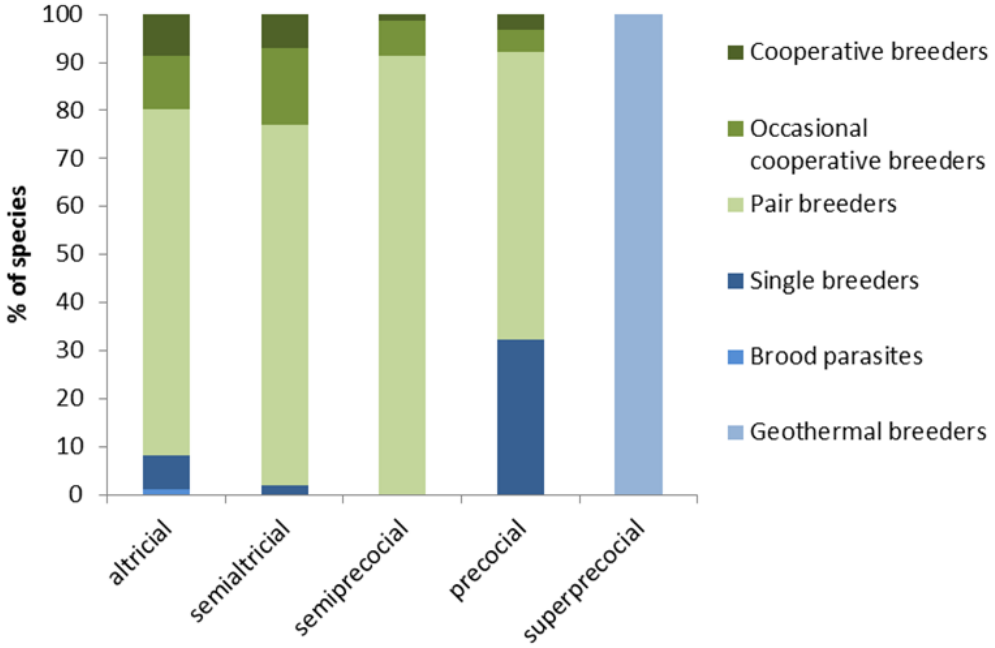


Figure 1.9: **Development mode and breeding type.** Percentages of species for the different breeding types (geothermal breeders, brood parasites, single breeders, pair breeders, occasional cooperative breeders, cooperative breeders) within development modes (altricial ($n = 1062$; geothermal breeders: 0%, brood parasites: 1.2%, single breeders: 6.9%, pair breeders: 72.3%, occasional cooperative breeders: 11%, cooperative breeders: 8.7%), semialtricial ($n = 177$; geothermal breeders: 0%, brood parasites: 0%, single breeders: 1.9%, pair breeders: 75%, occasional cooperative breeders: 16%, cooperative breeders: 7.1%), semiprecocial ($n = 159$; geothermal breeders: 0%, brood parasites: 0%, single breeders: 0%, pair breeders: 91.3%, occasional cooperative breeders: 7.3%, cooperative breeders: 1.5%), precocial ($n = 335$; geothermal breeders: 0%, brood parasites: 0%, single breeders: 32.3%, pair breeders: 59.8%, occasional cooperative breeders: 4.8%, cooperative breeders: 3.1%), superprecocial ($n = 4$; geothermal breeders: 100%, brood parasites: 0%, single breeders: 0%, pair breeders: 0%, occasional cooperative breeders: 0%, cooperative breeders: 0%)).

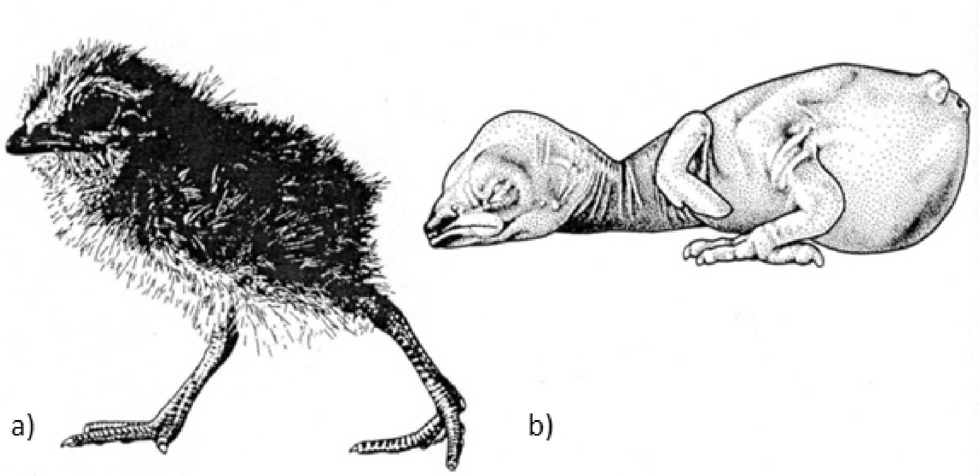


Figure 1.10: **Altricial and precocial neonate.** a) Precocial-3 neonate (Barred Buttonquail) and b) altricial-2 neonate (Java Sparrow) (according to Starck (1993)).

and semialtricial and a few other intermediate stages. A broad overview about this „altricial-precocial spectrum“ in birds was given by Starck and Ricklefs (1998). The different development modes defined according to Starck (1993) based on different characters are compared in table 1.2 (according to Starck and Ricklefs (1998)).

Starck (1993) differed between three precocial patterns (precocial 1-3) and two altricial patterns (altricial 1-2). Hatchlings described as „precocial 1“ have contour feathers (figure 1.10a) and forage independently in contrast to „precocial 3“ hatchlings, which are still fed by parents. The two altricial patterns differ between downy plumage and external feathers at hatching. The more altricial, the less they are covered by down (figure 1.10b).

There are huge differences concerning the development patterns in birds: the superprecocial megapodes are able to fly right after hatching and are comparable with mature birds, whereas parrots are totally altricial and still resemble an embryo after hatching (Starck and Ricklefs 1998). Concerning neuronal growth rates, precocial birds and mammals show high indices during embryonic development, ensued by low brain growth rates after hatching or birth, except in us humans, which show high neuronal growth both during and after gestation. Altricial species show the exact opposite pattern, the main part of brain growth occurring after the embryonic phase. These differences are compensated by the corresponding differences in parental metabolic allocation, being larger in precocials during incubation or gestation and in altricials after hatching or birth (Bennett and Harvey 1985a). This is also reflected in the time allocation of the different periods within the breeding season. In avian species, on the one hand, altricials show rather a short incubation but a rather long nestling period. On the other hand, precocials incubate their eggs for a rather long time, whereas time in the nest lasts only for 1 or 2 days. Further, the very short nestling period is compensated by long time feeding the offspring after they have left the nest (figure 1.12). The „brain growth spurts“ for different mammalian species were graphically illustrated by

Table 1.2: **Development modes.** Classification of different developmental modes in birds (according to Starck, 1993) based on a total of 11 characteristics according to Starck and Ricklefs (1998): 1) Downy hatchling plumage, 2) Motor activity, 3) Locomotor activity, 4) Follow parents, 5) Search food and feed alone, 6) Young fed by parents, 7) Stay in nest, 8) Eyes closed at hatching, 9) Without external feathers at hatching, a) No parent-chick interaction, b) Contour feathers at hatching.

| | Characteristics | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Development mode (Starck 1993) | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | a | b | Example avian family |
| Superprecocial | ✓ | ✓ | ✓ | | ✓ | | | | | ✓ | ✓ | *Megapodiidae* |
| Precocial 1 | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | | ✓ | *Anatidae* |
| Precocial 2 | ✓ | ✓ | ✓ | ✓ | (✓) | | | | | | | *Rheidae* |
| Precocial 3 | ✓ | ✓ | ✓ | ✓ | | ✓ | | | | | | *Rallidae* |
| Semiprecocial | ✓ | ✓ | ✓ | | | ✓ | | | | | | *Laridae* |
| Semialtricial | ✓ | ✓ | | | | ✓ | ✓ | | | | | *Ciconiidae* |
| Altricial 1 | ✓ | (✓) | | | | ✓ | ✓ | ✓ | | | | *Columbidae* |
| Altricial 2 | | (✓) | | | | ✓ | ✓ | ✓ | ✓ | | | *Psittacidae* |

Dobbing and Sands (1979) and are shown in figure 1.11. Vleck et al. (1980) found that precocial in contrast to altricial eggs are energetically more expensive for the mother, which supports the developmental allocation difference between pre - and posthatching period in brain growth. Thus, one can assume that in precocial species the length of incubation or gestation and the energy budgets during these periods are most important in relation to brain size, whereas in altricial ones, brain size rather is dependent on the postnatal nestling period (Isler and van Schaik in prep., Isler 2011). Martin et al. (2005) and Sacher and Staffeldt (1974) actually found evidence for such a pattern in placental mammals. For birds it is known that altricial species have relatively larger adult brains than precocial ones (Bennett and Harvey 1985a,b, Starck and Ricklefs 1998). Bennett and Harvey (1985a) suggest that, because precocial parents stop taking care of hatchlings quite early, this reduced energetic supply prevents them to grow bigger brains after hatching. In contrast, in altricial species parents are taking care of nestlings much longer, allowing them to grow larger brains (development hypothesis). The state of development of neonates is obviously strongly linked to the amount and manner of parental or alloparental care received after hatching. Thus, help must be most effective on brain size during gestation or incubation (acting on mother and indirectly on offspring for precocials) and during the postnatal period of brain growth in altricials.

## 1.6 Why birds?

Avian species build an interesting study group for several reasons. First, many studies already exist which make birds to one of the best studied taxa. Much information about behavioural, life history, ecological and physiological traits has been collected

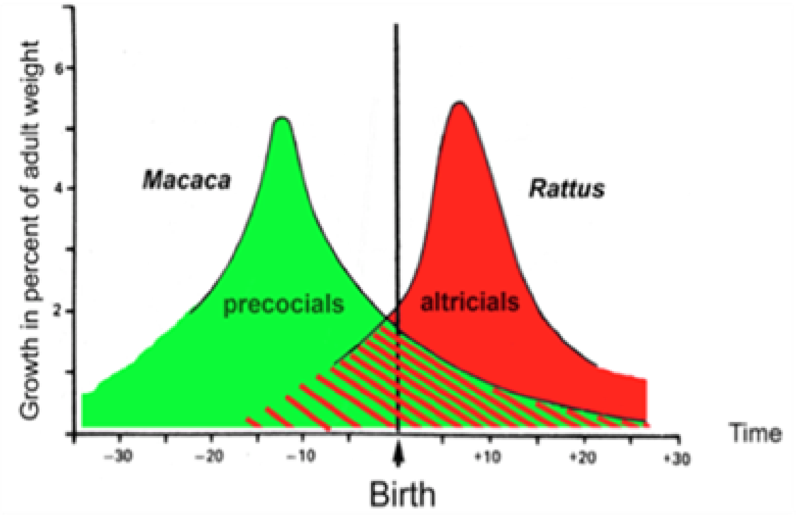
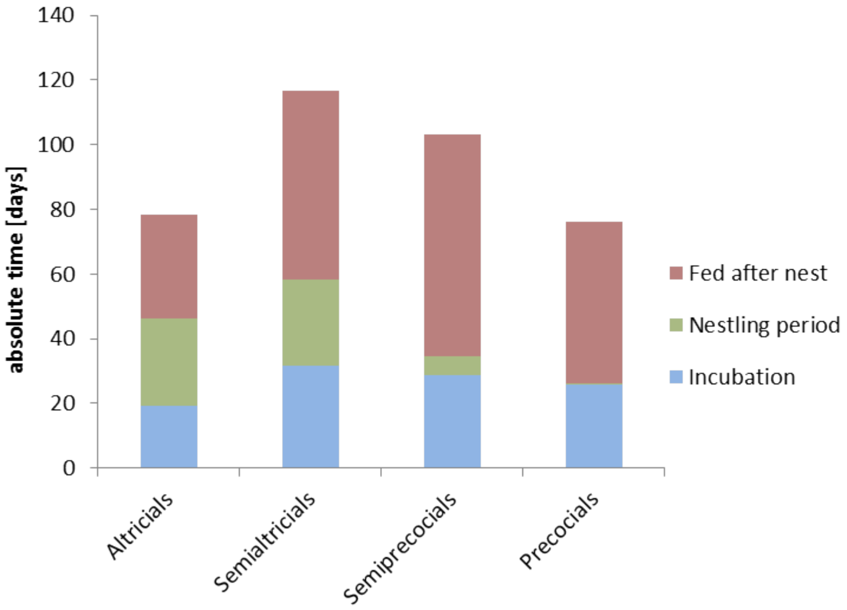


Figure 1.11: **Brain growth spurts.** Brain growth in percent of adult in a precocial (Macaca) and an altricial (Rattus) species during the pre - and postnatal period (according to Dobbing and Sands (1979) in Isler and van Schaik (in prep.)).



periods.png

Figure 1.12: **Average lengths of different breeding periods - in altricials, semi-altricials, semiprecocials and precocials.** The three main time periods of breeding shown separately for altricial ($n_{incubation}$=891, $n_{nestlingperiod}$=531, $n_{fedafternest}$=304), semi-altricial ($n_{incubation}$=150, $n_{nestlingperiod}$=12, $n_{fedafternest}$=44), semiprecocial ($n_{incubation}$=62, $n_{nestlingperiod}$=18, $n_{fedafternest}$=13) and precocial ($n_{incubation}$=292, $n_{nestlingperiod}$=245, $n_{Fedafternest}$=35) bird species. For each period the mean value of all available data is given in absolute days.

during the last two centuries. Counting to more or less 10‘000 species, birds show huge variation in all these different traits. Avian species are well-studied concerning the whole taxonomy and occupy all different kinds of habitats (Bennett and Owens 2002). For the purpose of this study, birds build an excellent study group as they show huge variation in relative brain size, development modes and social mating systems. 8 or 9% of all species are cooperative breeders and even more show complex social behaviour including courtship feeding. Most other species show biparental care (Cockburn 2006). Cooperative breeding provides additional energy inputs and may have an effect on the evolution of brain size. Moreover, the Machiavellian intelligence hypothesis proposes that living in social groups request certain cognitive abilities, as identifying ranks, sex, age and competitive and cheating behaviour of other group members (Byrne and Whiten 1997). Birds show other remarkable intellectual performances, such as the learning ability of certain tasks (Pepperberg 2002) or tool use (Lefebvre et al. 2002). Especially parrots and corvids, having relatively large brain sizes, show a whole range of cognitively demanding behaviours which are much more impressive than behaviours most other vertebrates. Concerning intelligence and cognitive abilities, the performance of parrots, corvids and other large-brained birds are even comparable to that of non-human primates (Striedter and Charvet 2008). Avian species exhibit abilities and perform tasks which once were thought to be limited to primates, and therefore, many of the adaptive benefit hypotheses mentioned in table 1.1 have been tested in birds as well. Several studies also considered the costs of growing and maintaining brains by testing diverse energy trade-offs and found encouraging results. For instance, Isler and van Schaik (2009b) found a negative correlation between brain size and $r_{max}$ in precocial avian species, but not in altricial species, where allomaternal offspring provisioning is rather frequent. To sum up, birds build an interesting study group for extending investigations on evolution of brain size not only in relation to adaptive benefits of higher cognitive abilities but also from a constraint perspective, including social or mating systems and development modes.

## 1.7 Questions and Hypotheses

The main aim of this study is to investigate in form of a comparative study whether energy subsidies during breeding are related to the evolution of large brains across birds, and how different development patterns influence this relationship. In a broader evolutionary context, this study aims to explain what allowed humans in comparison to great apes to have evolved huge brains and high reproductive rates at the same time.

Although some aspects of the energy trade-off hypothesis have already been tested in birds (Isler and van Schaik 2006a), various predictions from the expensive brain framework with the major focus on the production trade-off hypothesis are reanalysed with a new and more complete data set (including new quantification methods of reproductive effort and allomaternal energy subsidies). Especially the relationship between breeding systems and the reproduction trade-off is of main interest, as breeding types and differences in allomaternal care are expected to affect the relationship between brain size and reproduction differently. As promising results have been found in mammals, the association between breeding system and brain size is expected to be similar in birds. Avian species represent an optimal study group for these kinds of questions as they show huge variation in brain size as well as in breeding systems. The basic prediction is that additional amount of allomaternal care allows an increase in reproduction (fertility or $r_{max}$) and/or relative brain size. This leads to the prediction that relatively large-brained non-cooperative breeding species will reduce reproductive effort (fertility or $r_{max}$), whereas this negative correlation is expected to alleviate or even disappear in cooperatively breeding species (defined as the energy subsidies hypothesis). In a former study by Isler and van Schaik (2009b) the reproduction trade-off has been investigated distinguishing between altrical and precocial species, assuming that in altricial species allomaternal care is much more common compared to precocial species. In this study new data is available which allows for the direct distinction between non-cooperatively breeding and cooperatively breeding species.

### Expensive brain and energy subsidies hypotheses

Several hypothesis and predictions will be tested which are derived from these main predictions and the expensive brain framework (adapted from Isler and van Schaik (2006a, 2009a, in prep.); Isler (2011))(all the following hypotheses always incorporate correction for body mass):

#### 1. Metabolic constraint hypothesis

a) Assuming that the total energy turnover constrains brain size, I predict that the basal metabolic rate correlates positively with relative brain size.

b) Due to a study in marsupials (Isler 2011), it is now evident that a direct metabolic constraint can be obscured by a strong trade-off between relative brain size and offspring production. Assuming the same phenomenon across avian species, I expect relative brain size to correlate positively with BMR if $r_{max}$ values are held constant (analogous for the correlation between $r_{max}$ and BMR if relative brain size values are held constant).

#### 2. Production trade-off hypothesis

a) *Reproduction and brain size.* Correcting for the amount of allomaternal care (measured by energetic expenditure during chick rearing, number of caretakers or breeding type) (ca. 90% of all bird species breed in pairs, which is regarded as allomaternal care), I predict a negative correlation between relative brain size and reproduction (fertility or $r_{max}$). From another perspective, one could argue that non-cooperatively breeding species (geothermal breeders, brood parasites and single breeders) are expected to show a negative correlation between reproductive rate ($r_{max}$) and brain size, whereas species with allomaternal care (pair or cooperative breeders) are expected to show no relationship between $r_{max}$ or fertility and brain size. Moreover, I am interested in what drives the negative correlation between r$_{max}$ and relative brain size.

b) *Clutch size and brain size.* To further investigate the reproduction trade-off, after controlling for the effect of amount of allomaternal care, relatively large-brained species of taxa groups having clutch sizes larger than two are predicted to exhibit reduced clutch sizes. Groups with smaller clutch sizes of only one or two eggs are expected to reduce birth rates, and slower development (e.g. delayed fledging or time of first flight). From the other perspective, for relatively large-brained geothermal and singly breeding species having clutch sizes larger than 2 are expected to exhibit reduced clutch sizes. Large-brained geothermal and single breeders with smaller clutch sizes of only one or two eggs per clutch are expected to reduce birth rates, and slower development (e.g. delayed fledging or reduced growth rates).

c) *Longevity and brain size.* Correcting for the amount of allomaternal care, relatively large-brained species with reduced reproduction (fertility or r$_{max}$) are expected to increase the annual adult survival and elongate their maximum reproductive lifespan (max. lifespan - AFR). Thus, I expect a positive correlation between relative brain size and maximum reproductive lifespan. From the other perspective, one could argue that for geothermal and singly breeding species, relatively large-brained species with reduced reproduction (fertility or r$_{max}$) are expected to elongate their maximum reproductive lifespan (max. lifespan - AFR).

d) *„Grey ceiling“.* The relatively largest-brained taxa with reduced reproduction are expected to be very close to their „grey ceiling“ (maximum viable brain size), showing quite low r$_{max}$ values and thus, are expected to be classified as vulnerable or endangered on the worldwide scale. Therefore, high endangered species are expected to show low r$_{max}$ values and relatively large brain sizes. Thus, I predict a negative correlation between r$_{max}$ and the status on the worldwide scale (1=not globally threatened, 2=rare, 3=vulnerable, 4=endangered) and a positive correlation between relative brain size and the worldwide status.

### 3. Energy subsidies hypothesis

a) *Brain size or reproduction.* Before the energy subsidies hypothesis can be tested, I need to look at a possible correlation between total energy amount per breeding season and number of caretakers. A positive correlation is expected. Then, the amount of allomaternal care is expected to correlate positively with relative brain size and/or reproduction (fertility or r$_{max}$).

- Amount of allomaternal care positively correlates with relative brain size: The more help available, the more energy is invested in brains rather than reproduction, which means that compensation by an elongation in reproductive lifespan is required for nonetheless evolutionary stable populations. Thus, I predict a positive correlation between the amount of allomaternal care and reproductive lifespan.

- Amount of allomaternal care positively correlates with reproduction (fertility or r$_{max}$): The more help available, the more energy is invested in reproduction rather than in brains and thus, no compensation by elongated reproductive lifespan is required. Therefore, I expect the amount of allomaternal care not to positively correlate with maximum reproductive lifespan.

b) *Energetic load per caretaker.* The lower the energetic load per caretaker (in this case only mother or father), the more energy they are able to invest in maintenance of their own brains. I predict a negative correlation between the total energetic load per breeding parent and relative brain size and positive correlation between the energetic load per caretaker and reproduction (r$_{max}$ or fertility).

c) *Energetic input per offspring.* Offspring which are bred in presence of additional allomaternal care are expected to receive a higher amount of energy. I predict that the total energetic input per offspring correlates positively with relative brain size.

### 4. Energy subsidies, egg mass and altriciality

a) *Mate feeding.* Additional allomaternal care in form of mate feeding during egg production, egg laying and incubation is expected to either positively correlate with egg mass or brain mass. If egg mass positively correlates with mate feeding (dummy variable), this means that the extra energy from mate feeding is invested in egg mass. If brain mass positively correlates with mate feeding (dummy variable), this means that the extra energy from mate feeding is rather invested in brain size. If both, egg mass and brain mass are correlated with mate feeding, the extra energy is invested in both.

b) *Allomaternal care and egg mass.* According to the study of Russel et al. (2007), within the same species (*Malurus cyaneus*) mothers with additional amount of allomaternal lay smaller eggs than mothers without helpers. The premature (smaller hatch weight) state of hatchlings are compensated by the support of allomaternal helpers later in development (during pre- and post-fledging period). I will test for a correlation between the amount of allomaternal care and egg mass on an interspecific level.

c) *Altriciality.* Help is supposed to be most effective for offspring during the postnatal period, as then energy flows directly to the offspring. I predict that the more additional amount of allomaternal help is available during the chick rearing period, the more precocial species to show altricial characteristics such as relatively smaller eggs and clutch sizes or shorter incubation periods (shift towards altriciality).

### Alternative hypotheses

Several alternative explanations exist to explain variation in relative brain size (see 1.2 Hypotheses explaining brain size variation).

### 5. Development hypothesis

Relative brain size is expected to be bigger in more altricial species, as there the offpsring are provisioned much more often by parents and helpers after hatching (e.g. Pagel and Harvey 1985 a,b).

- I expect the amount of allomaternal care (energetic input, number of caretakers, breeding type) to have stronger effects on relative brain size than developmental aspects per se. Thus, I predict that including the amount of allomaternal care yields a better statistical model than just including development mode alone.

### 6. Maternal energy hypothesis

Assuming that the mother‘s energetic investment per offspring is strongly effecting relative brain size, a positive correlation between maternal energetic load per offspring and relative brain size of offspring would be expected (e.g. Martin 1981, 1996).

- As in most avian groups both parents (mother and father) are breeding, I expect that the total energetic input per offspring is stronger correlated with relative brain size than only the maternal energetic input per offspring.

### 7. Time vs. energetic constraints

If time mainly constrains relative brain size (e.g. maturational constraint hypothesis), various time estimations in development such as incubation, pre-fledging, post-fledging parental care and time to independence are expected to correlate positively with encephalization. Time of first flight would be expected to correlate positively with relative brain size as well, as fledglings are much more dependent on help of parents and alloparental helpers in terms of feeding and protection during the time they are not able to fly. Further, time to adult size which seems to be especially important for superprecocial and precocial species leaving their nests right after hatching, is expected to be positively related to encephalization (assuming the later offspring reach adult size, the longer their brains need to grow and the longer they are provisioned by parents/helpers).

- I predict that differences in amount of allomaternal care (energetic investments per offspring, number of caretakers or breeding type) are responsible for variation in relative brain size rather than time constraints. Thus, I expect amount of allomaternal care (energetic input per offspring, number of caretakers or breeding type) to correlate stronger with relative brain size than the duration of parental care.

### 8. Social brain hypothesis

This hypothesis claims that the more complex social groups in cooperatively breeding species would allow for larger brains to become a selective advantage (e.g. Dunbar 1998). To test whether the effects of complex social demands or energetic constraints are behind this, I include social patterns during breeding season in the analyses, where for example a gregarious lifestyle per se does not mean additional energy.

- I expect that allomaternal care is linked to extra energy inputs and that the effects of cooperative breeding (allomaternal care) on relative brain size are stronger than the effects of a gregarious lifestyle per se.

# 2 Material and Methods

## 2.1 Comparative approach

The methodological basis of this project is the comparative approach. Comparative studies are crucial to understand evolution in a broader framework, to detect general evolutionary principles and to infer these on to other taxa and lineages. It is important to consider that an evolutionary pattern observed within a species does not necessarily need to appear across species and vice versa. The advantage of experimental studies is that all factors except the one of interest can be controlled. However, for some evolutionary questions it is simply impossible to study them in form of an experimental approach. One example would be investigating the effect of sociality on relative brain size as it has been done to test for the social brain hypothesis. First, one is not able to force individuals of a species to be social in order to compare them to the non-social ones. Second and most important, the aim of such an evolutionary question is not to detect such a pattern within a species but rather across species. Due to genetic, morphological and physiological constraints the intraspecific trait variation is not large enough to detect certain evolutionary patterns within a species (Bennett and Owens 2002). Often, patterns found across species are mixed up with patterns found within species. To make an example, in a recent study by Navarrete et al. (2011) a negative relationship between relative brain size and adipose tissue has been found across a wide range of mammalian species. This does not imply that obese individuals have smaller brains and are less intelligent, it rather claims that species with larger brains have little adipose tissue compared to species with smaller relative brain sizes.

The aim of this study is to find a general pattern about the cohesion between the amount of allomaternal care and relative brain size across a wide range of bird species. For investigating such a general evolutionary question the comparative approach is very well suited.

## 2.2 Data set

### 2.2.1 Basis data set

The original data set was provided by Karin Isler and built the foundation for this comparative research project. The data on several different variables of morphology/physiology, ecology and life history, mainly collected by Karin Isler, were compiled from literature . Already collected **morphological/physiological data** (adult body mass; adult brain mass; egg mass; basal metabolic rate (BMR); field metabolic rate during the non-breeding period ($FMR_{non-breeding}$)) were compiled from several compilations, mainly by Mlikovski (1989a,b,c, 1990), Iwaniuk and Nelson (2003) and Schönwetter (1960-1978). Already collected **life history data** (breeding type; nest building; incubation; time of fledging; time of first flight; time to adult size; time until offspring are fed after they have left the nest; clutch size (number of eggs per clutch);

broods per year; age at first reproduction (AFR); annual adult survival; longevity (= maximum lifespan)) were mainly compiled from del Hoyo et al. (1992-2011), Schönwetter (1960-1978) and Iwaniuk and Nelson (2003).
Although the data provided by Karin Isler represented a huge compilation, data collection on all these variables was not complete, as new data and many new compilations (e.g. new volumes of del Hoyo et al. (1992-2011)) have become available. Therefore, I compiled further data on these variables to enhance the existing data collection (further details see sections 2.2.2 and 2.3).

### 2.2.2 Extended data set

I compiled further data on given and new variables from the literature resulting in a data set of 1756 avian species from 179 different families. Data on morphology, physiology and life history are not complete for all the species. However, the data set includes only species for which complete phylogenetic information is available (number of collected data (= number of species data is available for) on each variable is given in table 2.5).
In contrast to the basic data set, the extended data set additionally contains the following variables: body mass range (including mass of ♀/♂); number of caretakers during different development periods; social pattern; courtship/mate feeding; development mode; status on the worldwide scale and field metabolic rates during incubation and chick rearing period. Especially data on field metabolic rates during the incubation and the chick rearing period and the exact number of caretakers are essential to quantify reproductive effort and allomaternal energy subsidies. The compiled data set containing 1756 species built the foundation for all analyses of this study.

## 2.3 Data collection

Further data and variables were assembled from various literature sources, whereby most information was collected from 'The Handbook of the Birds of the World' by del Hoyo et al. (1992-2011) and BWPi (The Birds of the Western Palearctic on interactive DVD-ROM (2004)). These two encyclopaedias cover wide ranges of information about taxonomy, behaviour, morphology, life history and habitats on almost all known avian species on earth. All the common English family names were compiled from the Internet Bird Collection (IBC) (http://ibc.lynxeds.com), where the information is provided by the Handbook of the Birds of the World (del Hoyo et al. 1992-2011).
Table 2.5 lists the data distribution on the different variables and their levels as well as their detailed definitions. The different variables are categorized into six classes: „*Morphology/physiology*“, „*Life history I (caretakers)*“, „*Life history II (durations)*“, „*Life history III (others)*“, „*Life history IV (fertility)*“, „*Others*“.

### 2.3.1 Morphological and physiological data

***Brain mass***

Data on brain mass were collected from several publications (Boire and Baron 1994; Cril and Quiring 1940; Mlikovski 1989 a,b,c,1990; Jersion in Mlikovski 1989b; Lapicque in Mlikovski 1990; Graber and Graber in Mlikovski 1990; Hrdlicka in Mlikovski 1989a,b, 1990; Hrdlicka, Vaughien and Skvorcova in Mlikovski 1990; Garamszegi et al. 2002; Girard in Mlikovski 1990; Armstrong and Bergeron 1985; Iwaniuk and Nelson 2002,2003; Iwaniuk and Hurd 2005; Portmann 1947 in Mlikovski 1990; Portmann and Vischer in Mlikovski 1990; Rehkamper et al. 1991 a,b; Schuck-Paim et al. 2008; Senglaub in Mlikovski 1989c; Skvorcova in Mlikovski 1990; Waterlot 1912 in Mlikovski 1989c, 1990; Löhmer and Ebinger 1980 in Mlikovski 1989c). Data refers to fully adult individuals and the values represent the means of female and male brain mass or endocranial volume.

Measurements of total relative brain mass (adjusted to body mass) rather than the relative sizes of separate brain structures are included in the analyses for several reasons. First of all, the costs arising from brain growth and maintenance affect the whole brain and not particular brain structures. The only cost differences appear between unmyelinated grey and myelinated white matter, namely the costs for unmyelinated axons are up to ten times higher than for myelinated axons (Wang et al. 2008). However, both types, grey and white matter, cover the whole brain. Second, Finlay et al. (1995, 2001) found coordinated size changes among major brain subdivisions: changes in sizes of individual parts of the brain change with total brain size, whereby selection on particular structures for certain functions can occur. Moreover, several cerebral subdivisions are used simultaneously during cognitive performances and are anatomically connected, which again supports the idea of correlated evolution of volumetric change among brain components (Barton 2006). Third, often only data on whole brain sizes are available.

***Body mass***

The already collected data on non sex-specific body mass in the basic data set were collected from the same publications as brain mass (section 2.3.1). Furthermore, I collected data on body mass ranges for each sex in order to derive accurate estimates of mean body mass (compiled from del Hoyo (1992-2011)). In cases where data on several subspecies were available, whenever possible the value of the subspecies named identical to the one in the data set was used, else the median value of all subspecies was used. The estimates of sex-specific mean body mass were calculated based on multiple PGLS regression models (section 2.4.2) of 52 species (where for each sex the range (minimum and maximum) as well as the exact mean of body mass were available):

$$\female : \text{mean body mass} = -0.018 + (0.402 * \text{min. body}) + (0.592 * \text{max. body}) \tag{2.1}$$

$$\male : \text{mean body mass} = 0.015 + (0.462 * \text{min. body}) + (0.530 * \text{max. body}) \qquad (2.2)$$

In total I estimated 1501 female and 1504 male body mass means. In order to avoid pseudo correlations concerning morphological and physiological traits as well as life history traits, all the analyses needed to be controlled for body size. I used non sex-specific body mass as a covariate (mainly collected from Mlikovsi (1989a, 1989b, 1989c, 1990): average of female and male body mass used as a species mean value (see Iwaniuk and Nelson (2002)) because of several reasons. First, body size dimorphism is not very common in birds. In only 25% of all species included in the data set the difference between the sexes is sufficiently significant that separate values were given in del Hoyo (1992-2011). The stronger body size dimorphism in mammals, compared to birds, might be explained by the fact that in mammals males mostly do not help to care for young which allows them to have a bigger optimal body size than the females, whereas in birds, mostly both parents care for young, which results in only a very weak sexual body dimorphism.
Second, brain size is not really sex-specific, in general, sexual dimorphism is much more expressed in body mass (Isler and van Schaik 2009a). Thus, it makes no sense to adjust non sex-specific brain mass to sex-specific body mass. Part of the analyses including life history data were as well additionally corrected for female body mass instead of non sex-specific body mass. However, the results did not differ in the level of significance. Therefore, all the results presented are based on non sex-specific body mass data. Whenever possible, data on any morphological, physiological or life history variable and body mass were taken from the same study.

### *Egg mass*

Data on egg mass were collected from several publications (Alisauskas 1986; Bancroft 1984; Birkhead et al. 1988; del Hoyo (1992-2011); Evans 1969; Forbes and Ankney 1988; Hoyt 1979; Mead et al. 1987; Mueller 1986; Murphy and Fleischer 1986; Murphy 1988; O'Connor 1979; Paganelli et al. 1974; Poole 1985; Rohwer 1988; Schönwetter 1960-1987; Slagsvold et al. 1984; Warham 1983). The mass was mostly estimated from the measurements of external dimensions.

### *BMR, $FMR_{non-breeding}$, $FMR_{incubation}$ and $FMR_{chick-rearing}$*

According to Ricklefs et al. (1996, p. 1047), BMR represents the „minimum energetic cost of maintaining cells and organs in readiness for higher levels of activity“, whereas FMR is defined as „the daily energy expenditure measuring the rate of energy metabolism of an active organism“. BMR is measured in Watt and FMR in kJ/day.

Already collected data on basal metabolic rate (BMR) were compiled from Daan (1990) and McKechnie and Wolf (2004), building 97% of all BMR data. Data on BMR of McKechnie and Wolf (2004) fulfil the following conditions: 1) measured within the thermoneutral zone; 2) measurements came only from postabsorptive individuals; 3) measured during „the rest phase of the circadian cycle in darkened chambers“; 4) species means result from sample sizes of at least 3 individuals. BMR data compiled from Daan (1990) fulfil the first three of these conditions. Further data on BMR were collected from a few other compilations: Williams 1988, 1993, 1996; Engstrand 2002; Koteja 1991; McNab 2009; Wheathers and Sullivan 1989; Yom-Tov and Wright 1993. Most data on FMR during the non-breeding period (FMR$_{non-breeding}$) were compiled from Nagy (1999). Further FMR$_{non-breeding}$ data were collected from a few other sources (FMR$_{non-breeding}$: Bennett and Harvey 1987; Koteja 1991; Nagy 1987). All measurements came from free living individuals which were fully independent of parental feeding. I additionally collected data on FMR during the incubation (FMR$_{incubation}$) and the chick rearing period (FMR$_{chick-rearing}$) in order to properly quantify the amount of allomaternal (data on FMR$_{incubation}$: Tinbergen and Williams 2002; Bech et al. 2002; Chapell et al. 1993; Flint and Nagy 1984; Parker and Holm 1990; Bennett and Harvey 1987; Shaffer 2004; Green et al. 2009; Williams 1993, 1996, 2001; data on FMR$_{chick-rearing}$: Tinbergen and Williams 2002; Tatner 1992; Bech et al. 2002; Chapell et al. 1993; Shaffer 2004; Williams 2001; Gabrielsen 1991; Utter and Lefebvre 1973; Wheather et al. 2002; Tieleman 2004). All the values represent averages of males and females in case where data was available for both sexes. If data for different stages within incubation or chick rearing periods were given, as well mean values were used. Information for FMR$_{incubation}$ was available for a total number of 47 species and for FMR$_{chick-rearing}$ I found data for 32 species. As information on FMR$_{incubation}$ and FMR$_{chick-rearing}$ is available only for few species, FMR$_{incubation}$/FMR$_{chick-rearing}$ values were approximated for other species using multiple PGLS regression models (section 2.4.2).

#### Multiple PGLS regression model for estimating FMR$_{incubation}$

To estimate field metabolic rates during incubation for a larger range of bird species, I calculated a multiple PGLS regression model including different predictor parameters (body mass, BMR, FMR$_{non-breeding}$, number of individuals incubating, duration of incubation, clutch mass (clutch size * egg mass), development mode and their interactions). The best model fit based on Akaike information criterion (AIC) included body mass, BMR, development mode, duration of incubation, number of individuals incubating and the interaction of body mass and development mode (table 2.1). First, body mass has a negative effect on the energy spent during incubation. This can be explained by the surface-to-volume ratio: larger species need transfer less heat to the eggs compared to small-bodied species (cited in Clutton-Brock (1991 a)). Second, as one would expect, duration of incubation and number of individuals incubating are negatively correlated with FMR$_{incubation}$. In other words, the longer the duration of incubation lasts and the more individuals involved during incubation, the less energy is spent per individual per day. Development mode is negatively correlated with $\text{FMR}_{incubation}$, which means that the more altricial the less energy is spent during incubation. Altricial species invest much more in growth after hatching. In contrast to BMR, $\text{FMR}_{non-breeding}$ did not have an influence on $\text{FMR}_{incubation}$. Furthermore, clutch mass did not have an effect on $\text{FMR}_{incubation}$, i.e. energy invested during incubation is not dependent on the total egg mass. Other parameters such as the ambient temperature and the structure or location of the nest might have an influence on $\text{FMR}_{incubation}$ as well but could not be considered in the model (cited in Clutton-Brock 1991a). Using the parameter estimates shown in table 2.1, I approximated $\text{FMR}_{incubation}$ for a total number of 192 species. The raw and estimated data of $\text{FMR}_{chick-rearing}$ is shown in figure 2.1a.

Table 2.1: **Multiple PGLS regression model for estimating $\text{FMR}_{incubation}$.** Multiple PGLS regression model for estimating $\text{FMR}_{incubation}$: given are the sample size (n), Akaike information criterion (AIC), Pagels' lambda ($\lambda$) as well as slopes and corresponding p-values. Significant effects are shown in italics.

| n | AIC | lambda | predictor variable | p-value | slope |
|---|---|---|---|---|---|
| 21 | 12.58 | 0 | body mass | 0.31 | -0.39 |
| | | | BMR | *0.04* | 0.7 |
| | | | development type | *0.02* | -0.77 |
| | | | incubation duration | *0.0008* | -1.18 |
| | | | # individuals incubating | 0.27 | -0.21 |
| | | | body mass * development type | *0.046* | 0.14 |

### *Multiple PGLS regression model for estimating $\text{FMR}_{chick-rearing}$*

To estimate field metabolic rates during chick rearing period for a larger range of bird species, I calculated a multiple PGLS regression model including different predictor parameters (body mass, BMR, $\text{FMR}_{non-breeding}$, number of individuals feeding young in the nest, time of first flight, clutch mass (clutch size * egg mass), development mode and their interactions). Because development differences in time of leaving the nest are crucial (precocials in contrast to altricials leave the nest right after hatching which results in fledging periods equal to zero), I used time of first flight instead of time of fledging as a measurement for the duration of the growth period. However, the length of the growth period seems not to account for any variation of $\text{FMR}_{chick-rearing}$. The best model fit based on AIC was found including body mass, BMR, $\text{FMR}_{non-breeding}$, development mode, number of individuals feeding young in nest and flight (0: flightless, 1: aerial) (table 2.2). In contrast to $\text{FMR}_{incubation}$, $\text{FMR}_{chick-rearing}$ correlates significantly with $\text{FMR}_{non-breeding}$. Many different factors influencing $\text{FMR}_{chick-rearing}$ (e.g. diet, habitat, climate) as well as high variability between species concerning „feeding offspring“ patterns (e.g. locations of food resources, if parents actively feed young or only passively) make it difficult to find a better model estimating $\text{FMR}_{chick-rearing}$. Such a high variability in various parameters is likely only found during the chick-rearing period because during incubation there is much less room for variation. In total FMR$_{chick-rearing}$ data was approximated for 37 species. The raw and estimated data of FMR$_{chick-rearing}$ is shown in figure 2.1b.

Table 2.2: **Multiple PGLS regression model for estimating FMR$_{chick-rearing}$.** Multiple PGLS regression model for estimating FMR$_{chick-rearing}$: given are the sample size (n), Akaike information criterion (AIC), Pagels' lambda ($\lambda$) as well as slopes and corresponding p-values. Significant effects are shown in italics.

| **n** | **AIC** | **lambda** | **predictor variable** | **p-value** | **slope** |
|---|---|---|---|---|---|
| 18 | -18.88 | 0 | body mass | 0.11 | 0.2 |
| | | | BMR | 0.09 | 0.26 |
| | | | FMR$_{non-breeding}$ | *<0.0001* | 0.66 |
| | | | development type | 0.07 | 0.12 |
| | | | # individuals feeding young in nest | 0.23 | -0.19 |
| | | | flight | *<0.0001* | 0.185 |

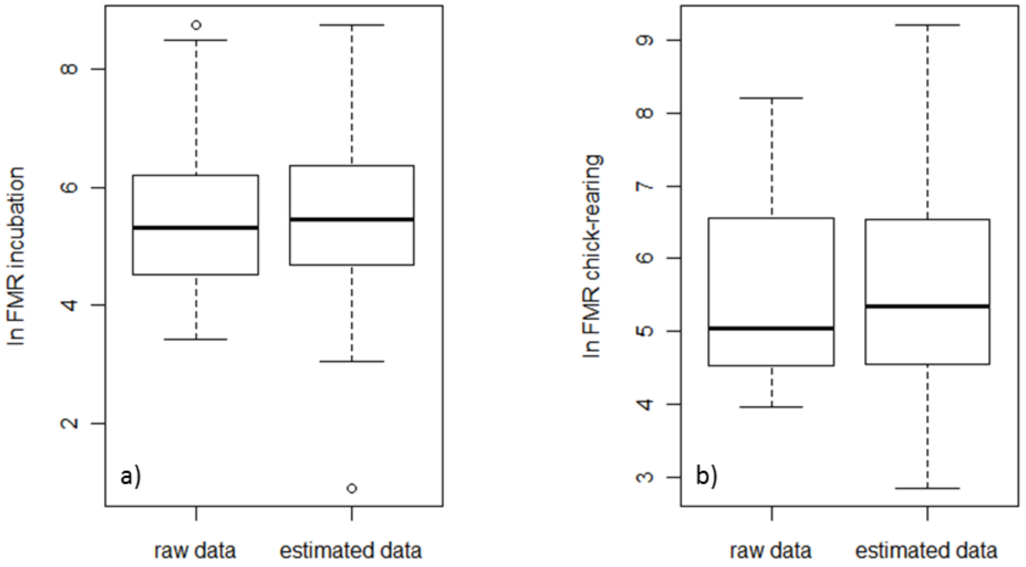


Figure 2.1: **Raw and estimated FMR data.** Raw and estimated data of FMR$_{incubation}$ and FMR$_{chick-rearing}$. a) Raw ln FMR$_{incubation}$ ($mean \pm SD = 5.62 \pm 1.35$ ($n = 49$) and estimated ln FMR$_{incubation}$ data ($mean \pm SD = 5.54 \pm 1.84$) ($n = 239$). b) Raw ln FMR$_{chick-rearing}$ ($mean \pm SD = 5.50 \pm 1.19$) ($n = 32$) and estimated FMR$_{chick-rearing}$ data ($mean \pm SD = 5.56 \pm 1.37$) ($n = 61$). The horizontal lines in the boxes represents the median, the hinges represent the 25% and 75% quartiles. The whiskers indicate the 1.5*interquartile range and blank data points represent outliers.

***Quantification of reproductive effort and allomaternal energy subsidies*** The main challenge was to quantify the amount of help a breeding pair and its offspring receive. This quantification needs to represent the parental/helper energetic load and the energetic input received per offspring. Not only lengths of different development periods (incubation, pre - and postfledging periods) and the corresponding number of helpers are important. Of major interest is the energy spent during these periods in order to distribute the costs during different breeding periods. Therefore, data on field metabolic rates (FMR) of parents during incubation and chick rearing periods were collected in order to quantify the costs during different breeding periods. As described in the previous two sections, body mass, BMR, FMR$_{non-breeding}$, duration of incubation, number of individuals incubating, number of individuals feeding young in nest, flight (aerial; flightless) and development mode were used as predictor parameters of FMR$_{incubation}$/FMR$_{chick-rearing}$ for further species. Out of these estimated values I quantified the energetic load per caretaker/all caretakers during the incubation respectively the chick rearing period and the energetic input per offspring as follows: First, in equation 2.3 and 2.5 the difference between FMR$_{incubation}$/FMR$_{chick-rearing}$ and BMR are calculated to get standardized FMR$_{incubation}$/FMR$_{chick-rearing}$. Second, the $\Delta FMR_{inc}/\Delta FMR_{chick}$ are then multiplied by the time of incubation respectively duration of chick rearing (=time of first flight=TFF) (equations 2.4 and 2.6). These values represent the total energetic load per caretaker. The sum of the total energetic loads of all caretakers is calculated by multiplying with the number of caretakers helping during the corresponding period (equations 2.7 and 2.8). In equations 2.9 and 2.10 the total energetic input per offspring is calculated by dividing by the sum of the energetic loads of all caretakers by clutch size.

$$\Delta FMR_{inc} \text{ (kJ/day)} = \text{FMR}_{inc} \text{ (kJ/day)} - \text{BMR (kJ/day)} \tag{2.3}$$

$$\text{total } \Delta FMR_{inc} \text{ (kJ)} = \Delta FMR_{inc} \text{ (kJ/day)} * \text{incubation (days)} \tag{2.4}$$

Corresponding calculations for energetic load during chick rearing period:

$$\Delta FMR_{chick} \text{ (kJ/day)} = \text{FMR}_{chick} \text{ (kJ/day)} - \text{BMR (kJ/day)} \tag{2.5}$$

$$\text{total } \Delta FMR_{chick} \text{ (kJ)} = \Delta FMR_{chick} \text{ (kJ/day)} * \text{TFF (days)} \tag{2.6}$$

Total energetic load for all caretakers:

$$\text{E}_{sum(incubation)} = \text{total } \Delta FMR_{inc} \text{ (kJ)} * \text{total number of caretakers} \tag{2.7}$$

$$\text{E}_{sum(chick)} = \text{total } \Delta FMR_{chick} \text{ (kJ)} * \text{total number of caretakers} \tag{2.8}$$

Total energetic input per offspring:

$$\text{E}_{offspring(incubation)} = \frac{\text{E}_{sum(incubation)}}{\text{clutch size}} \tag{2.9}$$

$$\text{E}_{offspring(chick)} = \frac{\text{E}_{sum(chick)}}{\text{clutch size}} \tag{2.10}$$

For the calculations of total $\Delta FMR_{incubation}/\Delta FMR_{chick}$ I consider time until first flight as the main chick rearing period for precocial as well as altricial species, as by that time the offspring reach about adult size (Bennett and Owens 2002). Further, I assume caretakers to have their biggest breeding effort by feeding and protecting the young during the time those are unable to fly. After they are able to fly, they are probably largely independent.

For the calculations of $\text{E}_{sum(incubation)}/\text{E}_{sum(chickrearing)}$ either the number of individuals feeding (in altricials) or protecting (in precocials) the offspring was used. In cases where the difference between $\text{FMR}_{incubation}/\text{FMR}_{chick-rearing}$ and BMR (equations ( 2.3) and ( 2.5)) resulted in negative values, data seem to be not reliable, and thus, these species were excluded from the analyses (4% of data for $\text{FMR}_{incubation}$; 4.5% of data for $\text{FMR}_{chick-rearing}$). For altricial species, where data on TFF was not available, time of fledging was used as a measurement for the chick rearing period, as TFF and

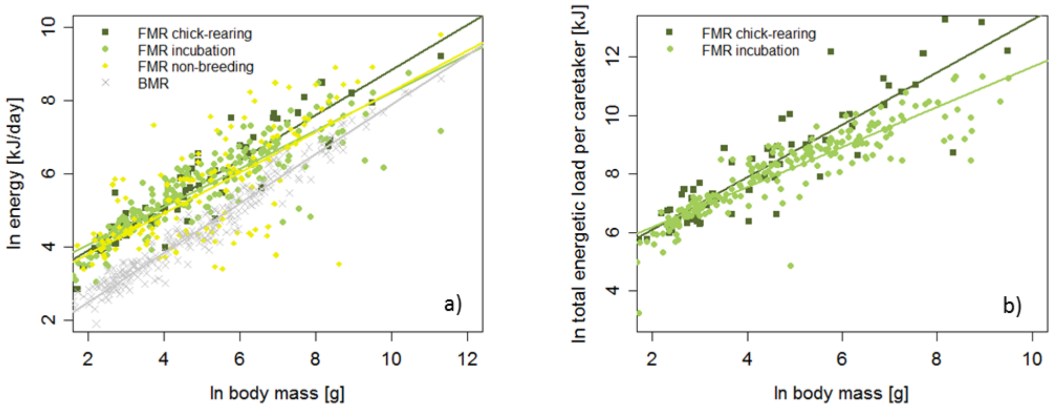


Figure 2.2: **Energetic measurements.** Least-square regressions of ln daily energetic measurements (ln BMR, ln FMR$_{non-breeding}$ , ln FMR$_{incubation}$ (estimated), ln FMR$_{chick-rearing}$ (estimated)) on ln body mass. n(BMR) = 255; n(FMR$_{non-breeding}$) = 154; n(FMR$_{incubation}$) = 239; n(FMR$_{chick-rearing}$) = 69. b) Least-square regressions of ln total energetic load per caretaker (for the total incubation and chick-rearing period, calculated from equations (2.4) and (2.6) based on estimated values) on ln body mass (n(FMR$_{incubation}$) = 215; n(FMR$_{chick-rearing}$) = 61).

time of fledging mostly coincide in altricial species. Data on total $\Delta FMR_{chick}$ and E$_{sum(chickrearing)}$ for the total of 59 species is listed in table 2.3.

For the analyses investigating the effect of help, I used three alternative quantifications for the amount of allomaternal care: energetic measurements, number of caretakers and breeding type. The energetic measurements representing the amount of allomaternal care are based on the FMR$_{chick-rearing}$. The energetic breeding effort is highest during the chick-rearing period including feeding young and thus, is roughly representing total breeding effort (cited in Clutton-Brock 1991a). The energetic expenditure during incubation is very similar to FMR$_{non-breeding}$ or even BMR and thus, might not be an appropriate measurement for the amount of allomaternal care (figure 2.2 a,b).

Furthermore, for properly testing the maternal energy hypothesis, larger sample sizes of maternal investment and total investment per offspring were needed. Therefore, approximations for the total and maternal energy invested in an offspring were used. The total energy per offspring was estimated by the growth mass (adult body mass - egg mass) multiplied by time of first flight (TFF), whereas as an approximation for the maternal load, growth mass multiplied by TFF was divided by the total number of caretakers. As a second approach, daily input per offspring and daily maternal load per offspring was calculated, representing time independent measurements (the approximations from above not multiplied by TFF).

Table 2.3: **Estimated FMR$_{chick-rearing}$ data.** Data on mean number of caretakers, total $\Delta FMR_{chick}$ [kJ] and E$_{sum(chick)}$ [kJ] of all the 59 species data is available for.

| Genus species | Family | # caretakers | total $\Delta FMR_{chick}$ | E$_{sum(chick)}$ |
|---|---|---|---|---|
| *Lagopus lagopus* | *Phasianidae* | 2 | 9166.4 | 18332.8 |
| *Branta bernicla* | *Anatidae* | 2 | 48654.2 | 97308.3 |
| *Somateria mollissima* | *Anatidae* | 1 | 180672.6 | 180672.6 |
| *Melanerpes formicivorus* | *Picidae* | 5 | 2677.3 | 13386.3 |
| *Colius striatus* | *Coliidae* | 3 | 581.9 | 1745.7 |
| *Platycercus zonarius* | *Psittacidae* | 2 | 8099.1 | 16198.3 |
| *Nyctea scandiaca* | *Strigidae* | 2 | 61811.5 | 123623.1 |
| *Asio otus* | *Strigidae* | 2.5 | 9497.4 | 23743.5 |
| *Geophaps plumifera* | *Columbidae* | 2 | 756.4 | 1512.8 |
| *Tringa totanus* | *Scolopacidae* | 2 | 7666.7 | 15333.5 |
| *Arenaria interpres* | *Scolopacidae* | 2 | 5573.2 | 11146.5 |
| *Calidris alba* | *Scolopacidae* | 2 | 1707.0 | 3414.0 |
| *Haematopus ostralegus* | *Haematopodidae* | 2.5 | 15067.0 | 37667.5 |
| *Larus argentatus* | *Laridae* | 2 | 60201.4 | 120402.8 |
| *Larus ridibundus* | *Laridae* | 2 | 2727.8 | 5455.7 |
| *Rissa tridactyla* | *Laridae* | 2 | 22532.7 | 45065.3 |
| *Uria aalge* | *Alcidae* | 2.5 | 76988.1 | 192470.2 |
| *Uria lomvia* | *Alcidae* | 2 | 31334.8 | 62669.6 |
| *Cepphus grylle* | *Alcidae* | 2 | 21937.8 | 43875.6 |
| *Aethia pusilla* | *Alcidae* | 2 | 7049.6 | 14099.1 |
| *Accipiter nisus* | *Accipitridae* | 2.5 | 10062.7 | 25156.9 |
| *Falco tinnunculus* | *Falconidae* | 2.5 | 8128.0 | 20319.9 |
| *Falco sparverius* | *Falconidae* | 2.5 | 4146.0 | 10364.9 |
| *Aptenodytes patagonicus* | *Spheniscidae* | 2 | 200207.3 | 400414.5 |
| *Eudyptes chrysolophus* | *Spheniscidae* | 2 | 6127.9 | 12255.9 |
| *Pterodroma macroptera* | *Procellariidae* | 2 | 193202.6 | 386405.3 |
| *Pelecanoides georgicus* | *Pelecanoididae* | 2 | 19522.0 | 39044.1 |
| *Pelecanoides urinatrix* | *Pelecanoididae* | 2 | 22696.5 | 45393.1 |
| *Diomedea exulans* | *Diomedeidae* | 2 | 525688.5 | 1051377.1 |
| *Diomedea chrysostoma* | *Diomedeidae* | 2 | 585308.2 | 1170616.5 |
| *Oceanites oceanicus* | *Hydrobatidae* | 2 | 7201.2 | 14402.5 |
| *Oceanodroma leucorhoa* | *Hydrobatidae* | 2 | 4424.0 | 8848.0 |
| *Phylid. novaehollandiae* | *Meliphagidae* | 2.5 | 694.3 | 1735.7 |
| *Acanthor. tenuirostris* | *Meliphagidae* | 2 | 430.0 | 860.0 |

(to be continued)

| | | | | |
|---|---|---|---|---|
| *Cinclus cinclus* | *Cinclidae* | 2 | 4914.5 | 9829.0 |
| *Sialia mexicana* | *Turdidae* | 2.5 | 1488.3 | 3720.7 |
| *Turdus merula* | *Turdidae* | 2 | 2632.2 | 5264.4 |
| *Muscicapa striata* | *Muscicapidae* | 2 | 559.7 | 1119.5 |
| *Ficedula hypoleuca* | *Muscicapidae* | 2.5 | 653.7 | 1634.2 |
| *Ficedula albicollis* | *Muscicapidae* | 2.5 | 855.2 | 2137.9 |
| *Erithacus rubecula* | *Muscicapidae* | 2.5 | 617.4 | 1543.4 |
| *Oenanthe oenanthe* | *Muscicapidae* | 2.5 | 1009.6 | 2523.9 |
| *Sturnus vulgaris* | *Sturnidae* | 2.5 | 4175.4 | 10438.4 |
| *Auriparus flaviceps* | *Polioptilidae* | 2 | 314.3 | 628.6 |
| *Parus major* | *Paridae* | 2 | 1279.8 | 2559.5 |
| *Parus caeruleus* | *Paridae* | 2.5 | 866.5 | 2166.3 |
| *Tachycineta bicolor* | *Hirundinidae* | 2.5 | 2192.3 | 5480.8 |
| *Riparia riparia* | *Hirundinidae* | 2 | 1472.0 | 2944.0 |
| *Hirundo rustica* | *Hirundinidae* | 2.5 | 1733.4 | 4333.6 |
| *Delichon urbica* | *Hirundinidae* | 2 | 1764.5 | 3528.9 |
| *Zosterops lateralis* | *Zosteropidae* | 2 | 399.7 | 799.4 |
| *Alauda arvensis* | *Alaudidae* | 2 | 741.4 | 1482.7 |
| *Nectarinia violacea* | *Nectariniidae* | 2 | 778.6 | 1557.1 |
| *Passer domesticus* | *Passeridae* | 2 | 1253.0 | 2505.9 |
| *Prunella modularis* | *Prunellidae* | 3.25 | 550.6 | 1789.6 |
| *Estrilda troglodytes* | *Estrildidae* | 2 | 316.8 | 633.5 |
| *Fringilla montifringilla* | *Fringillidae* | 2 | 1237.7 | 2475.5 |
| *Junco hyemalis* | *Emberizidae* | 2 | 595.6 | 1191.2 |
| *Passerculus sandwichensis* | *Emberizidae* | 2 | 536.0 | 1072.0 |

### 2.3.2 Life history data

#### *Life history I - caretakers*

The first life history category (*„Life history I (caretakers)“*) contains variables on number of caretakers (parents + helpers = caretakers) assisting during different breeding periods (number of caretakers incubating, feeding and protecting the offspring before and after they have left the nest). Data on the number of caretakers were collected from del Hoyo (1992-2011). In case of cooperative breeders, the values represent the sum of the two parents and the average of the given range of number of helpers. In case of occasional cooperative breeders, number of parents (one or two) and the half of the average of number of helpers were added up. In cases where no explicit number of helpers was given, I used 2.5 for occasional cooperative breeders or 3 for cooperative breeders. Furthermore, if one parent is investing much more than the other, the number of parents was set to 1.5. The number of caretakers is crucial for quantifying reproductive effort and allomaternal energy subsidies during breeding.

#### *Life history II - durations*

Category *„Life history II (durations)“* contains duration estimates of various life history traits, development and breeding periods. These include the durations of incubation and fledging periods, time of first flight (TFF); time to adult size; age at first reproduction (AFR) and longevity. Already collected data were compiled from several sources (Altman and Dittmer 1972; Alvarez 1975; Beissinger 1986; Boersma 1982; Botkin and Miller 1974; Brabraud et al. 1999; Bryant 1988; BWPi 2004; Carey and Judge 200; Chastel et al. 1993; Chernichko 1998; Clapp et al. 1982, 1983; del Hoyo (1992-2011); Delannoy and Cruz (1988); Doherty et al. 2004; El-Wailly 1966; Gaillard et al. 1989; Grzimek 1970; Higgins 1999; Holland et al. 1982; Iwaniuk and Nelson 2003; Juniper 1998; Kaverkina and Babich 1987; Kennard 1975; Klimcievicz et al. 1983; Klimcievicz and Futcher 1987,1989; Klomp 1970; Langley 1983; Marion and Fleetwood 1974; Martin and Clobert 1996; Martin 1995; Moreau and Moreau 1940; Mougin and ven Beveren 1979; Newton 1988; Ollason and Dunnet 1988; Pierotti and Annette 1995; Prather and Cruz 1995; Ricklefs 2000; Russel et al. 2004; Scolaro 1990; Staav 1998; Williams and Croxall 1991; Worth 1940; Yorio et al. 2001; Yosef 2001; Zammuto 1986). I collected further data from del Hoyo (1992-2011) and BWPi (2004). Generally, if ranges of durations were given, average values were used. Whenever possible, data on longevity was used from from wild records, but if not available, captive records were used. If both were available, I used data of wild records. In some species the difference between longevity and AFR were very small compared to close related species, incicating the lack of observations rather than realistic data. Thus, eight species were excluded from the analyses. Time measurements are crucial for the quantification of the reproductive effort. The different breeding and development periods are graphically illustrated in figure 2.3.

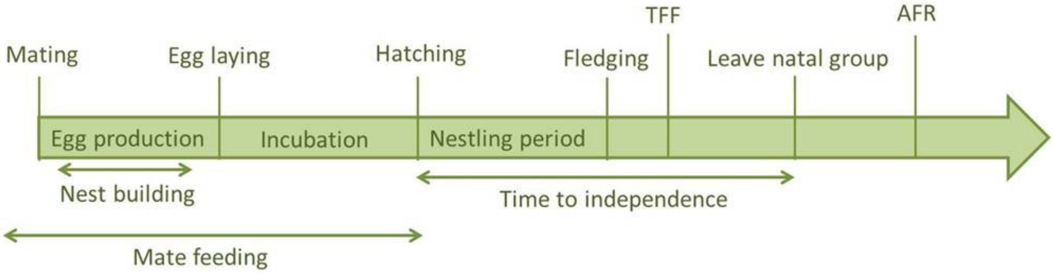


Figure 2.3: **Life history.** Graphic representation of different breeding and development periods in avian life history. Mate feeding occurs mostly during courtship, egg production and incubation. The time between leaving eggs (= hatching) and leaving nests (= fledging) is called nestling period or time to fledging. After a certain period of time offspring leave nests and start to fly (= TFF). Offspring reach their independence when they no longer stay with their parents or whithin family groups and leave their natal territory.

### ***Life history III - others***

The third life history category („*Life history III (others)*“) contains different kinds of other life history traits such as social pattern and mate feeding, breeding type and development mode.

Social pattern refers to the social organisation during breeding season and the data was used to test for the social brain hypothesis. In the analyses social pattern, compiled from del Hoyo (1992-2011), was treated as a continuous variable: 1= territorial solitary; 2 = territorial pair; 2.5 = territorial pair / family group; 3 = territorial family group; 4 = tolerant; 5 = colonial (further details are found in table 2.5). Furthermore, I collected data on mate feeding (0 = no mate feeding; 1 = mate feeding) in order to quantify the amount of allomaternal care during the incubation period (collected form del Hoyo (1992-2011)).

The breeding types are classified according to Cockburn (2006) representing a stepwise increase in the amount of allomaternal care (table 2.4).

Data on the different development modes were compiled from Starck 1993 and was assigned on family levels. A detailed description of the classification is given in table 1.2. Although detailed information about nestling morphology and behaviour is lacking for many species, species can be assigned on the family level to one of these eight development gradations. The highest variation in development stage at hatching is observed on the level of avian orders and most avian families show the same ontogenetic mode (Starck 1993). For the analyses Precocial 1, 2 and 3 as well as Altricial 1 and 2 each were pooled together in one group (numerical coding: superprecocial = 0; precocial 1 + 2 + 3 = 1; semiprecocial = 2; semialtricial = 3; altricial 1 + 2 = 4). In general, I treated categorical variables as continuous variables which allowed for applying multiple regression models.

Table 2.4: **Breeding types.** Breeding type classification after Cockburn (2006). Given is the numerical coding used for the analyses, the definiton of each breeding type and some examples of avian families.

| **Breeding type** | **Numerical coding** | **Definition** | **Examples** |
|---|---|---|---|
| Brood parasites | 0.01 | Escape the effort of rearing young by laying own eggs in foreign nests | *Cuculidae* |
| Geothermal | 0 | Escape the effort of rearing young by using geothermal heat to incubate eggs | *Megapodiidae* |
| Single breeding | 1 | Care for young provided by either sex, male or female | *Anatidae* |
| Pair breeding | 2 | Care for young provided by both sexes, parents (male and female) | *Columbidae*,<br>*Corvidae*,<br>*Spheniscidae* |
| Occasional cooperative breeding | 2.5 | Sometimes more than two adults care for or defend brood (breeding type added by Karin Isler) | *Accipitridae*,<br>*Falconidae*,<br>*Meliphagidae* |
| Cooperative breeding | 3 | More than two adults care for or defend brood | *Psittacidae*,<br>*Accipitridae* |

### *Life history IV - fertility*

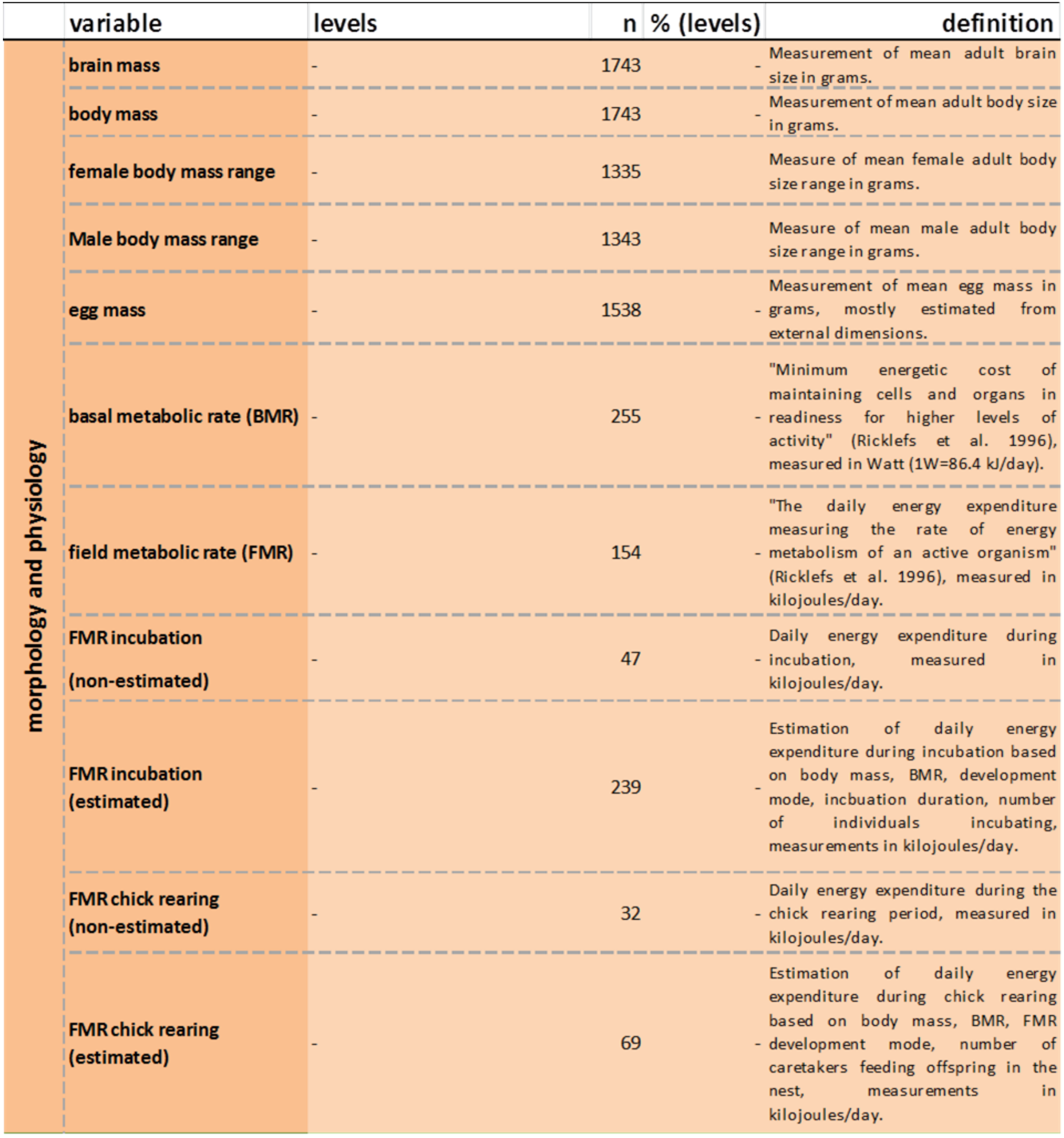
The last life history category (*„Life history IV (fertility)“*) contains numerical measurements of reproduction and parental fitness including clutch size, broods per year, annual fertility, maximum rate of population increase ($r_{max}$) and annual adult survival. Data collected by Karin Isler were compiled from the following publications: Alvarez 1975; Bent 1946; Crawford et al. 1999; del Hoyo 1992-2011; Delestrade and Stoyanov 1995; Doherty et al. 2004; Higgins 1999; Klomp 1970; Mallory et al. 2002; Martin and Clobert 1996; Martin 1995; Pruett-Jonest et al. 1981; Russell et al. 2004; Yom 1992; Yorio et al. 2001; Zammuto 1985. I collected further data from del Hoyo (1992-2011). Data on clutch size represent the mean of a given range of number of eggs per clutch. Annual fertility is calculated by clutch size times the number of broods per year. Data on $r_{max}$ were calculated from Cole‘s (1954) equation ((maximum lifespan - AFR) and average annual fertility), using Mathematica 8.0.1. As in some species the difference between longevity and AFR are very small compared to close related species, data on $r_{max}$ of eight species were excluded from the analyses.

### 2.3.3 Other data

This category contains the „status on the worldwide scale“ and flight. „Status on the worldwide scale“ classifies how threatened a species is for extinction according to the gradation of del Hoyo (1992-2011) (table 2.5). For the analyses I used the following numerical coding: 1 = not globally threatened; 2 = rare; 3 = vulnerable; 4 = endangered.

Data on flight (whether a species is flightless (= 0) or aerial (= 1)) were compiled from Burish et al. (2004) and Iwaniuk et al. (2004). As there seems to be a fundamental difference between flightless and aerial species concerning $\mathrm{FMR}_{non-breeding}$, in some analyses this factor needed to be included as a covariate.

Table 2.5: **Variables.** Data distribution on the different variables and their levels. For each variable number of species data have been collect for, percentages of total number of species of the particular levels of a variable and definitions are given. The different variables are categorized into six classes: „Morphology/physiology“, „Life history I (caretakers)“, „Life history II (durations)“, „Life history III (others)“, „Life history IV (fertility)“ and „others“.



| | variable | levels | n | % (levels) | definition |
|---|---|---|---|---|---|
| morphology and physiology | **brain mass** | - | 1743 | - | Measurement of mean adult brain size in grams. |
| | **body mass** | - | 1743 | - | Measurement of mean adult body size in grams. |
| | **female body mass range** | - | 1335 | | Measure of mean female adult body size range in grams. |
| | **Male body mass range** | - | 1343 | | Measure of mean male adult body size range in grams. |
| | **egg mass** | - | 1538 | - | Measurement of mean egg mass in grams, mostly estimated from external dimensions. |
| | **basal metabolic rate (BMR)** | - | 255 | - | "Minimum energetic cost of maintaining cells and organs in readiness for higher levels of activity" (Ricklefs et al. 1996), measured in Watt (1W=86.4 kJ/day). |
| | **field metabolic rate (FMR)** | - | 154 | - | "The daily energy expenditure measuring the rate of energy metabolism of an active organism" (Ricklefs et al. 1996), measured in kilojoules/day. |
| | **FMR incubation (non-estimated)** | - | 47 | - | Daily energy expenditure during incubation, measured in kilojoules/day. |
| | **FMR incubation (estimated)** | - | 239 | - | Estimation of daily energy expenditure during incubation based on body mass, BMR, development mode, incbuation duration, number of individuals incubating, measurements in kilojoules/day. |
| | **FMR chick rearing (non-estimated)** | - | 32 | - | Daily energy expenditure during the chick rearing period, measured in kilojoules/day. |
| | **FMR chick rearing (estimated)** | - | 69 | - | Estimation of daily energy expenditure during chick rearing based on body mass, BMR, FMR development mode, number of caretakers feeding offspring in the nest, measurements in kilojoules/day. |

(to be continued)

| | | | | | |
|---|---|---|---|---|---|
| **Life history I** | **mate feeding** | yes | 298 | 87.39% | Feeding mates (mostly females) during courtship, egg laying and incubation. Mostly female is fed by male during incubation, either in or/and out of the nest. |
| | | no | 43 | 12.61% | |
| | **how many incubate** | - | 1595 | - | Number of individuals involved in incubation. |
| | **how many feed in the nest** | - | 1565 | - | Number of individuals feeding hatchlings. |
| | **how many feed after nest** | - | 861 | - | Number of individuals feeding fledglings. |
| | **how many protect in nest** | - | 381 | - | Number of individuals protecting hatchlings. |
| | **how many protect after nest** | - | 573 | - | Number of individuals protecting fledglings. |
| | **number of caretakers** | - | 1447 | - | Maximal recorded number of caretakers during incubation or nest feeding period. |
| **Life history II** | **duration of incubation** | - | 1429 | - | Variable period of time during which individuals are incubating eggs (time between egg laying and hatching), measured in days. |
| | **time to fledging** | - | 828 | - | Age at which offspring leave the nests (time spent in the nest between hatching and fledging), measured in days. |
| | **time of first flight (TFF)** | - | 1282 | - | Age at which fledglings are first able to fly, measured in days, often coincides with the time of reaching full coat of feathers (Iwaniuk and Nelson 2003, del Hoyo 1992-2011). |
| | **time to adult size** | - | 23 | - | Age at which birds reach their adult size, measured in days. Mostly, adult body mass is reached by the time of first flight (Bennett and Owens 2002). |
| | **days feeding after nest** | - | 402 | - | Period of time after fledging during which fledglings are fed by parents or helpers, measured in days. |
| | **age at first reproduction (AFR)** | - | 816 | - | Age at which birds reproduce for the first time, measured in years. |
| | **longevity** | - | 697 | - | Measure of maximal recorded life span in years. |

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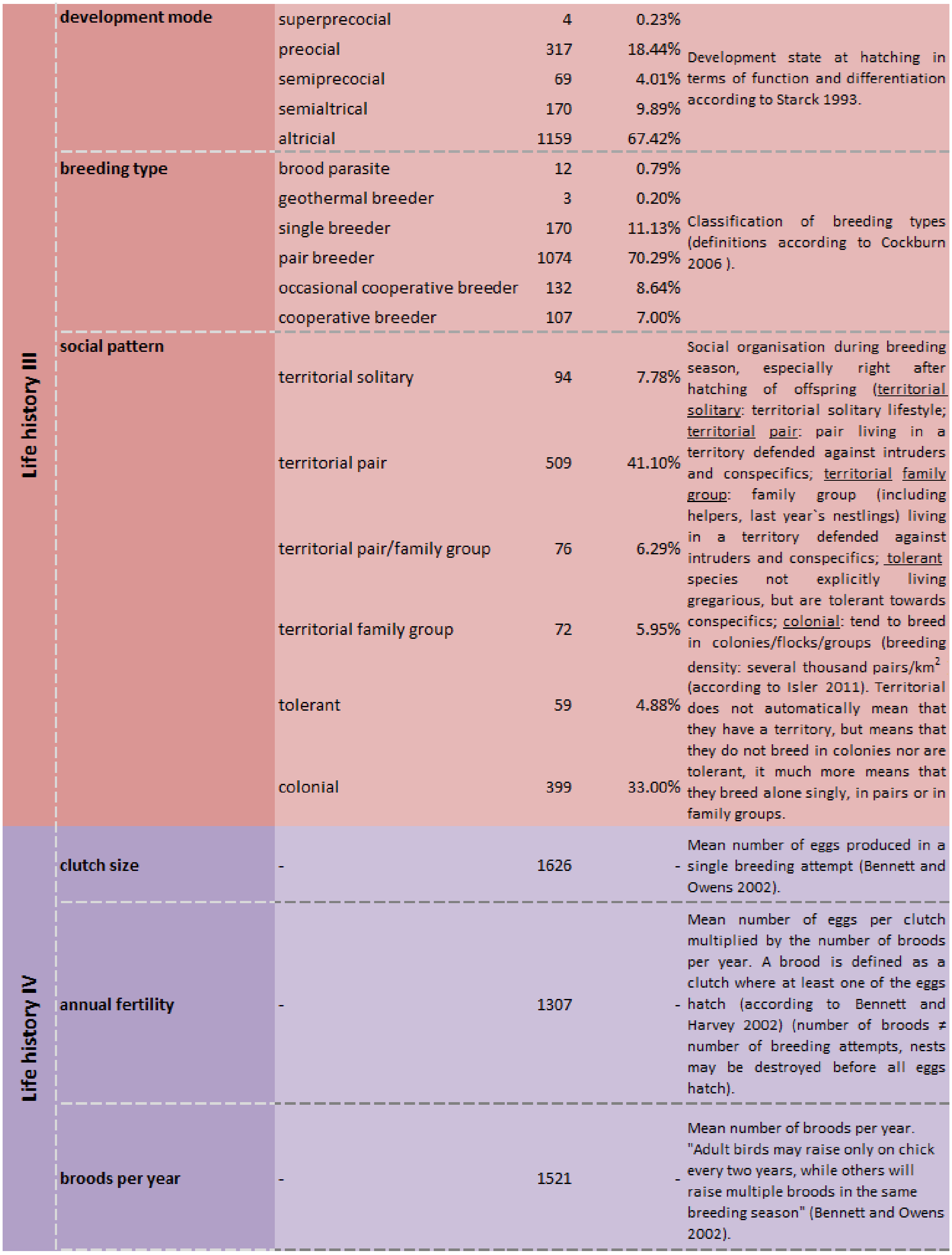


| | | | | | |
|---|---|---|---|---|---|
| **Life history III** | **development mode** | superprecocial | 4 | 0.23% | Development state at hatching in terms of function and differentiation according to Starck 1993. |
| | | preocial | 317 | 18.44% | |
| | | semiprecocial | 69 | 4.01% | |
| | | semialtrical | 170 | 9.89% | |
| | | altricial | 1159 | 67.42% | |
| | **breeding type** | brood parasite | 12 | 0.79% | Classification of breeding types (definitions according to Cockburn 2006 ). |
| | | geothermal breeder | 3 | 0.20% | |
| | | single breeder | 170 | 11.13% | |
| | | pair breeder | 1074 | 70.29% | |
| | | occasional cooperative breeder | 132 | 8.64% | |
| | | cooperative breeder | 107 | 7.00% | |
| | **social pattern** | territorial solitary | 94 | 7.78% | Social organisation during breeding season, especially right after hatching of offspring (territorial solitary: territorial solitary lifestyle; territorial pair: pair living in a territory defended against intruders and conspecifics; territorial family group: family group (including helpers, last year`s nestlings) living in a territory defended against intruders and conspecifics; tolerant species not explicitly living gregarious, but are tolerant towards conspecifics; colonial: tend to breed in colonies/flocks/groups (breeding density: several thousand pairs/$km^2$ (according to Isler 2011). Territorial does not automatically mean that they have a territory, but means that they do not breed in colonies nor are tolerant, it much more means that they breed alone singly, in pairs or in family groups. |
| | | territorial pair | 509 | 41.10% | |
| | | territorial pair/family group | 76 | 6.29% | |
| | | territorial family group | 72 | 5.95% | |
| | | tolerant | 59 | 4.88% | |
| | | colonial | 399 | 33.00% | |
| **Life history IV** | **clutch size** | - | 1626 | - | Mean number of eggs produced in a single breeding attempt (Bennett and Owens 2002). |
| | **annual fertility** | - | 1307 | - | Mean number of eggs per clutch multiplied by the number of broods per year. A brood is defined as a clutch where at least one of the eggs hatch (according to Bennett and Harvey 2002) (number of broods ≠ number of breeding attempts, nests may be destroyed before all eggs hatch). |
| | **broods per year** | - | 1521 | - | Mean number of broods per year. "Adult birds may raise only on chick every two years, while others will raise multiple broods in the same breeding season" (Bennett and Owens 2002). |

(to be continued)

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| **Life history IV** | **Maximum rate of population increase ($r_{max}$)** | - | 471 | - | Intrinsic population growth rate (Cole 1954) under optimum conditions given in year$^{-1}$. Calculated from (maximum lifespan - AFR) and average annual fertility. Cole`s equation (1954): $1=e^{-r} + b(e^{-r\alpha} -e^{-r(\omega+1}$ (b= annual fecundity, α = minimum age at first reproduction (AFR) and ω = maximum age at last reproduction, where ω is used as maximum lifespan and additionally maximum reproductive period (MaxRP) is defined as max. lifespan minus AFR) (after Isler & van Schaik 2009). |
|  | **Annual adult survival (%)** | - | 292 |  | Adult survival rate in percentage. "Annual rate among individuals above the modal at first breeding" (Bennett and Owens 2002). |
| **Others** | **status on worldwide scale** | not globally threatened (ngt) | 1565 | 0.9607 | How threatened a species is for extinction (according to del Hoyo et al. 1992-2011). Not globally threatened; rare: taxa with small world populations that are not at present endangered or vulnerable, but are at risk; vulnerable: taxa believed likely to move into the endangered category in the near future if the causal factors continue operating; endangered: taxa in danger of extinction and whose survival is unlikely if the causal factors continue operating. |
|  |  | rare | 7 | 0.43% |  |
|  |  | vulnerable | 39 | 2.39% |  |
|  |  | endangered | 18 | 1.10% |  |
|  | **flight** | flightless | 38 | 2.21% | Locomotion: either flightless or aerial (Bennett and Owens 2002). |
|  |  | aerial | 1685 | 97.79% |  |

## 2.4 Statistical analyses

### 2.4.1 Data transformation

All morphological, physiological and life history variables (except development mode; breeding type; number of caretakers; status on the worldwide scale) were $\log_e$ transformed before analyses, to generate normal distributions.

### 2.4.2 Phylogenetic analyses

Analyses were conducted using comparative methods, which account for the phylogenetic relationships between the species. Because to a certain extent, all species share common ancestors respectively common evolutionary histories, they cannot be regarded as independent of each other in a cross-species analysis (Harvey and Pagel 1991). More closely related species may show similarities in certain traits due to their

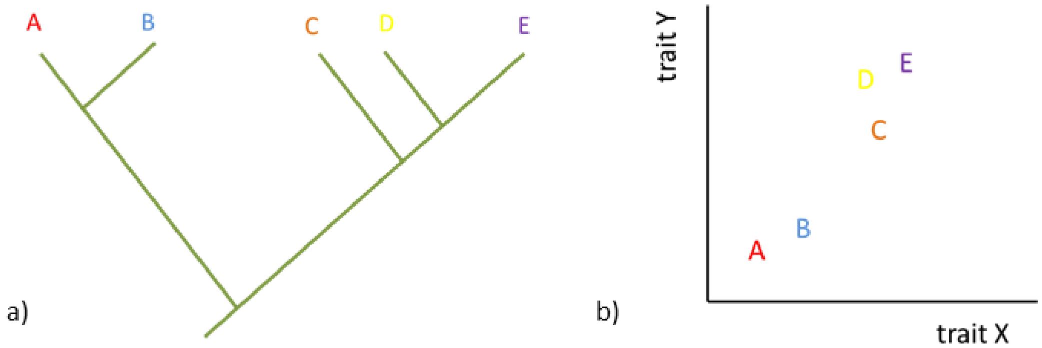
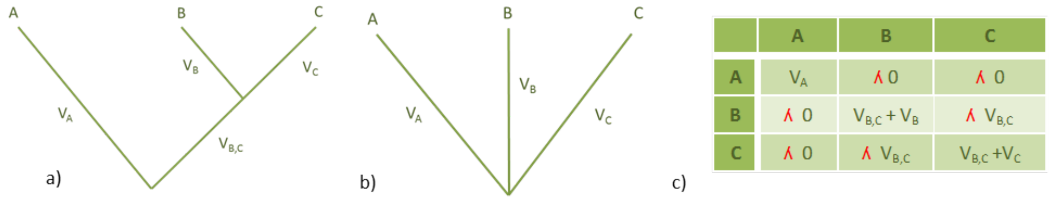


Figure 2.4: **Phylogenetic non-independence.** a) Phylogenetic tree with five terminal taxa groups (A, B, C, D, E). b) Comparison of two traits (X, Y) for each taxa group. More closely related species show similarities in traits due to their common evolutionary history. Phylogenetic comparative methods are needed to correct for their common evolutionary history (figure according to Freeman and Herron, 2007).

common evolutionary history (figure 2.4), and to correct for such phenomena phylogenetic comparative methods are needed. Therefore, the evolutionary relationships among the studied species need to be estimated and a phylogenetic tree with estimated branch lengths is required to properly apply comparative methods. To get phylogenetically independent data I applied phylogenetic generalized least-squares regressions (PGLS) (Grafen 1989). Non-independence of taxa groups is taken into account by expressing the phylogeny in form of a variance-covariance matrix (figure 2.5). This matrix is then used as a complex error term in a regression least-squares model ($Y = X * b + \varepsilon$, Y=dependent variable, X=independent variable (predictor), b=regression coefficient, $\varepsilon$=error term). The off-diagonal values of the variance-covariance matrix stand for the common evolutionary history of two corresonding species (figure 2.5)(Garland and Ives 2000, Rohlf 2001, Nunn 2011). In the PGLS regression models I did not include interaction terms because they never showed significant p-values, probably because interactions do not make sense in an independent contrasts model (Isler, personal communication).

Additionally, for analyses with very large sample sizes the family average of each variable was calculated and non-phylogenetic generalized least-squares (GLS) regressions were applied. This is an alternative method to PGLS regression models, which does not incorporate phylogenetic relationship directly in the analyses but rather corrects for it based on family levels. In fact, main brain size differences evolved very early in the history of birds (Nealen and Ricklefs 2001), thus, brain size variation occurs mainly between families than within families.
Morphological traits such as brain and body mass are known to show high phylogenetic signals (Blomberg et al. 2003; O‘Neill and Dobson 2008; Böhning-Gaese and Oberrath 1999). Therefore, in most analyses it was necessary to account for phylogenetic relationships in order to get proper results. The PGLS function automatically esti-



|  | A | B | C |
|---|---|---|---|
| A | $V_A$ | $\lambda$ 0 | $\lambda$ 0 |
| B | $\lambda$ 0 | $V_{B,C} + V_B$ | $\lambda$ $V_{B,C}$ |
| C | $\lambda$ 0 | $\lambda$ $V_{B,C}$ | $V_{B,C} + V_C$ |

Figure 2.5: **Phylogeny and variance-covariance matrix.** Phylogenetic tree with corresponding variance-covariance matrix. a) Phylogenetic tree with lambda ($\lambda$) = 1. b) Phylogenetic tree with lambda ($\lambda$) = 0 („star phylogeny“)). c) Variance-covariance matrix: The diagonal elements (e.g. $V_A$) represent the variances, whereas the off-diagonal values ($V_{B,C}$) represent the covariances respecitvely the time of shared evolution in the phylogenetic tree. The red symbols represent lambda ($\lambda$) and are direct proportional to times of shared evolution. According to AnthroTree Workshop 2011, Isabella Capellini.

mates lambda and tests for its‘ significance using a likelihood ratio test. Lambda ($\lambda$) estimates how strong two traits correlate because of common evolutionary history ($\lambda$ varies between 0 and 1, if $\lambda$ is significantly different from 0, phylogenetic corrections are needed) (Pagel 1999). Lambda adjusts the off-diagonal values of the variance-covariance matrix which represents the time of shared evolutionary time (figure 2.5) (Nunn 2011). A lambda of 0 means that there is no phylogenetic signal at all, there is no shared evolutionary time between species which ends up in a so called „star phylogeny“ (Nunn 2011, p. 108) (figure 2.5 b). A lambda of 1 means that the evolutionary model complies with a Brownian motion model (figure 2.5 a) (Nunn 2011). If due to small sample sizes lambda estimates were neither significantly different from 0 nor from 1, I ran the analyses both with fixed lambda values of 0 (no covariance between trait and phylogeny) and 1 (covariance between trait and phylogeny following a Brownian motion model).

In all multiple PGLS regressions and multiple GLS regressions of family averages body mass was included as a covariate. Further, in all but a few analyses development mode was added as a covariate.

Phylogenetic comparative methods were run in RStudio (version 0.95.256) (R Development Core Team 2011) using the package caper (Orme 2011). Descriptive statistics were produced using the reporttools (Rufiback 2009) in RStudio and further non-phylogenetic analyses were conducted in RStudio and JMP (version 8.0). Figures were done in RStudio, Microsoft Excel 2010, Microsoft PowerPoint 2010 and Dendroscope (Huson et al. 2007).

### 2.4.3 Phylogeny

Phylogenetic comparative analyses are based on a supertree including 1756 avian species (179 families within 26 orders), where taxonomy followed Sibley and Monroe (1990).

The constructed phylogenetic tree used for the phylogenetic analyses in this study is mainly based on the supertree proposed by Davis (2008) and on the results of a phylogenetic study by Hackett et al. (2008).

The tree of Davis (2008) (total of 5985 species) was built on the strict consensus of 2000 trees run in Paup and information was collected from a total of 748 published phylogenetic trees (Davis 2008). Detailed information can be found on http://linnaeus.zoology.gla.ac.uk/∼ rpage/birdsupertree/, Bird Supertree Project. Hackett et al. (2008) used nuclear DNA sequences from 19 independent loci to construct a new robust avian evolutionary tree and detected a lot of unrecognized interordinal relationships such as the one between passerines and parrots.

Furthermore, the supertree as a combination by Davis (2008) and Hackett et al. (2008) was supplemented in order to reach consensus with the compiled data set. Especially species for which rare but essential data are available (e.g data on BMR or FMR) needed to be additionally included in the given tree. The exact phylogenetic relatedness for these additionally included species were taken from a few other sources, where all the phylogenetic relationships are based on molecular data (table 2.6) (Rutkowski et al. 2007; Schweizer et al. 2009; Kennedy and Page 2002). Species with conflicting taxanomic information are listed in table 2.7.

Because no branch lengths are available for the constructed tree, they were assigned to 1. Thus, the assumed model of evolutionary change is the so called speciational model, which is a special case of the Brownian motion model (Nunn 2011). This assumes that all changes occur at the same level when new species evolve and these changes are independent from any other evolutionary changes within the phylogenetic tree (Nunn 2011). The polytomies were resolved by setting them to 0-length branches. As caper only accepts unrooted trees as input files, an outgroup has been added to phylogenetic group of interest (ingroup contains 1756 avian species). For a simple illustration of the constructed tree see figure 2.6. I used the program Mesquite (version 2.74) for assigning branch lengths, resolving polytomies and including/deleting species from the given tree. For interactive visualization of the bird supertrees I used the programs FigTree (version 1.3.1) and Dendroscope (Huson et al. 2007).

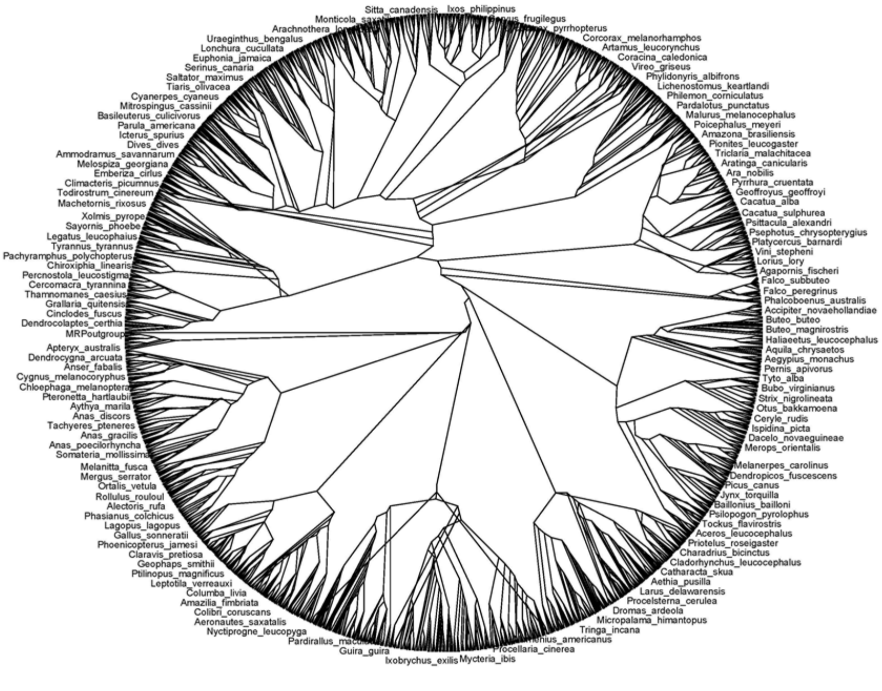


Figure 2.6: **Phylogeny.** A simple illustration of the constructed tree containing 1756 avian species. Only part of all the species names are shown. The tree is unrooted and thus, contains an outgroup (seen on the left hand side). For illustration the program Dendroscope (Huson et al. 2007) was used.

Table 2.6: **Bird species additionally included in phylogenetic tree.** Bird species which were additionally included in the phylogenetic tree. Given are the source of the corresponding phylogenetic trees and on what the phylogenetic relationships are based.

| **Family** | **Genus species** | **Source phylogeny** | **Phylogenetic relationships based on . . .** |
|---|---|---|---|
| *Picidae* | *Dendrocopos minor* | Rutkowski et al. 2007 | . . . hypervariable domain of mitochondrial DNA control region. |
| *Picidae* | *Dendrocopos medius* | Rutkowski et al. 2007 | . . . hypervariable domain of mitochondrial DNA control region. |
| *Psittacidae* | *Loriculus philippensis* | Schweizer et al. 2009 | . . . on 3219 bp of three nuclear genes. |
| *Procellariidae* | *Pterodroma alba* | Kennedy and Page 2002 | . . . a combination of seven seabird phylogenies (based on behavioral, DNA-DNA hybridization, isozyme, life history, morphological, and sequence data) using matrix representation with parsimony. |

Table 2.7: **Conflicting taxonomic information.** Bird species with conflicting taxonomic information.

| Family | Genus species | Note |
|---|---|---|
| *Psittacidae* | *Amazona auropalliata* | According to the original tree based on Davis (2008) and Hackett et al. (2008), A. ochrocephala is considered as three different species: itA. ochrocephala, *A. oratrix* and *A. auropalliata.* However, in del Hoyo (1992 – 2011), *A. ochrocephala* is considered as a single species, therefore data for only this species are available. |
| *Psittacidae* | *Amazona oratrix* | See note of *Amazone auropalliata.* |
| *Anatidae* | *Anas laysanensis* | According to the original tree based on Davis (2008) and Hackett et al. (2008), *Anas platyrhynchos* is considered as three different species: *Anas laysanensis*, *Anas wyvilliana* and *Anas platyrhynchos.* However, in del Hoyo (1992-2011) *Anas platyrhynchos* is considered as a single species, therefore therefore data for only this species are available . |
| *Anatidae* | *Anas wyvilliana* | See note of *Anas laysanensis.* |
| *Burhinidae* | *Esacus neglectus* | According to del Hoyo (1992-2011) considered as *Esacus magnirostris* (considered as the correct name). In the original tree based on Davis (2008) and Hackett et al. (2008), *Esacus neglectus* as well as *Esacus magnirostris* are included, but complete data is only available for *Esacus magnirostris.* |
| *Pycnonotidae* | *Pycnonotus tricolor* | According to del Hoyo (1992-2011) considered as *Pycnonotus barbatus.* In the original tree based on Davis (2008) and Hackett et al. (2008) both species names occur. |
| *Accipitridae* | *Accipiter griseogularis* | According to del Hoyo (1992-2011) considered as *Accipiter novaehollandiae.* In the original tree based on Davis (2008) and Hackett et al. (2008) both species names occur. |

# 3 Results

## 3.1 Descriptive statistics

Descriptive statistics on all nominal and continuous variables are given in table 3.1 and 3.2.

Table 3.1: **Nominal variables.** Given are levels, sample size, corresponding % and cumulative % ($\sum$%).

| **Variable** | **Levels** | **n** | % | $\sum$% |
|---|---|---|---|---|
| Flight | flightless | 38 | 2.2 | 2.2 |
| | aerial | 1685 | 97.8 | 100.0 |
| | all | 1723 | 100.0 | |
| Status | not globally threatened | 1565 | 96.1 | 96.1 |
| | rare | 7 | 0.4 | 96.5 |
| | vulnerable | 39 | 2.4 | 98.9 |
| | endangered | 18 | 1.1 | 100.0 |
| | all | 1629 | 100.0 | |
| Mate feeding | No | 43 | 12.7 | 12.7 |
| | Yes | 296 | 87.3 | 100.0 |
| | all | 339 | 100.0 | |
| Breeding Type | geothermal breeders | 3 | 0.2 | 0.2 |
| | brood parasites | 12 | 0.8 | 1.0 |
| | single breeders | 170 | 11.1 | 12.1 |
| | pair breeders | 1080 | 70.8 | 82.9 |
| | occasional cooperative breeders | 152 | 10.0 | 92.9 |
| | cooperative breeders | 109 | 7.1 | 100.0 |
| | all | 1526 | 100.0 | |
| Social pattern | territorial solitary | 94 | 15.0 | 15.0 |
| | territorial pair/family group | 76 | 12.1 | 27.1 |
| | tolerant | 59 | 9.4 | 36.5 |
| | colonial | 399 | 63.5 | 100.0 |
| | all | 628 | 100.0 | |
| Development mode | Superprecocial | 4 | 0.2 | 0.2 |
| | Precocial | 317 | 18.4 | 18.7 |
| | Semiprecocial | 69 | 4.0 | 22.7 |
| | Semialtricial | 170 | 9.9 | 32.6 |
| | Altricial | 1159 | 67.4 | 100.0 |
| | all | 1719 | 100.0 | |

Table 3.2: **Continuous variables.** Given are sample size, number of missing values (**#NA**), minimum, maximum, median ($\widetilde{\mathbf{x}}$), mean ($\bar{x}$), standard deviation (**s**), 25% quantile (q1), 75% quantile (q3) and interquartile range (IQR).

| **Variable** | **n** | **#NA** | **Min** | **Max** | $\widetilde{\mathbf{x}}$ | $\bar{\mathbf{x}}$ | **s** | $\mathbf{q_1}$ | $\mathbf{q_3}$ | **IQR** |
|---|---|---|---|---|---|---|---|---|---|---|
| Brain mass [g] | 1743 | 13 | 0.1 | 47.9 | 1.8 | 3.8 | 5.0 | 0.9 | 4.8 | 3.9 |
| Body mass [g] | 1743 | 13 | 2.7 | 80000.0 | 92.0 | 674.3 | 2841.3 | 25.8 | 450.2 | 424.5 |
| Body mass (male) [g] | 1556 | 200 | 2.5 | 116671.2 | 100.1 | 708.6 | 3598.9 | 27.2 | 452.3 | 425.1 |
| Body mass (female) [g] | 1553 | 203 | 2.5 | 92715.0 | 100.0 | 689.7 | 3336.1 | 26.4 | 465.3 | 439.0 |
| Egg mass [g] | 1538 | 218 | 0.3 | 1692.3 | 8.5 | 31.9 | 71.8 | 2.9 | 35.7 | 32.7 |
| BMR [W] | 255 | 1501 | 0.0 | 63.1 | 0.8 | 3.0 | 6.7 | 0.3 | 2.6 | 2.3 |
| $\text{FMR}_{non-breeding}$ [kJ/day] | 154 | 1602 | 30.0 | 18000.0 | 202.5 | 837.3 | 1896.6 | 77.8 | 679.1 | 601.3 |
| Raw $\text{FMR}_{incubation}$ [kJ/day] | 47 | 1709 | 31.0 | 6377.2 | 204.5 | 771.9 | 1368.0 | 92.5 | 491.0 | 398.5 |
| Estimated $\text{FMR}_{incubation}$ [kJ/day] | 239 | 1517 | 2.5 | 6377.2 | 232.3 | 506.5 | 749.0 | 108.1 | 581.4 | 473.2 |
| Total $\text{FMR}_{incubation}$ per caretaker [kJ] | 215 | 1541 | 25.4 | 171080.0 | 3763.5 | 8318.9 | 16916.3 | 974.6 | 8513.9 | 7539.3 |
| Total $\text{FMR}_{incubation}$ for all caretakers [kJ] | 203 | 1553 | 0.0 | 342160.1 | 6452.0 | 17192.8 | 37175.6 | 1917.7 | 15589.6 | 13671.9 |
| Total energetic input per offspring (incubation) [kJ] | 202 | 1554 | 0.0 | 342160.1 | 1494.6 | 9503.2 | 31133.9 | 454.1 | 5556.6 | 5102.4 |
| Raw $\text{FMR}_{chickrearing}$ [kJ/day] | 32 | 1724 | 52.9 | 3645.8 | 156.6 | 514.8 | 759.3 | 92.9 | 699.0 | 606.1 |
| Estimated $\text{FMR}_{chickrearing}$ [kJ/day] | 69 | 1687 | 17.4 | 10010.4 | 211.0 | 740.4 | 1474.6 | 95.3 | 696.0 | 600.6 |
| Total $\text{FMR}_{chickrearing}$ per caretaker [kJ] | 61 | 1695 | 314.3 | 585308.2 | 2727.8 | 36091.0 | 105606.4 | 778.6 | 10062.7 | 9284.2 |
| Total $\text{FMR}_{chickrearing}$ for all caretakers [kJ] | 59 | 1697 | 628.6 | 1170616.5 | 8848.0 | 72689.4 | 211699.5 | 1963.7 | 31412.2 | 29448.5 |
| Total energetic input per offspring (chick rearing) [kJ] | 59 | 1697 | 140.8 | 1170616.5 | 1947.5 | 61717.4 | 212220.8 | 416.6 | 14250.8 | 13834.2 |
| Number of caretakers | 1447 | 309 | 0.0 | 12.5 | 2.0 | 2.0 | 0.8 | 2.0 | 2.0 | 0.0 |
| Incubation duration [d] | 1429 | 327 | 10.0 | 79.5 | 20.5 | 22.5 | 10.0 | 14.5 | 27.0 | 12.5 |
| Time of fledging [d] | 836 | 920 | 0.0 | 345.0 | 14.0 | 18.5 | 23.8 | 1.0 | 23.0 | 22.0 |
| Time of first flight [d] | 1282 | 474 | 2.5 | 350.8 | 28.0 | 36.4 | 29.4 | 16.1 | 49.0 | 32.9 |
| Time to adult size [d] | 23 | 1733 | 16.0 | 579.0 | 49.0 | 120.0 | 155.5 | 29.0 | 110.0 | 81.0 |
| Days feeding after nest [d] | 415 | 1341 | 0.0 | 366.0 | 24.5 | 38.3 | 47.0 | 14.0 | 41.2 | 27.2 |
| Duration of total parental care [d] | 262 | 1494 | 0.1 | 292.8 | 39.0 | 54.4 | 47.3 | 30.0 | 60.9 | 30.9 |
| Age at first reproduction [y] | 816 | 940 | 0.2 | 10.0 | 1.0 | 1.9 | 1.5 | 1.0 | 2.1 | 1.1 |
| Longevity [y] | 697 | 1059 | 3.1 | 120.0 | 13.0 | 16.5 | 12.6 | 8.7 | 20.8 | 12.2 |
| Clutch size | 1626 | 130 | 1.0 | 21.0 | 3.3 | 3.7 | 2.4 | 2.0 | 4.5 | 2.5 |
| Broods per year | 1329 | 427 | 0.5 | 10.0 | 1.0 | 1.3 | 0.6 | 1.0 | 1.0 | 0.0 |
| Annual fertility | 1307 | 449 | 0.5 | 48.0 | 4.0 | 5.0 | 3.8 | 2.5 | 6.5 | 4.0 |
| Annual adult survival [%] | 292 | 1464 | 0.1 | 1.0 | 0.7 | 0.7 | 0.2 | 0.5 | 0.8 | 0.3 |
| $\text{R}_{max}$ | 471 | 1285 | 0.0 | 4.4 | 0.9 | 1.0 | 0.6 | 0.5 | 1.4 | 0.9 |

## 3.2 Metabolic constraint hypothesis

**Prediction Hypothesis 1a**: Assuming that the total energy turnover constrains brain size, basal metabolic rate is predicted to correlate positively with relative brain size.

**Results Hypothesis 1 a**: To investigate whether the total energy turnover constrains brain size I looked at the correlation between basal metabolic rate (BMR) and brain size using multiple phylogenetic generalized least square (PGLS) regression models. After controlling for the effect of body size, BMR and brain size do not show a positive correlation as would be expected from the metabolic constraint hypothesis (model A; table 3.3) (figure 3.1 a). Additionally controlling for the effects of development mode and the factor if a species is flightless or aerial (dummy variable: 0=flightless; 1=aerial) does also not affect the relationship between BMR and relative brain size(model B, C and D; table 3.3).

**Prediction Hypothesis 1 b**: Relative brain size is predicted to correlate positively with BMR if $r_{max}$ values are held constant (analogous for the correlation between $r_{max}$ and BMR if relative brain size values are held constant).

**Results Hypothesis 1 b**: Due to a study in marsupials (Isler 2011), it is now evident that a direct metabolic constraint can be obscured by a strong trade-off between relative brain size and offspring production. In birds, I also found a trade-off between brain size and reproduction ($r_{max}$ or fertility) or at least a trend (PGLS regression ($r_{max}$): n=447; multiple $r^2$=0.20, brain mass: slope=-0.15, p=0.13, corrected for body size and development mode); (PGLS regression (fertility): n=1263; multiple $r^2$=0.05, brain mass: slope=-0.26, p=0.0002, corrected for body size and development mode) and thus, it can be assumed that the same phenomenon exists across avian species. I constructed a model which contains BMR as the dependent variable and body size, brain size and fertility or $r_{max}$ (as a measurement of reproduction) as independent variables. However, even if fertility or $r_{max}$ values are held constant, there is no positive link between basal metabolism and relative brain size (whereas negative correlations are observed between BMR and fertility/$r_{max}$ if relative brain size values are held constant) (model E and G; table 3.3; figure 3.2 a,b). Furthermore, additionally controlling for flight does not affect the relationship between BMR and relative brain size (model F and model H; table 3.3).
Moreover, I also looked at the correlation between field metabolic rates ($FMR_{non-breeding}$: daily energy expenditure based on the active state of an individual during the non-breeding period) and relative brain size instead BMR and relative brain size. One might assume that higher energy expenditure in the active state (including the energy spent for the brain growth and maintenance) is coupled with larger relative brain sizes. After controlling for the effects of body size, development mode and flight, I found no relationship between $FMR_{non-breeding}$ and relative brain size (model I, J, K and L; table 3.3; figure 3.1 b). Further, as $FMR_{non-breeding}$ shows a strong trend

towards a trade-off with $r_{max}$, but not with fertility (PGLS regression ($r_{max}$): n=68; multiple $r^2$=0.61, $r_{max}$: slope=-0.30, p=0.06, corrected for body size and development mode) ; (PGLS regression (fertility): n=125; multiple $r^2$=0.37, fertility: slope=0.16, p=0.23, corrected for body size and development mode), the relationship between $\mathrm{FMR}_{non-breeding}$ and relative brain size might be alleviated by the relationship between $\mathrm{FMR}_{non-breeding}$ and $r_{max}$. Additionally correcting for $r_{max}$ leads to a strong negative relationship between $\mathrm{FMR}_{non-breeding}$ and relative brain size (model M and N; table 3.3). Surprisingly, correcting for fertility, which did not show trade-off with $\mathrm{FMR}_{non-breeding}$, has as well an effect. $\mathrm{FMR}_{non-breeding}$ and relative brain size show a negative correlation (model O and P; table 3.3).

To sum up, no positive relationship between the total energy turnover (BMR) and relative brain size was found. Even after correcting for the effect of reproduction ($r_{max}$ or fertility), no correlation is observed. Interestingly, I found a negative relationship between $\mathrm{FMR}_{non-breeding}$ and relative brain size after correcting for the effect of reproduction, which postulates that large-brained species have rather low daily energy expenditures.

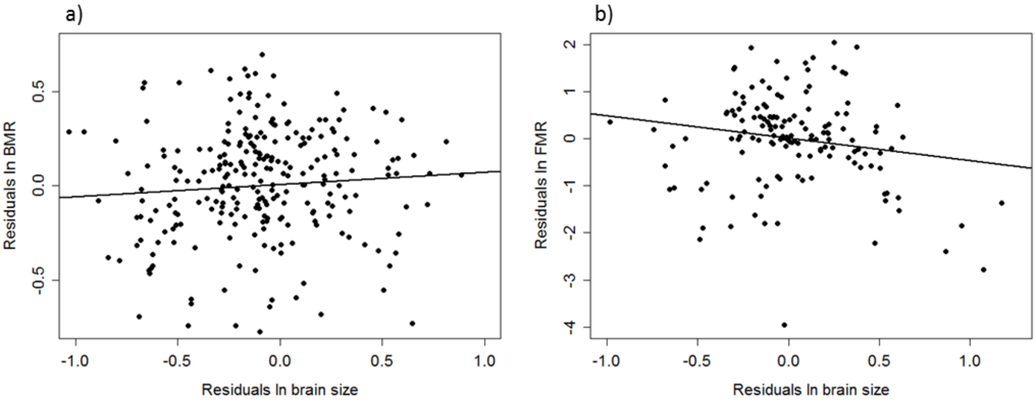


Figure 3.1: **BMR and FMR vs. brain size.** a) Least-square regression of the residuals of ln BMR on the residuals of ln brain mass (PGLS: n=245, p=0.35(-)). b) Least-square regression of the residuals of ln FMR on the residuals of ln brain mass (PGLS: n=144, p=0.69(+)). All residuals indicate correction for body size.

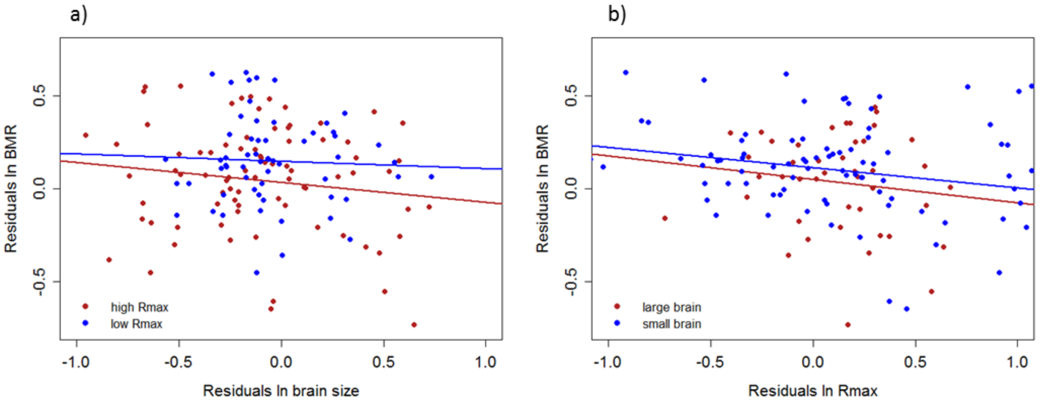


Figure 3.2: **BMR vs. brain size and $r_{max}$.** a) Least-square regressions of the residuals of ln BMR on the residuals of ln brain mass, shown separately for species with high (residuals >0) (n = 81) and low (residuals < 0) $r_{max}$ values (n=60). b) Least-square regressions of the residuals of ln BMR on the residuals of ln $r_{max}$ shown separately for large-brained (residuals > 0) (n = 47) and small-brained species (residuals < 0) (n = 94). Corresponds to model E in table 3.1. All residuals indicate correction for body size.

Table 3.3: Multiple PGLS regressions for ln BMR, ln FMR and ln brain mass, body mass, development mode, ln $r_{max}$, ln fertility, flight (ln BMR and ln FMR as dependent variables and ln brain mass, ln body mass, ln $r_{max}$, ln fertility and flight as independent varibales). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$). In the different models different covariates are included (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | **brain mass** | | **body mass** | | **development** | | **$r_{max}$** | | **fertility** | | **flight** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **BMR** | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| model A | 245 | 0.91 | 0.93 | 0.810, 0.990 | 0.35 | -0.07 | *<0.0001* | 0.76 | - | - | - | - | - | - | - | - |
| model B | 245 | 0.92 | 0.92 | 0.782, 0.984 | 0.25 | -0.08 | *<0.0001* | 0.77 | - | - | - | - | - | - | 0.06 | 0.21 |
| model C | 236 | 0.92 | 0.93 | 0.828, 0.992 | 0.46 | -0.05 | *<0.0001* | 0.74 | 0.48 | 0.02 | - | - | - | - | - | - |
| model D | 236 | 0.92 | 0.93 | 0.807, 0.988 | 0.38 | -0.07 | *<0.0001* | 0.76 | 0.52 | 0.02 | - | - | - | - | 0.15 | 0.17 |
| model E | 130 | 0.94 | 0.88 | 0.695, 0.974 | 0.84 | 0.02 | *<0.0001* | 0.66 | 0.13 | -0.06 | *<0.0001* | -0.18 | - | - | - | - |
| model F | 130 | 0.95 | 0.85 | 0.615, 0.961 | 0.95 | -0.005 | *<0.0001* | 0.67 | 0.15 | -0.05 | *<0.0001* | -0.18 | - | - | 0.06 | 0.25 |
| model G | 201 | 0.93 | 0.87 | 0.707, 0.960 | 0.2 | -0.1 | *<0.0001* | 0.76 | 0.93 | -0.003 | - | - | *0.04* | -0.07 | - | - |
| model H | 201 | 0.93 | 0.85 | 0.669, 0.952 | 0.15 | -0.11 | *<0.0001* | 0.78 | 0.87 | -0.005 | - | - | *0.05* | -0.06 | 0.1 | 0.17 |
| **FMR** | | | | | | | | | | | | | | | | |
| model I | 144 | 0.92 | 0.59 | 0.280, 0.832 | 0.69 | 0.02 | *<0.0001* | 0.63 | - | - | - | - | - | - | - | - |
| model J | 144 | 0.92 | 0.6 | 0.288, 0.836 | 0.76 | 0.01 | *<0.0001* | 0.63 | - | - | - | - | - | - | 0.5 | -0.11 |
| model K | 141 | 0.92 | 0.49 | 0.184, 0.766 | 0.98 | -0.001 | *<0.0001* | 0.64 | 0.83 | -0.008 | - | - | - | - | - | - |
| model L | 141 | 0.92 | 0.5 | 0.191, 0.772 | 0.9 | -0.006 | *<0.0001* | 0.63 | 0.85 | -0.007 | - | - | - | - | 0.53 | -0.1 |
| model M | 68 | 0.98 | 0 | NA, 0.239 | *0.005* | -0.15 | *<0.0001* | 0.68 | 0.7 | -0.01 | *<0.0001* | -0.2 | - | - | - | - |
| model N | 68 | 0.98 | 0 | NA, 0.185 | *0.003* | -0.16 | *<0.0001* | 0.67 | 0.73 | -0.01 | *<0.0001* | -0.21 | - | - | 0.12 | -0.24 |
| model O | 125 | 0.96 | 0 | NA, 0.647 | *0.04* | -0.08 | *<0.0001* | 0.67 | 0.87 | -0.004 | - | - | *<0.0001* | -0.15 | - | - |
| model P | 125 | 0.96 | 0 | NA, 0.583 | *0.02* | -0.09 | *<0.0001* | 0.66 | 0.79 | -0.007 | - | - | *<0.0001* | -0.16 | 0.21 | -0.16 |

## 3.3 Production trade-off hypothesis

**Prediction Hypothesis 2a**: Correcting for the amount of allomaternal care (measured by energetic expenditure during chick rearing period, number of caretakers or breeding type), a negative correlation between relative brain size and reproduction (fertility or r$_{max}$) is predicted. From another perspective, non-cooperatively breeding species (brood parasites, geothermal and single breeders) are expected to show a negative correlation between reproductive rate (r$_{max}$) and brain size, whereas species with allomaternal care (pair or cooperative breeders) are expected to show no relationship between r$_{max}$ or fertility and brain size.

**Results Hypothesis 2 a**: Over all, fertility correlates negatively with relative brain size, whereas r$_{max}$ showed no correlation. Additionally controlling for the amount of allomaternal care, using either total energetic input per breeding season, total number of caretakers or breeding type, had no effect on the relationship between reproduction (fertility or r$_{max}$) and relative brain size (table 3.4).
However, when looking at the reproduction trade-off separately for brood parasites, geothermal/single breeders and pair/cooperative breeders, I found a negative correlation between r$_{max}$ and brain size for species with no allomaternal care (brood parasites, geothermal and singly breeding species) (table 3.5, figure 3.3 a). Pair and cooperative breeders show no relationship at all between the reproductive rate (r$_{max}$) and brain size (table 3.5). The same pattern is observed if using fertility (number of eggs per year = clutch size * number of breeding season per year) instead of r$_{max}$ as a measurement of reproduction: brood parasites, geothermal and single breeders show a strong negative correlation between fertility and brain size (table 3.5, figure 3.3 b), whereas pair and cooperative breeders show a alleviated relationship between brain size and fertility (table 3.5) and if looking at cooperatively breeding species separately, this trade-off even completely disappears (table 3.5). To sum up, non-cooperative breeders show a production trade-off, whereas species with allomaternal care almost fully elude this trade-off.

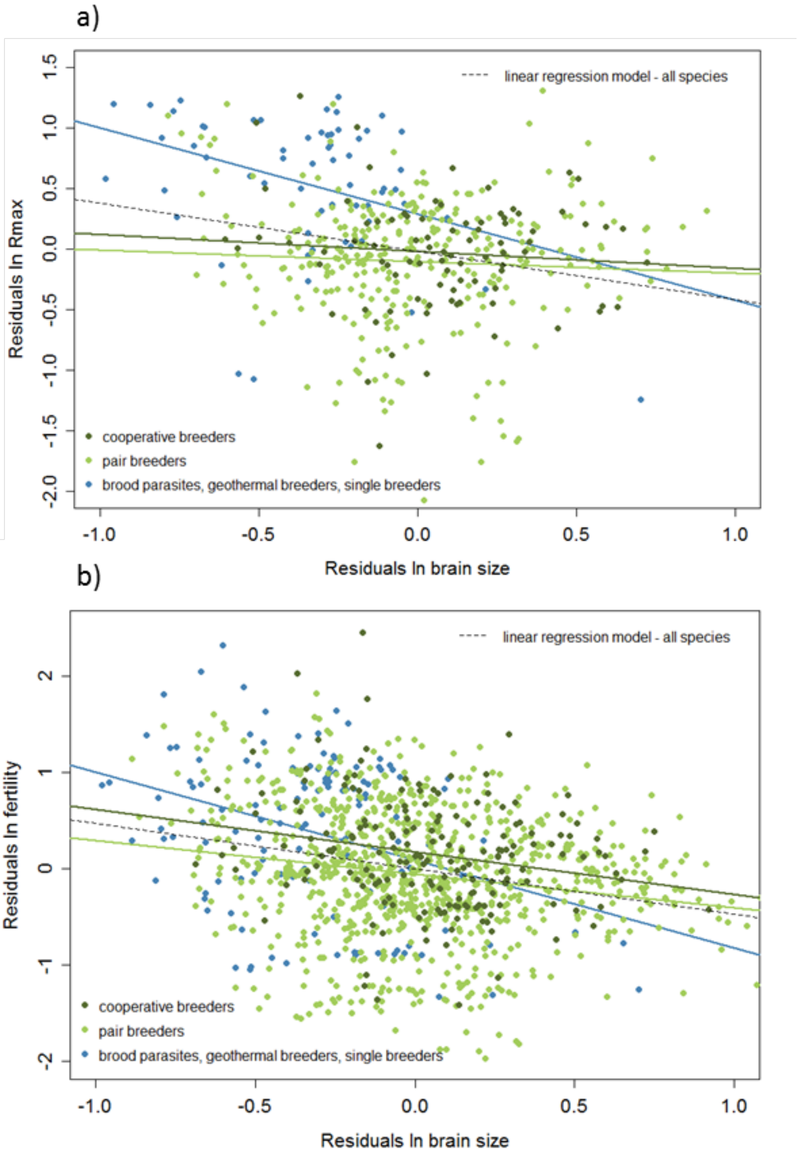


Figure 3.3: **$\mathbf{r}_{max}$ and annual fertility vs. brain size.** a) Least square-regression of the residuals of ln $r_{max}$ on the residuals of ln brain mass shown for brood parasites/geothermal breeders/single breeders, pair and cooperatie breeders separately (PGLS: brood parasites,geothermal/single breeders: n=58, p=0.07(-); pair breeders: n=295, p=0.48(-); cooperative breeders: n=86, p=0.73(-)). b) Least-square regression of the residuals of ln fertility on the residuals of ln brain mass, shown for brood parasites/geothermal breeders/single breeders, pair and cooperative breeders seperately (PGLS: brood parasites, geothermal/single breeders: n=123, p=0.001(-); pair breeders: n=844, p=0.003(-); cooperative breeders: n=176, p=0.41(+)). The dashed lines indicate the least-square regressions of all species. All residuals indicate correction for body size.

Table 3.4: Multiple PGLS regressions of ln fertility and ln r$_{max}$ (ln $r_{max}$ and ln fertility as dependent variables, ln brain mass, ln body mass and development mode, total energetic input per breeding season, number of caretakers and breeding type as independent variables). Correcting the analyses either for total energetic input number of caretakers or for breeding type. Given are the sample size (n), multiple r$^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | **brain mass** | | **body mass** | | **development** | | **total energetic input** | | **number of caretakers** | | **breeding type** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | r$^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **fertility** | 56 | 0.11 | 0.98 | 0.849, NA | 0.25 | -0.46 | 0.55 | 0.15 | 0.35 | 0.13 | - | - | - | - | - | - |
| | 56 | 0.28 | 0.96 | 0.791, NA | 0.8 | 0.1 | 0.86 | 0.04 | 0.89 | 0.02 | 0.001 | -0.28 | - | - | - | - |
| | 1056 | 0.06 | 0.97 | 0.941, 0.982 | *0.003* | -0.22 | 0.81 | 0.1 | *0.03* | -0.1 | - | - | - | - | - | - |
| | 1056 | 0.06 | 0.97 | 0.943, 0.983 | *0.003* | -0.22 | 0.83 | 0.01 | *0.04* | -0.1 | - | - | 0.09 | 0.03 | - | - |
| | 1056 | 0.06 | 0.97 | 0.941, 0.982 | *0.003* | -0.22 | 0.81 | 0.01 | *0.03* | -0.1 | - | - | - | - | 0.97 | 0.001 |
| **r$_{max}$** | 42 | 0.06 | 1 | 0.843, NA | 0.77 | -0.17 | 0.97 | -0.01 | *0.78* | 0.05 | - | - | - | - | - | - |
| | 42 | 0.18 | 0.99 | 0.752, NA | 0.42 | 0.51 | 0.64 | -0.16 | *0.89* | -0.02 | 0.03 | -0.32 | - | - | - | - |
| | 416 | 0.2 | 0.99 | 0.960, NA | 0.32 | -0.1 | *0.01* | -0.16 | 0.34 | -0.05 | - | - | - | - | - | - |
| | 416 | 0.2 | 0.99 | 0.960, NA | 0.32 | -0.1 | *0.01* | -0.16 | 0.34 | -0.05 | - | - | 0.87 | 0.006 | - | - |
| | 416 | 0.2 | 0.99 | 0.960, NA | 0.32 | -0.1 | *0.01* | -0.16 | 0.34 | -0.05 | | | - | - | 0.99 | 0.0009 |

Table 3.5: Multiple PGLS regressions ln $r_{max}$ and ln fertility for all species, brood parasites, geothermal and single breeding species, pair breeding species, cooperatively breeding species and pair and cooperativley breeding species (ln $r_{max}$ and ln fertility as dependent variables, ln brain mass, ln body mass and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | **brain mass** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **all species** | $r_{max}$ | 447 | 0.2 | 0.98 | 0.948, 1.00 | 0.12 | -0.15 | *0.03* | -0.13 | 0.37 | -0.05 |
| | fertility | 1054 | 0.06 | 0.97 | 0.942, 0.982 | *0.007* | -0.2 | 0.99 | -0.0001 | *0.02* | -0.12 |
| **brood parasites, geothermal/single breeders** | $r_{max}$ | 58 | 0.4 | 1 | 0.950, NA | 0.07 | -0.33 | 0.99 | 0.002 | *0.0009* | -0.38 |
| | fertility | 123 | 0.18 | 1 | 0.969, NA | *0.001* | -0.69 | *0.005* | 0.43 | *0.008* | -0.4 |
| **pair breeders** | $r_{max}$ | 295 | 0.14 | 0.98 | 0.936, NA | 0.48 | -0.09 | 0.1 | -0.13 | 0.91 | -0.007 |
| | fertility | 844 | 0.05 | 0.94 | 0.904, 0.966 | *0.003* | -0.23 | 0.43 | 0.04 | 0.18 | -0.07 |
| **cooperative breeders** | $r_{max}$ | 86 | 0.38 | 0.89 | 0.725, 0.982 | 0.73 | -0.07 | 0.12 | -0.21 | 0.6 | 0.05 |
| | fertility | 176 | 0.12 | 0.87 | 0.685, 0.966 | 0.41 | 0.18 | *0.04* | -0.28 | 0.44 | 0.08 |
| **pair/cooperative breeders** | $r_{max}$ | 381 | 0.16 | 0.98 | 0.943, NA | 0.49 | -0.08 | *0.02* | -0.16 | 0.88 | -0.009 |
| | fertility | 1020 | 0.05 | 0.95 | 0.917, 0.970 | *0.04* | -0.16 | 0.54 | -0.03 | 0.33 | -0.05 |

To find out what factors drive the negative correlation between $r_{max}$ and relative brain size in geothermal and singly breeding species, I run PGLS models using either brain size or $r_{max}$ as dependent variables and fertility and maximum reproductive lifespan (components of $r_{max}$) as independent variables (correcting for body size and development mode) (see table 3.6). Fertility more often shows significant correlations with either brain size or $r_{max}$ than maximum reproductive lifespan. This suggests that the reproduction trade-off is rather driven by fertility than maximum reproductive lifespan.

Table 3.6: Multiple PGLS regressions of ln $r_{max}$ and ln brain mass for brood parasites, geothermal/singly breeding species and pair/cooperatively breeding species (ln $r_{max}$ and ln brain mass as dependent variables and ln maximum reproductive lifespan, ln ferility, ln body mass and development mode as indpendent variables). The p-values and slopes are only given for ln maximum reproductive lifespan and ln fertility (significant effects are shown in italics).

| | | **brood parasites/ geothermal/single breeders** | | **pair/cooperative breeders** | |
|---|---|---|---|---|---|
| | | p-value | slope | p-value | slope |
| $r_{max}$ | max RP | *0.005* | 0.14 | 0.26 | 0.03 |
| | fertility | *<0.0001* | 0.73 | *<0.0001* | 0.74 |
| brain mass | max RP | 0.39 | 0.05 | 0.27 | 0.02 |
| | fertility | 0.08 | -0.15 | 0.15 | -0.03 |

**Prediction Hypothesis 2b**: Correcting for the amount of allomaternal care, relatively large-brained species of taxa groups having clutch sizes larger than two are predicted to exhibit reduced clutch sizes, except groups with smaller clutch sizes of only one or two eggs are expected to reduce birth rates, and slower development (e.g. delayed fledging or time of first flight). From the other perspective, relatively large-brained geothermal and singly breeding species having clutch sizes larger than 2 are expected to exhibit reduced clutch sizes. Large-brained geothermal and single breeders with smaller clutch sizes of only one or two eggs per clutch are expected to reduce birth rates, and slower development (e.g. delayed fledging or reduced growth rates).

**Results Hypothesis 2 b**: In order to correct for the life history pace, all the analyses were corrected for longevity. Taxa groups with clutch sizes larger than two, show mostly strong negative correlations of clutch size with relative brain size, with or without correcting for the amount of allomaternal care (number of caretakers or breeding type). In the samples where corrected for the amount of allomaternal care in form of energetic measurements, no such negative correlation is observed (table 3.7). Furthermore, for taxa groups with clutch sizes larger than two, the TFF positively correlates with relative brain size or shows at least a trend, whereas time of fledging is not correlated with relative brain size (no difference if including number of caretakers or breeding type as covariates). For the sample where total energy is included as a covariate, the positive correlation and trend with time of first flight and fledging disappear after controlling for total energy input per breeding season.
Between species having clutch sizes smaller or equal to two, clutch size is not correlated to relative brain size anymore, as expected. Moreover, in the big samples (correcting for number of caretakers and breeding type), I found broods per year as a measurement for birth rate to show negative trends with relative brain size (table 3.7), meaning that large brained species tend to reduce the number of broods per year. In taxa groups which reduce cluch size with increasing brain size, these negative trends completely disappear. Contrarily to my initial prediction, I did not find a positive correlation between TFF or fledging and relative brain size (table 3.7). Only in the sample in which I did not correct for total energy, a positive trend between TFF and relative brain size was observed, but there the sample size might be too small to give reliable results (n=10). In sum, this means that in taxa groups with clutch size smaller or equal to two, large-brained species do not reduce clutch size but reduce annual birth rates.
Over all, additionally correcting for the amount of allomaternal care seems not to make a difference concerning the relationships between clutch size, broods per year or time of development and relative brain size. Except if correcting for the effects of total energy per breeding season, the positive relationships between development duration and relative brain size in species with clutch sizes larger than two disappears.

Table 3.7: Multiple PGLS regressions for ln clutch size, ln broods per year, ln TFF, ln fledging and ln brain mass for species with clutch size larger than two and species with clutch sizes smaller or equal to two (ln clutch size, ln broods per year, ln TFF and ln fledging as dependent variables; ln brain mass, ln body mass, ln longevity development mode as well as total energetic input per breeding season, number of caretakers or breeding type as independent variables). The PGLS regressions are corrected for the amount of allomaternal care using either total energetic investment during whole chick rearing period, number of caretakers or breeding type. Given are the sample size (n), multiple $r^2$, Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | **brain mass** | | **body mass** | | **longevity** | | **development** | | **total energy** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **clutch size** | clutch > 2 | 43 | 0.05 | 0.88 | 0.398, NA | 0.25 | 0.33 | 0.37 | -0.17 | - | - | 0.41 | -0.09 | - | - |
| | | 43 | 0.21 | 0.92 | 0.532, NA | 0.62 | 0.13 | 0.12 | -0.29 | - | - | 0.72 | -0.04 | *0.01* | 0.24 |
| | clutch <= 2 | 16 | 0.1 | 0.24 | NA, NA | 0.34 | -0.45 | 0.37 | 0.26 | - | - | 0.47 | 0.08 | - | - |
| | | 16 | 0.58 | 0 | NA, 0.587 | 0.14 | 0.77 | 0.29 | -0.29 | - | - | 0.47 | -0.06 | *0.005* | -0.25 |
| **broods per year** | clutch > 2 | 41 | 0.35 | 0 | NA, 0.821 | 0.06 | -0.62 | 0.16 | 0.31 | - | - | 0.02 | 0.21 | - | - |
| | | 41 | 0.58 | 0 | NA, 0.686 | 0.19 | -0.36 | 0.006 | 0.53 | - | - | 0.03 | 0.17 | *<0.0001* | -0.45 |
| | clutch <= 2 | 15 | 0.66 | 1 | 0.294, NA | 0.25 | -0.39 | 0.73 | 0.07 | - | - | 0.13 | 0.19 | - | - |
| | | 15 | 0.74 | 1 | 0.207, NA | 0.96 | 0.02 | 0.6 | -0.11 | - | - | 0.2 | 0.15 | 0.09 | -0.09 |
| **TFF** | clutch > 2 | 37 | 0.31 | 1 | 0.740, NA | *0.06* | 0.48 | 0.17 | -0.22 | 0.23 | 0.13 | 0.37 | -0.08 | - | - |
| | | 37 | 0.43 | 1 | 0.709, NA | 0.2 | 0.32 | 0.07 | -0.27 | 0.49 | 0.07 | 0.66 | -0.04 | *0.02* | 0.18 |
| | clutch <= 2 | 10 | 0.68 | 1 | NA, NA | 0.5 | -1.04 | 0.38 | 0.71 | 0.92 | -0.04 | 0.37 | 0.59 | - | - |
| | | 10 | 0.97 | 0 | NA, 0.484 | 0.15 | 2.34 | 0.24 | -0.87 | 0.07 | 0.45 | *0.005* | 1.16 | *0.02* | -0.95 |
| **fledging** | clutch > 2 | 28 | 0.9 | 1 | 0.893, NA | 0.12 | 0.69 | 0.16 | -0.39 | 0.68 | 0.07 | *<0.0001* | 1.6 | - | - |
| | | 28 | 0.9 | 1 | 0.916, NA | 0.24 | 0.54 | 0.14 | -0.41 | 0.92 | 0.02 | *<0.0001* | 1.64 | 0.31 | 0.13 |
| | clutch <= 2 | | | | | | | *too small sample size* | | | | | | | |
| | | | | | | | | *too small sample size* | | | | | | | |

(to be continued)

|  |  |  |  |  |  | **brain mass** |  | **body mass** |  | **longevity** |  | **development** |  | **number of caretakers** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **clutch size** | clutch > 2 | 596 | 0.04 | 0.98 | 0.956, 0.996 | *<0.0001* | -0.29 | *0.0003* | 0.15 | - | - | 0.19 | -0.08 | - | - |
|  |  | 569 | 0.05 | 0.98 | 0.961, 1.000 | *<0.0001* | -0.3 | *0.0003* | 0.15 | - | - | 0.16 | -0.09 | 0.03 | 0.02 |
|  | clutch <= 2 | 124 | 0.06 | 0 | NA, 0.194 | 0.55 | 0.03 | 0.23 | -0.04 | - | - | *0.03* | -0.04 | - | - |
|  |  | 124 | 0.07 | 0 | NA, 0.178 | 0.46 | 0.04 | 0.2 | -0.05 | - | - | *0.03* | -0.04 | 0.14 | 0.03 |
| **broods per year** | clutch > 2 | 810 | 0.01 | 0.88 | 0.805, 0.923 | 0.99 | -0.0007 | 0.31 | -0.03 | - | - | 0.26 | -0.04 | - | - |
|  |  | 810 | 0.01 | 0.87 | 0.793, 0.919 | 0.88 | -0.008 | 0.34 | -0.03 | - | - | 0.22 | -0.05 | 0.07 | 0.03 |
|  | clutch <= 2 | 281 | 0.06 | 0.75 | 0.542, 0.884 | 0.13 | -0.13 | 0.68 | 0.02 | - | - | 0.29 | 0.04 | - | - |
|  |  | 281 | 0.07 | 0.74 | 0.535, 0.881 | 0.18 | -0.12 | 0.78 | 0.02 | - | - | 0.28 | 0.04 | 0.19 | 0.04 |
| **TFF** | clutch > 2 | 452 | 0.23 | 0.95 | 0.913, 0.979 | *0.007* | 0.18 | 0.14 | 0.06 | 0.12 | 0.04 | 0.22 | -0.06 | - | - |
|  |  | 452 | 0.23 | 0.95 | 0.913, 0.979 | *0.007* | 0.18 | 0.14 | 0.06 | 0.12 | 0.04 | 0.22 | -0.06 | 0.9 | -0.002 |
|  | clutch <= 2 | 118 | 0.42 | 0.81 | 0.572, 0.950 | 0.94 | -0.02 | 0.03 | 0.28 | 0.06 | 0.14 | 0.04 | 0.14 | - | - |
|  |  | 118 | 0.42 | 0.82 | 0.572, 0.950 | 0.89 | -0.03 | 0.03 | 0.29 | 0.06 | 0.14 | 0.05 | 0.14 | 0.63 | -0.06 |
| **fledging** | clutch > 2 | 310 | 0.26 | 0.9 | 0.782, 0.983 | 0.44 | 0.19 | *0.72* | 0.05 | 0.9 | 0.01 | <0.0001 | 1.6 | - | - |
|  |  | 310 | 0.26 | 0.9 | 0.782, 0.983 | 0.43 | 0.19 | *0.89* | 0.05 | 0.89 | 0.01 | <0.0001 | 1.6 | 0.8 | -0.01 |
|  | clutch <= 2 | 36 | 0.75 | 1 | NA, NA | 0.79 | -0.19 | *0.35* | 0.41 | 0.99 | 0.0005 | <0.0001 | 1.71 | - | - |
|  |  | 36 | 0.75 | 1 | NA, NA | 0.82 | -0.18 | *0.4* | 0.41 | 0.99 | 0.0006 | <0.0001 | 1.71 | 0.99 | 0.004 |

(to be continued)

|  |  |  |  |  |  | **brain mass** |  | **body mass** |  | **longevity** |  | **development** |  | **breeding type** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **clutch size** | clutch > 2 | 615 | 0.05 | 0.98 | 0.960, 1.00 | *<0.0001* | -0.3 | *<0.0001* | 0.17 | - | - | *0.03* | -0.13 | - | - |
|  |  | 615 | 0.05 | 0.98 | 0.959, 1.00 | *<0.0001* | -0.3 | *<0.0001* | 0.17 | - | - | *0.04* | -0.13 | 0.95 | 0.002 |
|  | clutch <= 2 | 126 | 0.05 | 0 | NA, 0.144 | 0.58 | 0.03 | 0.23 | -0.04 | - | - | *0.05* | -0.04 | - | - |
|  |  | 126 | 0.12 | 0 | NA, 0.130 | 0.29 | 0.06 | 0.12 | -0.06 | - | - | *0.02* | -0.04 | *0.004* | 0.13 |
| **broods per year** | clutch > 2 | 874 | 0.006 | 0.89 | 0.828, 0.925 | 0.82 | -0.01 | 0.53 | -0.02 | - | - | *0.78* | -0.01 | - | - |
|  |  | 874 | 0.008 | 0.88 | 0.826, 0.924 | 0.76 | -0.02 | 0.58 | -0.02 | - | - | *0.76* | -0.01 | 0.23 | 0.03 |
|  | clutch <= 2 | 284 | 0.06 | 0.77 | 0.588, 0.894 | 0.1 | -0.15 | 0.59 | 0.03 | - | - | *0.38* | 0.03 | - | - |
|  |  | 284 | 0.06 | 0.77 | 0.582, 0.891 | 0.11 | -0.14 | 0.63 | 0.03 | - | - | *0.39* | 0.03 | 0.51 | 0.03 |
| **TFF** | clutch > 2 | 479 | 0.22 | 0.97 | 0.942, 0.990 | *0.03* | 0.15 | *0.05* | 0.09 | 0.2 | 0.03 | 0.59 | -0.03 | - | - |
|  |  | 479 | 0.22 | 0.97 | 0.942, 0.990 | 0.03 | 0.15 | *0.05* | 0.09 | 0.2 | 0.03 | 0.59 | -0.03 | 0.89 | 0.004 |
|  | clutch <= 2 | 118 | 0.44 | 0.81 | 0.584, 0.945 | 0.85 | -0.04 | *0.03* | 0.27 | *0.02* | 0.18 | *0.01* | 0.17 | - | - |
|  |  | 118 | 0.44 | 0.81 | 0.584, 0.945 | 0.81 | -0.05 | *0.03* | 0.28 | *0.02* | 0.18 | *0.01* | 0.17 | 0.6 | -0.07 |
| **fledging** | clutch > 2 | 327 | 0.23 | 0.94 | 0.839, NA | 0.48 | 0.17 | 0.65 | 0.07 | 0.96 | 0.004 | *<0.0001* | 1.6 | - | - |
|  |  | 327 | 0.23 | 0.93 | 0.836, 1.000 | 0.47 | 0.17 | 0.67 | 0.06 | 0.91 | 0.01 | *<0.0001* | 1.59 | 0.64 | -0.05 |
|  | clutch <= 2 | 37 | 0.7 | 1 | 0.479, NA | 0.77 | -0.22 | 0.28 | 0.52 | 0.87 | 0.06 | *<0.0001* | 1.53 | - | - |
|  |  | 37 | 0.71 | 1 | 0.757, NA | 0.68 | -0.34 | 0.26 | 0.58 | 0.92 | 0.04 | *<0.0001* | 1.55 | 0.7 | -0.15 |

Moreover, investigating the production trade-off from another perspective, I analysed non-cooperatively breeding species and species with allomaternal care separately. In non-cooperatively breeding bird species I found a reproduction trade-off. Depending on clutch size, the production trade-off is expected to show different effects: relatively large-brained species having clutch sizes larger than 2 are expected to reduce clutch sizes, whereas groups with smaller clutches (clutch $< = 2$) are expected to reduce birth rates, and slow down development. All the following results are shown in table 3.8.

First, I looked at the relationship between clutch size and relative brain size within the non-cooperatively breeding species including **brood parasites, geothermal and single breeders**. Species where the clutch contains more than two eggs (**clutch>2**) show a negative trend between clutch size and brain size, as expected (figure 3.4 a). Moreover, for the same taxa group, after correcting for the effect of life history pace, I found neither a positive correlation between time of first flight (measurement for development time) and relative brain size nor a negative relationship between broods per year and relative brain size (figure 3.4 c). Between time of fledging and relative brain size a positive trend is observed (figure 3.4 e).
Within species which have clutch sizes smaller or equal to two (**clutch<=2**), clutch size is not negatively correlated with relative brain size anymore (figure 3.4 a). However, after correcting for the effect of life history pace I found no correlation between time of first flight or fledging (as a measurement for development time) and relative brain size (figure 3.4 e). However, these sample sizes are too small to detect any reliable results ($n = 6$; $n = 7$).

Second, in **pair and cooperatively breeding species** I found no negative correlation between reproductive rate and relative brain size. Species breeding in pairs or cooperativley having clutch sizes larger than two (**clutch>2**), showed still a negative correlation between clutch size and relative brain size (figure 3.4 b). Furthermore, they showed a weak trend between time of first flight and relative brain size, whereas fledging shows no correlation with relative brain size (figure 3.4 f).
Furthermore, pair and cooperative breeders having two or less eggs per clutch (**clutch <=2**) showed no relationship between clutch size and relative brain size (figure 3.4 b). Moreover, this taxa group shows a slight negative trend with broods per years, which is not observed in all other groups (figure 3.4 d). However, no correlation between time of first flight or fledging and relative brain size (figure 3.4 f) is observed.

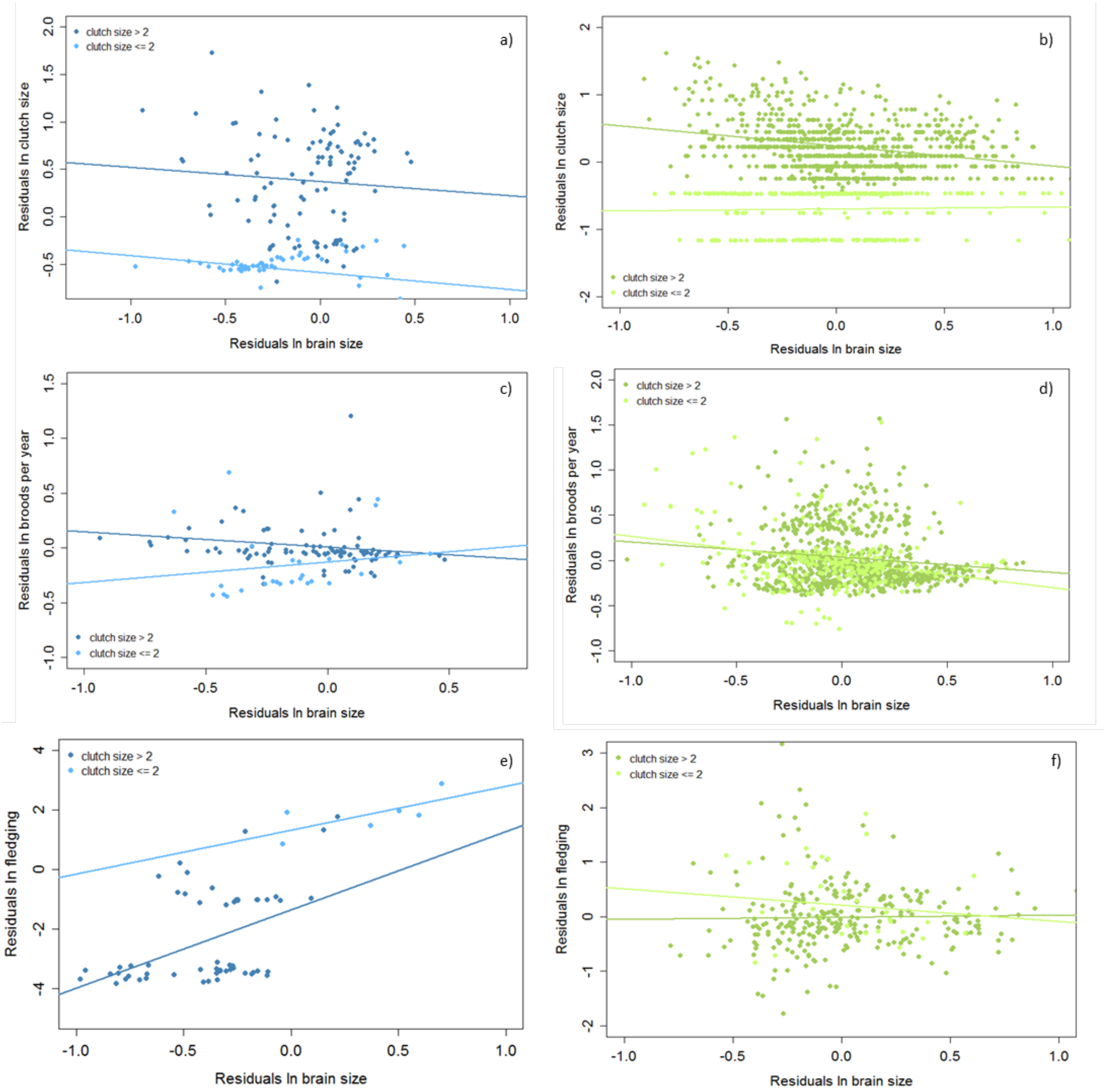


Figure 3.4: **Reproduction trade-off for different clutch sizes.** a) Least-square regressions of the residuals of ln clutch size on the residuals of ln brain mass for brood parasites, geothermal/single breeders. Residuals indicate correction for body size and development mode. (PGLS: clutch>2: n=102, p=0.12(+); clutch<=2: n=56, p=0.47(-)). b) Least-square regressions of the residuals of ln clutch size on the residuals of ln brain mass for pair and cooperative breeders. Residuals indicate correction for body size and development mode. Residuals indicate correction for body size. (PGLS: clutch>2: n=905, p<0.0001(-); clutch<=2: n=322, p=0.46(+)). c) Least-square regressions of the residuals of ln broods per year on the residuals of ln brain mass for brood parasites, geothermal/single breeders. Residuals indicate correction for body size and development mode. (PGLS: clutch>2: n=97, p=0.8(-); clutch<=2: n=26, p=0.99(+)). d) Least-square regressions of the residuals of ln broods per year on the residuals of ln brain mass for pair and cooperative breeders. Residuals indicate correction for body size and development mode. (PGLS: clutch>2: n=767, p=0.91(-); clutch<=2: n=254, p=0.09(-)). e) Least-square regressions of residuals of ln time of fledging on the residuals of ln brain mass for brood parasites, geothermal/single breeders. Residuals indicate correction for body size and development mode. (PGLS: clutch>2: n=61, p=0.13(+); clutch<=2: n=6, p=0.87(-)). f) Least-square regressions of the residuals of ln time of fledging on the residuals of ln brain mass for pair and cooperative breeders. Residuals of fledging indicate correction for body size, development mode and longevity. Residuals of brain size indicate correction for body size. (PGLS: clutch>2: n=300, p=0.47(+); clutch<=2: n=31, p=0.66(-)). All the regressions are shown separately for species with clutch sizes larger than two and species with clutch sizes smaller than.

Table 3.8: a) Multiple PGLS regressions of ln clutch size and ln brain mass for brood parasite/geothermal/singly breeding species and pair/cooperatively breeding species (ln clutch size as dependent variable and ln brain mass, ln body mass and development mode as independent variables). b) Multiple PGLS regressions of ln broods per year and ln brain mass for brood parasite/geothermal/singly breeding species and pair/cooperatively breeding species (ln broods per year as dependent variable and ln brain mass, ln body mass and development mode as independent variables). c) Multiple PGLS regressions of ln time of first flight (TFF) and ln brain mass for brood parasites/geothermal/singly breeding species and pair/cooperatively breeding species (ln TFF as dependent variable and ln brain mass, ln body mass, ln longevity and development mode as independent variables). d) Multiple PGLS regressions of ln time of fledging and ln brain mass for brood parasites/geothermal/singly breeding species and pair/cooperatively breeding species (ln fledging as dependent variable and ln brain mass, ln body mass, ln longevity and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$). (significant effects are shown in italics, NA = not available = unknown value).

| a) | | | | | | **brain mass** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **clutch size** | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **geothermal/single** | clutch $>$ 2 | 102 | 0.11 | 1 | 0.979, NA | 0.12 | -0.3 | *0.04* | 0.21 | *0.03* | -0.32 |
| **breeders** | clutch $<=$ 2 | 56 | 0.49 | 0 | NA, 0.380 | 0.47 | -0.09 | 0.72 | -0.04 | *0.02* | -0.13 |
| **pair/cooperative** | clutch $>$ 2 | 905 | 0.03 | 0.92 | 0.867, 0.951 | *<0.0001* | -0.23 | *0.0005* | 0.11 | 0.02 | 0.09 |
| **breeders** | clutch $<=$ 2 | 322 | 0.03 | 1 | 0.959, NA | 0.46 | 0.05 | 0.15 | -0.07 | *0.02* | -0.1 |

| b) | | | | | | **brain mass** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **broods per year** | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **geothermal/single** | clutch $>$ 2 | 97 | 0.005 | 1 | 0.962, NA | 0.8 | -0.04 | 0.65 | 0.04 | 0.86 | 0.02 |
| **breeders** | clutch $<=$ 2 | 26 | 0.22 | 0 | NA, 0.904 | 0.99 | 0.005 | 0.83 | -0.05 | 0.18 | -0.15 |
| **pair/cooperative** | clutch $>$ 2 | 767 | 0.009 | 0.84 | 0.756, 0.899 | 0.91 | -0.006 | 0.4 | -0.03 | 0.89 | 0.005 |
| **breeders** | clutch $<=$ 2 | 254 | 0.08 | 0.74 | 0.508, 0.886 | 0.09 | 0.15 | 0.66 | 0.03 | 0.22 | 0.04 |

(to be continued)

| c) | | | | | | brain mass | | body mass | | longevity | | development | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TFF** | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **geothermal/single** | clutch $> 2$ | 53 | 0.15 | 0.85 | 0.556, 0.997 | *0.03* | 0.72 | 0.14 | -0.25 | 0.95 | 0.009 | 0.23 | -0.21 |
| **breeders** | clutch $< = 2$ | 7 | 0.62 | 0 | NA, NA | 0.46 | -1.07 | 0.34 | 1.1 | 0.66 | -0.29 | variance = 0 | |
| **pair/cooperative** | clutch $> 2$ | 424 | 0.25 | 0.98 | 0.950, 0.992 | 0.14 | 0.1 | *0.006* | 0.12 | 0.12 | 0.04 | 0.75 | -0.02 |
| **breeders** | clutch $< = 2$ | 110 | 0.45 | 0.77 | 0.475, 0.934 | 0.98 | -0.004 | 0.05 | 0.26 | *0.01* | 0.19 | *0.02* | 0.16 |

| d) | | | | | | brain mass | | body mass | | longevity | | development | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **fledging** | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **geothermal/single** | clutch $> 2$ | 61 | 0.42 | 0.58 | 0.071, 0.867 | 0.13 | 1.15 | 0.33 | -0.4 | 0.8 | 0.11 | 0.0002 | 1.28 |
| **breeders** | clutch $< = 2$ | 6 | 0.95 | 0 | NA, NA | 0.87 | -0.6 | 0.68 | 1 | 0.78 | -0.8 | 0.48 | 1.05 |
| **pair/cooperative** | clutch $> 2$ | 300 | 0.32 | 1 | 0.989, NA | 0.47 | 0.16 | 0.39 | 0.12 | 0.75 | -0.02 | *<0.0001* | 1.57 |
| **breeders** | clutch $< = 2$ | 31 | 0.74 | 1 | NA, NA | 0.66 | -0.38 | 0.28 | 0.59 | 0.99 | 0.005 | *<0.0001* | 1.66 |

**Prediction Hypothesis 2c**: Correcting for the amount of allomaternal care, relatively large-brained species with reduced reproduction (fertility or r$_{max}$) are expected to increase the annual adult survival and elongate their maximum reproductive lifespan (max. lifespan - AFR). Thus, I expect a positive correlation between relative brain size and maximum reproductive lifespan. From the other perspective, one could argue that for geothermal and singly breeding species, relatively large-brained species with reduced reproduction (fertility or r$_{max}$) are expected to elongate their maximum reproductive lifespan (max. lifespan - AFR) and increase annual adult survival.

**Results Hypothesis 2 c**: I expected large-brained species with reduced reproduction to increase the annual adult survival or elongate their maximum reproductive lifespan in order to be nonetheless evolutionary stable. The data shows that longevity strongly positively correlates or at least shows a trend with relative brain size with and without correcting for the amount of allomaternal care (table 3.9). Annual adult survival shows slight trends towards a positive relationship with relative brain size in the data set where the energetic measurements are included. However, when including the number of caretakers and breeding type as covariates these trends disappear. Consistently, when looking at annual adult survival, I did not observe a substantial difference between models with and without the quantifications of allomaternal care as covariates.

Interestingly, in the large samples (controlling for number of caretakers or breeding type, table 3.9) longevity and annual adult survival show positive relationships (or at least strong) trends with number of caretakers and breeding type. In other words, the more allomaternal care in form of caretakers, the higher the adult survival.

Moreover, I looked at species with and without allomaternal care separately (results are shown in table 3.10 and figure 3.5). For non-cooperative breeders (brood parasites, geothermal and single breeders) where large-brained species have low reproductive rates, I expected annual adult survival and maximal reproductive lifespan to positively correlate with relative brain size. And in fact, in brood parasites, geothermal and singly breeding species, annual adult survival as well as longevity correlated positively with relative brain size. In pair and cooperatively breeding species I still found a positive correlation between longevity and relative brain size, whereas when looking at cooperatively breeding species separately, the positive correlation completely disappears. For annual adult survival the positive relationship with relative brain size already disappears in pair breeding species. These results suggest on the one hand that large-brained species with no allomaternal care need reduce mortality rates and elongate their maximum reproductive lifespan in order to be nonetheless evolutionary stable. On the other hand, in cooperatively breeding species no relationship between maximum reproductive lifespan and relative brain size is observed as they show an alleviated reproduction trade-off.

Table 3.9: Multiple PGLS regressions of ln longevity/squareroot (sqrt) annual adult survival and ln brain mass (ln longevity and sqrt annual adult survival as dependent variables, ln brain mass, ln body mass, development mode as well as ln total energetic input per chick rearing period, number of caretakers and breeding type as independent variables). Correcting the analyses either for total energy, number of caretakers or breeding type. Given are the sample size (n), multiple r$^2$, Akaike information criterion (AIC), Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$). (significant effects are shown in italics, NA = not available = unknown value).

|  |  |  |  |  |  | **brain mass** |  | **body mass** |  | **development** |  | **total energy** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | n | r$^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| longevity | 46 | 0.47 | 66.26 | 0 | NA, 0.557 | 0.08 | 0.61 | 0.39 | -0.18 | 0.06 | -0.14 | - | - |
|  | 46 | 0.47 | 67.94 | 0 | NA, 0.509 | 0.13 | 0.55 | 0.36 | -0.2 | 0.07 | -0.14 | 0.6 | 0.05 |
| ann.adult survival | 42 | 0.15 | -114.56 | 0.98 | 0.860, NA | 0.11 | 0.09 | 0.25 | -0.04 | 0.47 | -0.02 | - | - |
|  | 42 | 0.15 | -112.56 | 0.98 | 0.860, NA | 0.15 | 0.09 | 0.26 | -0.04 | 0.47 | -0.02 | 0.95 | -0.007 |
|  |  |  |  |  |  |  |  |  |  |  |  | **number of caretakers** |  |
|  |  |  |  |  |  |  |  |  |  |  |  | p-value | slope |
| longevity | 618 | 0.2 | 789.68 | 0.71 | 0.556, 0.828 | *0.001* | 0.33 | 0.68 | 0.03 | 0.1 | -0.07 | - | - |
|  | 618 | 2 | 789.1 | 0.71 | 0.561, 0.831 | *0.001* | 0.33 | 0.68 | 0.03 | 0.09 | -0.08 | 0.11 | 0.04 |
| ann.adult survival | 268 | 0.1 | -650.61 | 0.82 | 0.677, 0.917 | 0.37 | 0.02 | 0.45 | 0.01 | 0.6 | -0.006 | - | - |
|  | 268 | 0.12 | -654.21 | 0.82 | 0.668, 0.917 | 0.46 | 0.02 | 0.36 | 0.01 | 0.58 | -0.006 | 0.02 | 0.01 |
|  |  |  |  |  |  |  |  |  |  |  |  | **breeding type** |  |
|  |  |  |  |  |  |  |  |  |  |  |  | p-value | slope |
| longevity | 647 | 0.2 | 815.67 | 0.74 | 0.592, 0.844 | *0.0005* | 0.35 | 0.69 | 0.02 | 0.08 | -0.08 | - | - |
|  | 647 | 0.21 | 813.23 | 0.74 | 0.603, 0.848 | *0.0004* | 0.36 | 0.74 | 0.02 | 0.06 | -0.09 | *0.04* | 0.12 |
| ann.adult survival | 285 | 0.11 | -696.32 | 0.82 | 0.678, 0.916 | 0.72 | 0.008 | 0.14 | 0.02 | 0.96 | -0.005 | - | - |
|  | 285 | 0.12 | -697.203 | 0.82 | 0.675, 0.917 | 0.75 | 0.007 | 0.13 | 0.02 | 0.93 | -0.0009 | 0.09 | 0.02 |

Table 3.10: Multiple PGLS regressions of ln longevity, sqrt annual adult survival and ln brain mass for brood parasites/geothermal/singly breeding species, pair breeding species, cooperatively breeding species and pair/cooperatively breeding species (ln longevity and sgrt annual adult survival as dependent variable, ln brain mass, ln body mass and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics).

| | | | | | | **brain mass** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **brood parasites/ geothermal/single breeders** | longevity | 72 | 0.37 | 0.59 | 0.045, 0.871 | *0.01* | 0.55 | 0.39 | -0.11 | 0.57 | -0.05 |
| | ann. adult suvival | 20 | 0.71 | 0 | NA, 0.508 | *0.0002* | 0.31 | 0.003 | -0.13 | 0.87 | -0.004 |
| **pair breeders** | longevity | 446 | 0.2 | 0.78 | 0.609, 0.889 | *0.008* | 0.32 | 0.58 | 0.04 | 0.06 | -0.1 |
| | ann. adult suvival | 198 | 0.1 | 0.88 | 0.712, 0.961 | 0.57 | 0.01 | 0.42 | 0.01 | 0.49 | -0.008 |
| **cooperative breeders** | longevity | 127 | 0.21 | 0.76 | 0.414, 0.961 | 0.55 | 0.13 | 0.32 | 0.13 | 0.86 | -0.02 |
| | ann. adult suvival | 66 | 0.21 | 0.86 | 0.358, NA | 0.67 | -0.02 | 0.13 | 0.05 | 0.59 | 0.01 |
| **pair/cooperative breeders** | longevity | 573 | 0.19 | 0.78 | 0.635, 0.879 | *0.005* | 0.31 | 0.46 | 0.05 | 0.06 | -0.1 |
| | ann. adult suvival | 264 | 0.1 | 0.89 | 0.754, 0.961 | 0.82 | 0.005 | 0.15 | 0.02 | 0.8 | -0.003 |

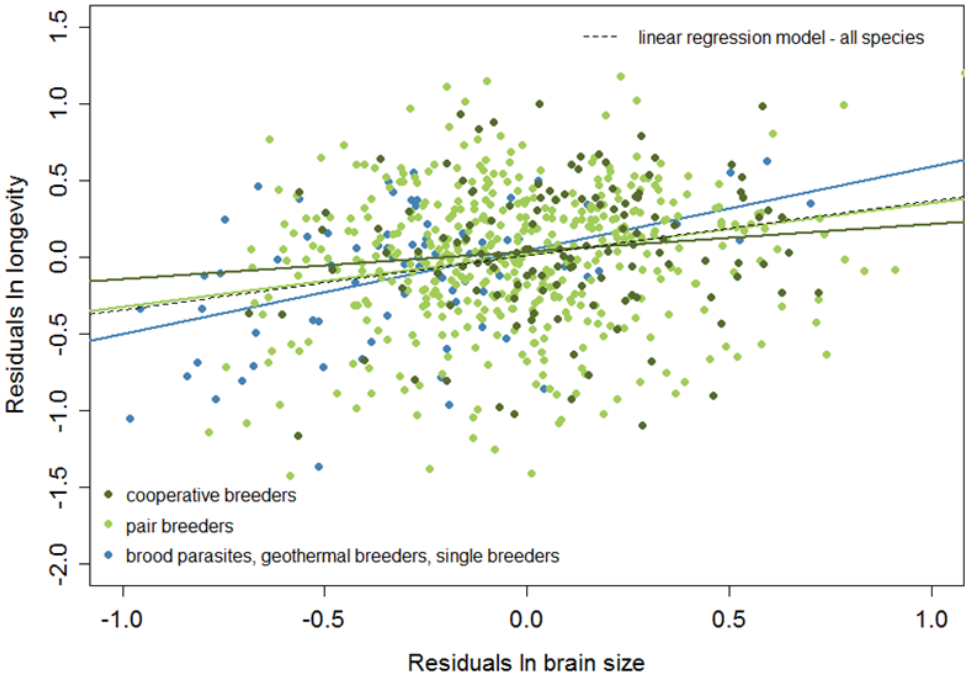


Figure 3.5: **Longevity vs. brain size.** Least-square regressions of the residuals of ln longevity on the residuals of ln brain mass shown for brood parasites/geothermal breeders/single breeders, pair and cooperative breeders separately. The dashed line indicates the least-square regression of all species species (PGLS: brood parasites, geothermal/single breeders: n = 72, p=0.01(+); pair breeders: n = 446, p=0.008(+); cooperative breeders: n = 127, p=0.55(+)). The residuals indicate correction for body size.

In summary across all species (using identical samples), annual adult fertility shows a negative correlation with relative brain size and longevity positively correlates with relative brain size (table 3.11, figure 3.6 a,b). $R_{max}$, which is calculated out of annual fertility and maximum reproductive lifespan, shows a very slight negative trend with relative brain size (table 3.11, figure 3.6 c).

Table 3.11: PGLS regression of ln annual fertility, ln longevity, ln $r_{max}$ and ln brain mass (ln annual fertility, ln longevity and ln $r_{max}$ as dependent variables; ln brain mass, ln body mass and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics).

| | | | | | **brain mass** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **fertility** | 447 | 0.09 | 0.95 | 0.915, 0.979 | *0.01* | -0.27 | 0.77 | 0.02 | 0.26 | -0.06 |
| **longevity** | 447 | 0.23 | 0.64 | 0.450, 0.783 | 0.06 | 0.2 | 0.1 | 0.11 | 0.1 | -0.01 |
| **$r_{max}$** | 447 | 0.2 | 0.98 | 0.948, 1.000 | 0.12 | -0.15 | *0.03* | -0.13 | 0.37 | -0.05 |

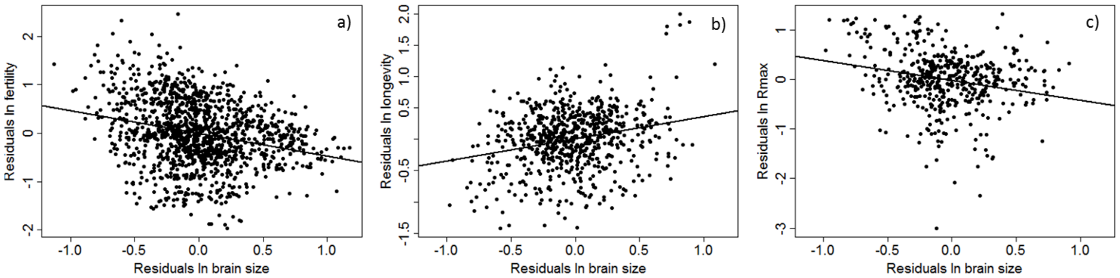


Figure 3.6: **Reproduction trade-off in birds.** Least-square regressions of (a) residuals of ln fertility (PGLS: n=447, p=0.01(-)), (b) residuals ln longevity (PGLS: n=447, p=0.06(+)), (c) residuals ln $r_{max}$ on the residuals of ln relative brain size PGLS: n=447, p=0.12(-). Residuals indicate correction for body mass.

**Prediction Hypothesis 2 d**: The relatively largest-brained taxa with reduced reproduction are expected to be very close to their „grey ceiling“ (maximum viable brain size), showing quite low $r_{max}$ values and thus, are expected to be classified as vulnerable or endangered on the worldwide scale. Therefore, high endangered species are expected to show low $r_{max}$ values and relatively large brain sizes. Thus, I predict a negative correlation between $r_{max}$ and the status on the worldwide scale (1=not globally threatened, 2=rare, 3=vulnerable, 4=endangered) and a positive correlation between relative brain size and the worldwide status.

**Results Hypothesis 2 d**: Interestingly, I found that bird species which on the worldwide scale are classified as rare, vulnerable or endangered predominantly have relatively low reproductive rates (residuals $< 0$) and large brain sizes (residuals $> 0$) (figure 3.7), which might be an indication of these species having reached their maximum viable brain size (= grey ceiling). I predicted that in taxa groups showing a strong reproduction trade-off (species without allomaternal care), large-brained species with very low rates of reproduction ($r_{max}$) to exhibit higher risk of extinction. However, the variation in the status of the worldwide scale (1=not globally threatened, 2=rare, 3=vulnerable, 4=endangered) within species with no allomaternal care (brood parasites, geothermal and single breeders) is too low for statistical testing. Thus, I needed to test the effect of reproduction ($r_{max}$ or fertility) on the status of the worldwide scale across all species ($r_{max}$ shows also a slightly negative trend across all species, table 3.11).
I found no significant correlations (model A and D; table 3.12), also not if additionally correcting the amount of allomaternal care (number of caretakers or breeding type; there is not enough data to correct for the total energetic input per breeding season) (model B, C, E and F; table 3.12). Relative brain size seems to have a positive effect on the status on the worldwide scale (model G, H and I; table 3.5). Further, I did not find significant relationships between the status on the worldwide scale and reproduction if relative brain size was held constant (PGLS regression status vs. $r_{max}$): n=404; multiple $r^2$=0.02; $\lambda$=0; $r_{max}$: slope=-0.03, p=0.34; brain mass: slope=0.09,

p=0.15; corrected for body size and development mode); (PGLS regression (status vs. fertility): n=1022; multiple $r^2$=0.02, $\lambda$=0.1; fertility: slope=-0.01, p=0.62; brain mass: slope=0.17, p=0.003, corrected for body size and development mode).

However, probability of a species being threatenend (either classified as rare, vulnerable or endangered) is highest in the bottom right square in figure 3.7 (probability=0.077), whereas in the top left square of figure 3.7, the probability of a species being endangered equals zero (probability in top right square=0.038; probability in bottom left square = 0.027). In summary, reproduction does not seem to have an effect on how endangered a certain species is, whereas with increasing brain size, species seem more likely to be endangered. However, endangered or vulnerable bird species dominantly seem to have rather low reproductive rates (residuals $< 0$) and large relative brain sizes (residuals $> 0$) (figure 3.7).

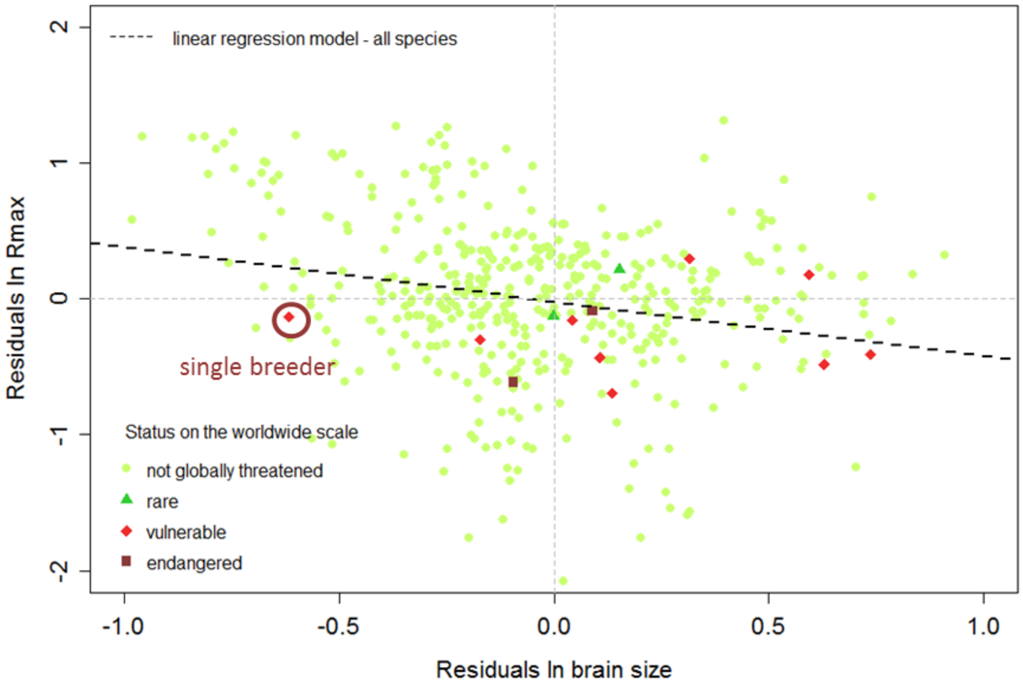


Figure 3.7: **Status on the worldwide scale.** Least square-regression of the residuals of ln $r_{max}$ on the residuals of ln brain mass shown for the different status on the worldwide scale (not globally threatened, rare, endangered and vulnerable) (n(„not globally threatened“) = 433; n(„rare“) = 2; n(„vulnerable“) = 9; n(„endangered“) = 2). Probability of a species being threatenend: top left square: 0%; top right square=3.8%, bottom left square=2.7%, bottom right square=7.7%. The only singly breeding species who has a critical classification on the worldwide scale is marked by a red circle.

Table 3.12: Multiple PGLS regressions of the status on the worldwide scale (not globally threatened = 1; rare = 2; vulnerable = 3; endangered = 4) and ln $r_{max}$, ln fertility, ln brain mass as well as the amount of allomaternal care in form of number of caretakers or breeding type (status on the worldwide scale as the dependent variable, ln $_{max}$, ln fertility, ln brain mass, ln body mass, development mode as well as number of caretakers and breeding type as independent variables). Given are the sample size (n), multiple $r^2$, Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

|  |  |  |  |  | **$r_{max}$** |  | **body mass** |  | **development** |  | **number of caretakers** |  | **breeding type** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **model A** | 404 | 0.02 | 0 | NA, 0.266 | 0.28 | -0.03 | 0.14 | 0.02 | 0.79 | 0.004 | - | - | - | - |
| **model B** | 404 | 0.03 | 0 | NA, 0.203 | 0.48 | -0.02 | 0.08 | 0.02 | 0.71 | -0.005 | *0.04* | 0.06 | - | - |
| **model C** | 404 | 0.03 | 0 | NA, 0.194 | 0.58 | *-0.01* | 0.08 | 0.02 | 0.68 | -0.006 | - | - | 0.05 | 0.08 |
|  |  |  |  |  | **fertility** |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  | p-value | slope |  |  |  |  |  |  |  |  |
| **model D** | 1022 | 0.007 | 0.15 | 0.079, 0.245 | 0.46 | -0.02 | *0.02* | 0.03 | 0.79 | -0.005 | - | - | - | - |
| **model E** | 1022 | 0.007 | 0.15 | 0.079, 0.245 | 0.46 | -0.02 | *0.02* | 0.03 | 0.79 | -0.006 | 0.94 | 0.002 | - | - |
| **model F** | 1022 | 0.007 | 0.15 | 0.079, 0.245 | 0.46 | -0.02 | *0.02* | 0.03 | 0.77 | -0.006 | - | - | 0.78 | 0.01 |
|  |  |  |  |  | **brain mass** |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  | p-value | slope |  |  |  |  |  |  |  |  |
| **model G** | 1022 | 0.02 | 0.1 | 0.039, 0.191 | *0.003* | 0.17 | *0.04* | -0.08 | 0.22 | -0.03 | - | - | - | - |
| **model H** | 1022 | 0.02 | 0.1 | 0.039, 0.191 | *0.003* | 0.17 | *0.04* | -0.08 | 0.22 | -0.03 | 0.99 | -0.0004 | - | - |
| **model I** | 1022 | 0.02 | 0.1 | 0.039, 0.191 | *0.003* | 0.17 | *0.04* | -0.08 | 0.22 | -0.03 | - | - | 0.89 | 0.005 |

## 3.4 Energy subsidies hypothesis

**Prediction Hypothesis 3 a**: Before the energy subsidies hypothesis can be tested, I need to look at a possible correlation between total energy amount per breeding season and number of caretakers. A positive correlation is expected. Then, the amount of allomaternal care is expected to correlate positively with relative brain size and/or reproduction (fertility or $r_{max}$).

- Amount of allomaternal care positively correlates with relative brain size: The more help available, the more energy is invested in brains rather than reproduction, which means that compensation by an elongation in reproductive lifespan is required for nonetheless evolutionary stable populations. Thus, I predict a positive correlation between the amount of allomaternal care and reproductive lifespan.
- Amount of allomaternal care positively correlates with reproduction (fertility or $r_{max}$): The more help available, the more energy is invested in reproduction rather than in brains and thus, no compensation by elongated reproductive lifespan is required. Therefore, I expect the amount of allomaternal care not to positively correlate with maximum reproductive lifespan.

**Results Hypothesis 3 a**: Total energetic investment per day and per breeding season does not significantly correlate with the number of caretakers or breeding type (PGLS regressions (per day): number of caretakers: n=59; multiple $r^2$=0.56; slope=0.21, p=0.32; breeding type: n=59, $r^2$=0.55, slope=0.20, p=0.46; corrected for body size and development mode) (PGLS regressions (per breeding season): number of caretakers: n=59; multiple $r^2$=0.62; slope=0.32, p=0.21; breeding type: n=49, $r^2$=0.61, slope=0.51, p=0.19; corrected for body size and development mode). The variation in number of caretakers and breeding type is however very low in that sample (only 1 single breeder, mainly pair breeders). For further analyses, I need to assume a positive link between these two variables.

The main aim of this study was to investigate whether energy subsidies during breeding are related to the evolution of large brains and/or an increase in reproduction in birds. In this context, I looked at the correlation between relative brain size and the amount of allomaternal care and reproduction ($r_{max}$, fertility, clutch size and egg mass) and the amount of allomaternal care. For measurements of the amount of allomaternal care I used three alternatives: total energetic input per chick rearing period (total energy inputs considering time and number of caretakers), total number of caretakers or breeding type. Besides of applying multiple PGLS regressions, I used another possible approach to get phylogenetically independent data: family means of the analysed variables applied in non-phylogenetic multiple regression models (GLS family means). All the following results are shown in table 3.13.

After correcting for body mass and development mode, I found relative brain size to correlate positively with the **total amount of energy** during chick rearing period (figure 3.9 a). Interestingly, $r_{max}$, fertility (number of eggs per year) and clutch size showed negative associations with the total energetic investment per breeding season (especially in the GLS regression model using family means) (figure 3.9 b). Moreover, after correcting for several confounding variables, egg mass positively correlated with the total amount of energy (figure 3.9 c). In other words, the more energy available during a breeding season, the more is invested in brain and egg mass and the less in reproductive rate/number of offspring. Therefore, longevity is expected to correlate positively with amount of allomaternal care. In the available data a very slight positive relationship is observed using PGLS method (figure 3.9 d).

Further, the **number of caretakers** can be used as an alternative measurement for the amount of allomaternal care. On the one hand, after correcting for the effects of body size and development mode, brain size does not correlate with the number of caretakers (figure 3.10 a). Furthermore, $r_{max}$ also did not show a correlation with the number of caretakers (figure 3.10 b), whereas fertility showed a positive relationship. Moreover, clutch size showed a positive trend with number of caretakers which disappears if applying GLS regression based on family means. Egg mass shows no correlation with number of caretakers (figure 3.10 c), however between longevity and number of caretakers a positive trend is observed (figure 3.10 d). Over all, no clear pattern can be found.

As a third measurement of the amount of allomaternal care, I used **breeding type** (0.01: brood parasites, 0: geothermal breeders, 1: single breeders, 2: pair breeders, 2.5: occasional cooperative breeders, 3: cooperative breedres). One simple way to analyse the differences in relative brain size between the different breeding types is to apply a non-phylogenetic analysis of covariance (ANCOVA). This analysis suggested that cooperatively breeding species have larger brains than pair breeding species and pair breeding species have larger brains than brood parasites, geothermal or singly breeding species (ANCOVA: Tukey‘s posthoc test: $p < 0.05$) (figure 3.8). However, the rather strong phylogenetic signal (maximum likelihood estimate of lambda ($\lambda$) = 0.85, maximum likelihood ration test: lower bound: 0.000, $p < 0.0001$; upper bound: 1.000, $p < 0.0001$) indicated that breeding type shows a significant association with phylogeny. Therefore, phylogenetic analyses are essential for properly testing the differences in relative brain size between the different breeding types. So far, different phylogenetic approaches have proposed to detect grade shifts between groups. I used a more recent and probably most common phylogenetic approach to investigate the possible grade shifts in relative brain size for different breeding types. I included breeding type as continuous variable in a multiple PGLS model to test whether there is a significant effect of breeding type on relative brain size after accounting for phylogenetic relatedness (similar approaches have been used in other studies: Fritz et al. 2009; Gartner et al. 2010). However, after taking the phylogenetic relatedness into account and correcting for the effects of body size and development, breeding type does not have a significant effect on brain size (table 3.13). Using family means does also not result in a significant effect of breeding type on relative brain size (GLS models with family means, table 3.13). To sum up, relative brain size, $r_{max}$, fertility and clutch size do not correlate with breeding type, whereas egg mass does show a positive correlation.

In summary, the different alternative measurements trying to quantify the amount of allomaternal care show no consistent pattern in relation to relative brain size and reproduction. First, regarding energetic measurements, with an increasing amount of allomaternal care, brain size increases whereas reproduction rather decreases. Thus, I predicted a positive correlation between the amount of allomaternal care and reproductive lifespan, where a slight positive trend is observed if using family means. Second, relative brain size as well as $r_{max}$ are not correlated with the number of caretakers, whereas fertility shows a positive correlation. Further, with an increasing number of caretakers a trend towards increasing longevity is observed (figure 3.10 d), which has not been expected. Third, breeding type shows only positive correlations with egg mass and longevity.

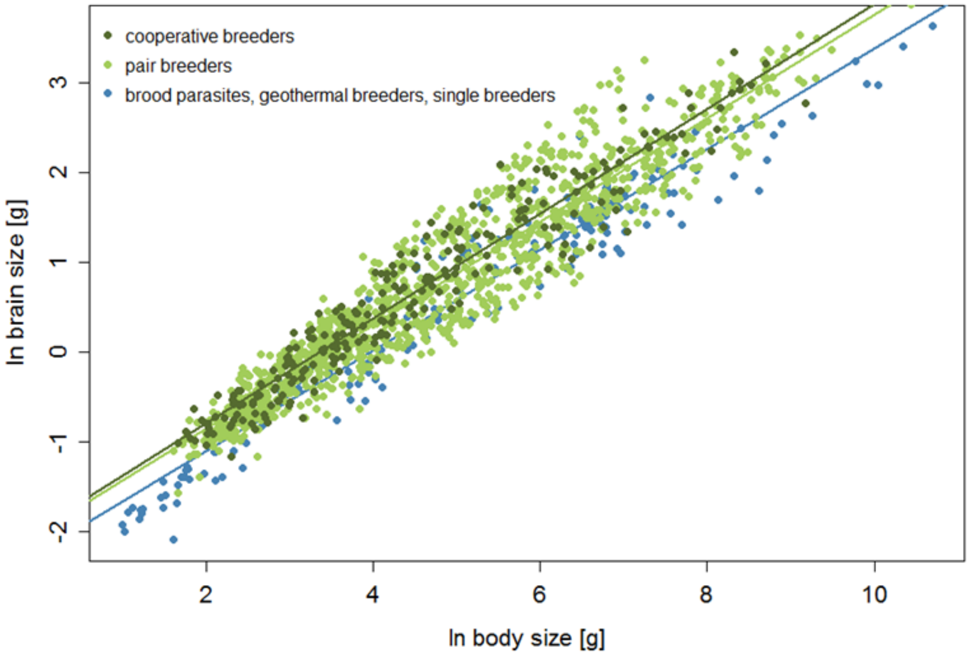


Figure 3.8: **Brain size vs. body size for the different breeding types.** Least-square regressions of ln brain mass on ln body size, shown separately for brood parasites/geothermal breeders/single breeders, pair and cooperatively breeding species (n(brood parasites, geothermal/single breeders) = 173; n(pair breeders) = 1071; n(cooperative breeders) = 261). ANCOVA: Tukey‘s posthoc test: $p < 0.05$.

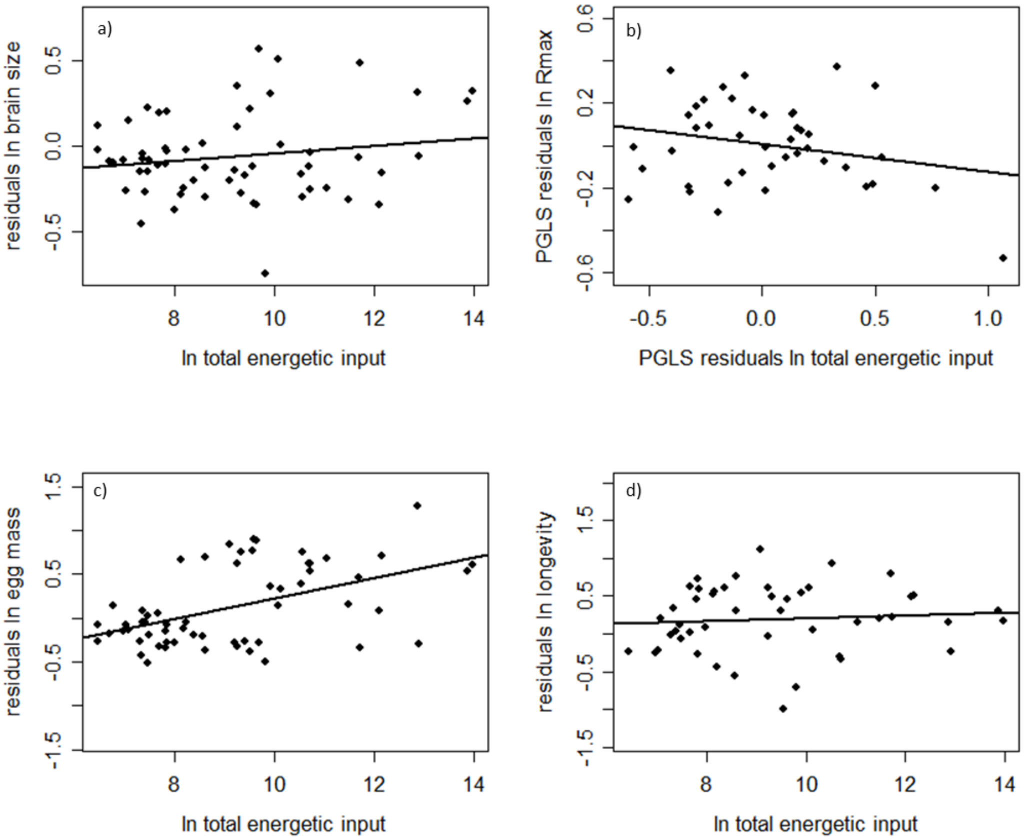


Figure 3.9: **Effects of total energetic input.** a) Least-square regressions of the residuals of ln brain mass on ln energy (PGLS: n = 59, p=0.0066(+)) (residuals of ln brain mass indicate correction for body mass). b) Least-square regressions of the residuals of ln $r_{max}$ (phylogenetic residuals corrected for body mass and development mode) on the residuals of ln energy (PGLS: n = 42, p=0.03(-)) (phylogenetic residuals corrected for body mass and development mode). c) Least-square regressions of the residuals of ln egg mass (corrected for body mass) on ln energy (PGLS: n = 59, p=0.0001(+)). d) Least-square regressions of the residuals of ln longevity (corrected for body mass) on ln energy (PGLS: n = 47, p=0.32(+)).

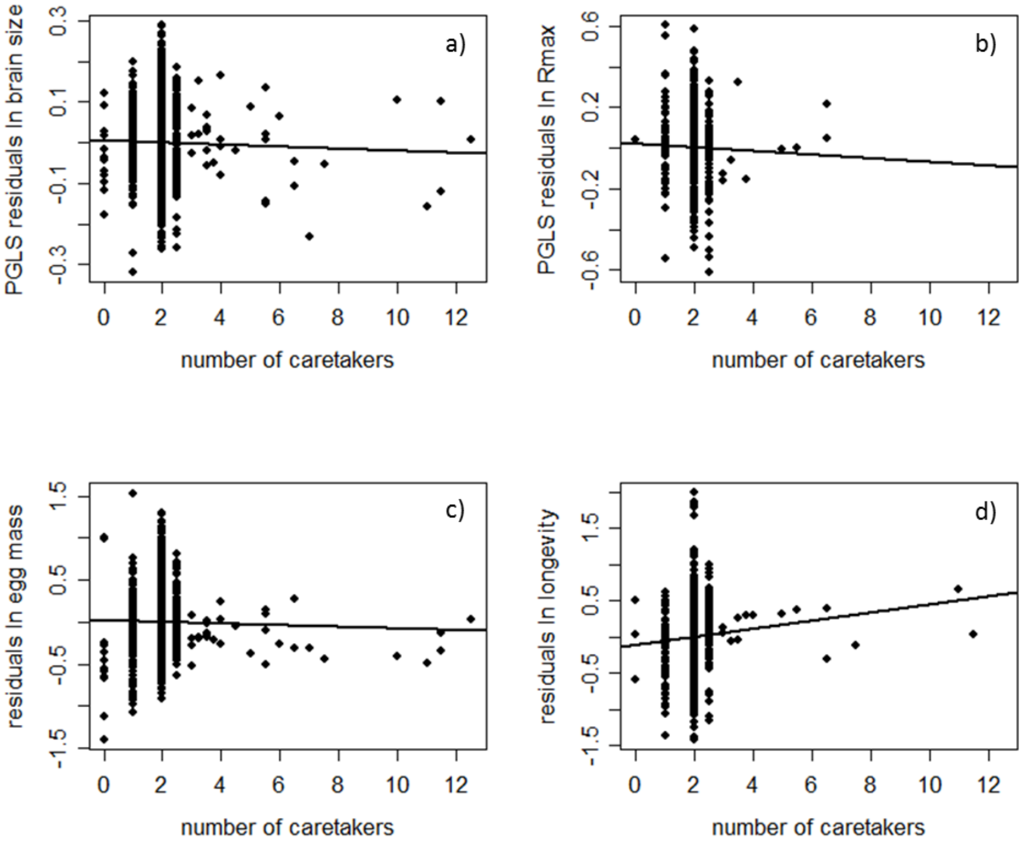


Figure 3.10: **Effects of number of caretakers.** a) Least-square regressions of the residuals of ln brain mass on number of caretakers (PGLS: n = 1413, p=0.78(+)) (residuals of ln brain mass indicate phylogenetic residuals corrected for body mass and development mode). b) Least-square regressions of the residuals of ln $r_{max}$ (phylogenetic residuals corrected for body mass and development mode) on number of caretakers (PGLS: n = 421, p=0.78(+)). c) Least-square regressions of the residuals of ln egg mass (corrected for body mass) on number of caretakers (PGLS: n = 1280, p=0.3 (-)). d) Least-square regressions of the residuals of ln longevity (corrected for body mass) on number of caretakers (PGLS: n = 618, p=0.1(+)).

Table 3.13: Multiple PGLS regressions and GLS regressions of familiy means of ln brain mass, ln r$_{max}$, ln fertility, ln clutch size, ln egg mass, ln longevity and ln total energy invested during the chick rearing period of all caretakers (E$_{sum(chick-rearing)}$), number of caretakers, breeding type (ln brain mass, ln r$_{max}$, ln fertility, ln clutch size, ln egg mass, ln longevity as dependent variables; ln total energy, number of caretakers, breeding type as well as ln body mass and development mode as independent variables). In the analyses including total energy, additionally brain mass and FMR$_{non-breeding}$ are included as covariates. Given are the sample size (n), multiple r$^2$, Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | **total energy** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | method | n | r$^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **brain size** | PGLS | 59 | 0.96 | 1 | 0.905, NA | *0.0006* | 0.09 | *<0.0001* | 0.52 | *0.001* | 0.13 |
| | GLM family means | 34 | 0.58 | - | - | 0.2 | -0.19 | *0.001* | 0.57 | *0.03* | -0.28 |
| **r$_{max}$** | PGLS | 42 | 0.17 | 0.98 | 0.732, NA | *0.03* | -0.27 | 0.41 | 0.1 | 0.78 | 0.04 |
| | GLM family means | 26 | 0.63 | - | - | *0.001* | -0.44 | 0.48 | 0.09 | 0.84 | 0.02 |
| **fertility** | PGLS | 56 | 0.28 | 0.96 | 0.795, NA | *0.0006* | -0.27 | 0.26 | 0.09 | 0.76 | 0.03 |
| | GLM family means | 33 | 0.59 | - | - | *0.00001* | -0.44 | 0.16 | 0.15 | 0.99 | 0.0001 |
| **clutch size** | PGLS | 59 | 0.04 | 1 | 0.888, NA | 0.65 | -0.03 | 0.37 | 0.06 | 0.19 | -0.13 |
| | GLM family means | 33 | 0.23 | - | - | *0.05* | -0.2 | 0.57 | 0.06 | *0.23* | -0.12 |
| **egg mass** | PGLS | 59 | 0.94 | 1 | 0.934, NA | *0.0001* | 0.15 | *<0.0001* | 0.59 | *0.01* | -0.14 |
| | GLM family means | 33 | 0.97 | - | - | *0.0001* | 0.28 | *<0.0001* | 0.54 | 0.008 | -0.16 |
| **longevity** | PGLS | 47 | 0.44 | 0 | NA, 0.676 | 0.32 | 0.1 | 0.32 | 0.1 | 0.27 | -0.07 |
| | GLM family means | 30 | 0.49 | - | - | 0.14 | 0.12 | 0.43 | 0.07 | 0.56 | -0.04 |

(to be continued)

|  |  |  |  |  |  | **number of caretakers** |  | **body mass** |  | **development** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  | method | n | r$^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **brain mass** | PGLS | 1413 | 0.87 | 0.95 | 0.925, 0.971 | 0.78 | 0.002 | *0.0001* | 0.59 | *0.0001* | 0.08 |
|  | GLM family means | 160 | 0.96 | - | - | 0.23 | 0.02 | *<0.0001* | 0.6 | *<0.0001* | 0.2 |
| **r$_{max}$** | PGLS | 421 | 0.19 | 0.99 | 0.965, NA | 0.78 | 0.01 | *<0.0001* | -0.22 | 0.21 | -0.07 |
|  | GLM family means | 89 | 0.37 | - | - | 0.59 | -0.07 | *<0.0001* | -0.24 | 0.24 | -0.08 |
| **fertility** | PGLS | 1091 | 0.05 | 0.96 | 0.936, 0.979 | *0.04* | 0.04 | *<0.0001* | -0.12 | *0.005* | -0.13 |
|  | GLM family means | 141 | 0.17 | - | - | 0.79 | 0.02 | *<0.0001* | -0.18 | *0.009* | -0.16 |
| **clutch size** | PGLS | 1353 | 0.05 | 0.98 | 0.960, 0.993 | 0.15 | 0.02 | *<0.0001* | -0.07 | *<0.0001* | -0.23 |
|  | GLM family means | 159 | 0.08 | - | - | 0.97 | 0.002 | *0.008* | -0.07 | *0.0008* | -0.15 |
| **egg mass** | PGLS | 1280 | 0.83 | 0.99 | 0.983, NA | 0.3 | -0.01 | *<0.0001* | 0.65 | *<0.0001* | -0.14 |
|  | GLM family means | 159 | 0.96 | - | - | 0.25 | -0.03 | *<0.0001* | 0.75 | *0.0002* | -0.1 |
| **longevity** | PGLS | 618 | 0.18 | 0.75 | 0.609, 0.854 | 0.1 | 0.04 | *<0.0001* | 0.22 | 0.41 | -0.04 |
|  | GLM family means | 113 | 0.55 | - | - | 0.08 | 0.07 | *<0.0001* | 0.22 | 0.96 | 0.002 |

|  |  |  |  |  |  | **breeding type** |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | p-value | slope |  |  |  |  |
| **brain mass** | PGLS | 1470 | 0.87 | 0.97 | 0.943, 0.983 | 0.33 | -0.01 | *<0.0001* | 0.59 | *<0.0001* | 0.07 |
|  | GLM family means | 168 | 0.96 | - | - | 0.39 | 0.04 | *<0.0001* | 0.6 | *<0.0001* | 0.2 |
| **r$_{max}$** | PGLS | 439 | 0.2 | 0.98 | 0.954, NA | 0.91 | 0.005 | *<0.0001* | -0.22 | 0.23 | -0.06 |
|  | GLM family means | 91 | 0.36 | - | - | 0.95 | 0.01 | *<0.0001* | -0.24 | 0.18 | -0.09 |
| **fertility** | PGLS | 1156 | 0.04 | 0.96 | 0.941, 0.981 | 0.38 | 0.03 | *<0.0001* | -0.11 | *0.01* | -0.11 |
|  | GLM family means | 148 | 0.17 | - | - | 0.54 | -0.08 | *<0.0001* | -0.19 | *0.005* | -0.17 |
| **clutch size** | PGLS | 1411 | 0.05 | 0.99 | 0.980, NA | 0.43 | 0.02 | *<0.0001* | -0.06 | *<0.0001* | -0.22 |
|  | GLM family means | 167 | 0.08 | - | - | 0.81 | -0.02 | *0.008* | -0.07 | *0.001* | -0.15 |
| **egg mass** | PGLS | 1336 | 0.84 | 1 | 0.994, NA | *0.005* | -0.04 | *<0.0001* | 0.65 | *<0.0001* | -0.12 |
|  | GLM family means | 165 | 0.96 | - | - | 0.2 | -0.08 | *<0.0001* | 0.75 | *0.001* | -0.1 |
| **longevity** | PGLS | 647 | 0.19 | 0.77 | 0.641, 0.867 | *0.05* | 0.1 | *<0.0001* | 0.23 | 0.35 | -0.04 |
|  | GLM family means | 113 | 0.54 | - | - | 0.61 | 0.06 | *<0.0001* | 0.22 | 0.98 | 0.001 |

**Prediction Hypothesis 3 b**: The lower the energetic load per caretaker (in this case only mother or father), the more energy they are able to invest in maintenance of their own brains. A negative correlation between the total energetic load per breeding parent and relative brain size and positive correlation between the energetic load per caretaker and reproduction ($r_{max}$ or fertility) are predicted.

**Results Hypothesis 3 b**: Contrarily to my initial prediction, relative brain size turned out to be positively correlated with total energetic load per caretaker (considering the total length of chick rearing), (figure 3.11, table 3.14). Even after additionally controlling for the effect of the duration of chick rearing period (=TFF), energetic load per caretaker still positively correlates with relative brain size (PGLS regression: n=59 multiple $r^2$=0.96; energy per caretaker: slope=0.08, p=0.01, corrected for body size, development mode and the duration of chick rearing period).
Furthermore, reproduction ($r_{max}$, annual fertility) shows a negative trend with the energetic load per caretaker, whereas egg mass shows a positive correlation (table 3.14). In other words, the more energy each caretaker invests during the chick rearing period, the larger the adult relative brain size and egg size, whereas number of offspring decreases with increasing energetic investment.
For comparative purpose, I also looked at the effect of daily energy expenditure during the non-breeding season ($FMR_{non-breeding}$) on relative brain size, using the biggest common sample. I found no correlation between relative brain size and $FMR_{non-breeding}$ (PGLS regression: n=49 multiple $r^2$=0.95; $FMR_{non-breeding}$: slope=0.07, p=0.24, corrected for body size, development mode and the factor flight).

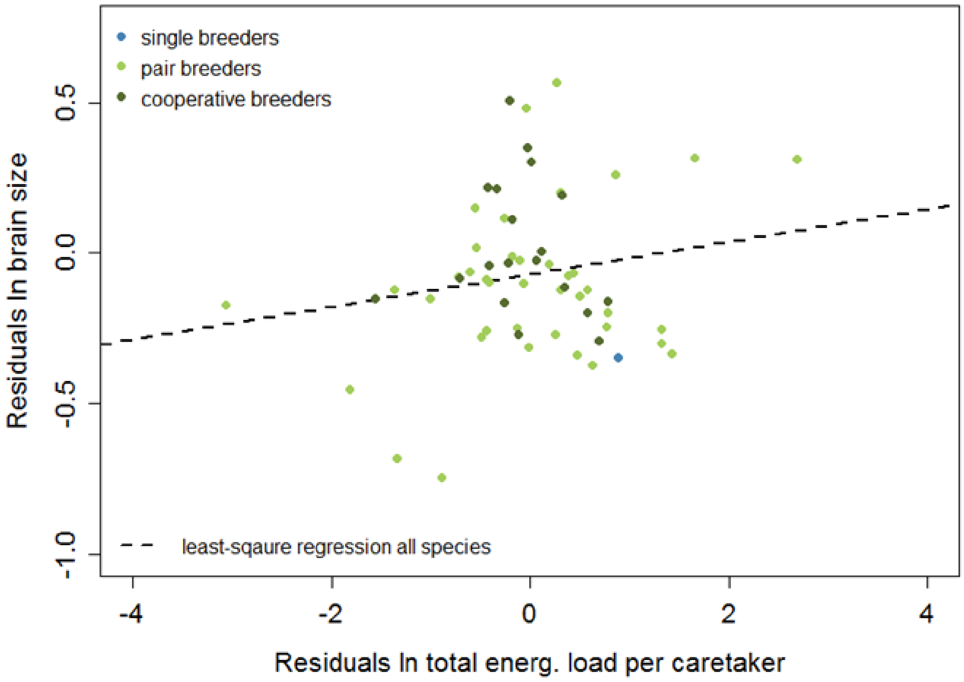


Figure 3.11: **Brain size vs. total energetic load per caretaker.** Least-square regression of the residuals of ln brain mass on the residuals of ln total energetic load per caretaker per chick rearing period (PGLS: n=60, p=0.0007(+) ). The residuals indicate correction for body size.

Table 3.14: PGLS regressions of ln brain mass, ln $r_{max}$, ln annual fertility, ln clutch size, ln egg mass, ln longevity and ln energetic load per caretaker (ln brain mass, ln $r_{max}$, ln annual fertility, ln clutch size, ln egg mass, ln longevity as dependent variables and ln energetic laod per caretaker as well as ln body mass and development as independent variables). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | **energ. load per caretaker** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **brain mass** | 60 | 0.96 | 1 | 0.903, NA | *0.0007* | 0.09 | *<0.0001* | 0.52 | *0.0007* | 0.14 |
| $\mathbf{r}_{max}$ | 42 | 0.18 | 0.98 | 0.724, NA | *0.03* | -0.28 | 0.34 | 0.12 | 0.89 | 0.02 |
| **fertility** | 57 | 0.29 | 0.96 | 0.807, NA | *0.0004* | -0.28 | 0.18 | 0.11 | 0.99 | -0.0005 |
| **clutch size** | 60 | 0.05 | 1 | 0.892, NA | 0.38 | -0.06 | 0.22 | 0.09 | 0.13 | -0.14 |
| **egg mass** | 60 | 0.94 | 1 | 0.940, NA | *<0.0001* | 0.16 | *<0.0001* | 0.58 | *0.02* | -0.12 |
| **longevity** | 46 | 0.44 | 0 | NA, 0.681 | 0.41 | 0.08 | 0.24 | 0.12 | 0.31 | -0.06 |

**Prediction Hypothesis 3 c**: Offspring which are bred in presence of additional amount of allomaternal care are expected to receive higher amount of energy. The total energetic input per offspring is predicted to correlate positively with relative brain size.

**Results Hypothesis 3 c**: As expected, I found that relative adult brain size correlates positively with total energetic investment per offspring per chick rearing period (PGLS regression: n=59 multiple $r^2$=0.95; energy per offspring: slope=0.06, p=0.01, corrected for body size and development mode) (figure 3.12)). After correcting for the effect of duration of the chick rearing period, the energetic input per offspring still shows a positive trend with relative brain size (PGLS regression: n=59 multiple $r^2$=0.96; energy per offspring: slope=0.05, p=0.09, corrected for body size, development mode and duration of the chick rearing period).

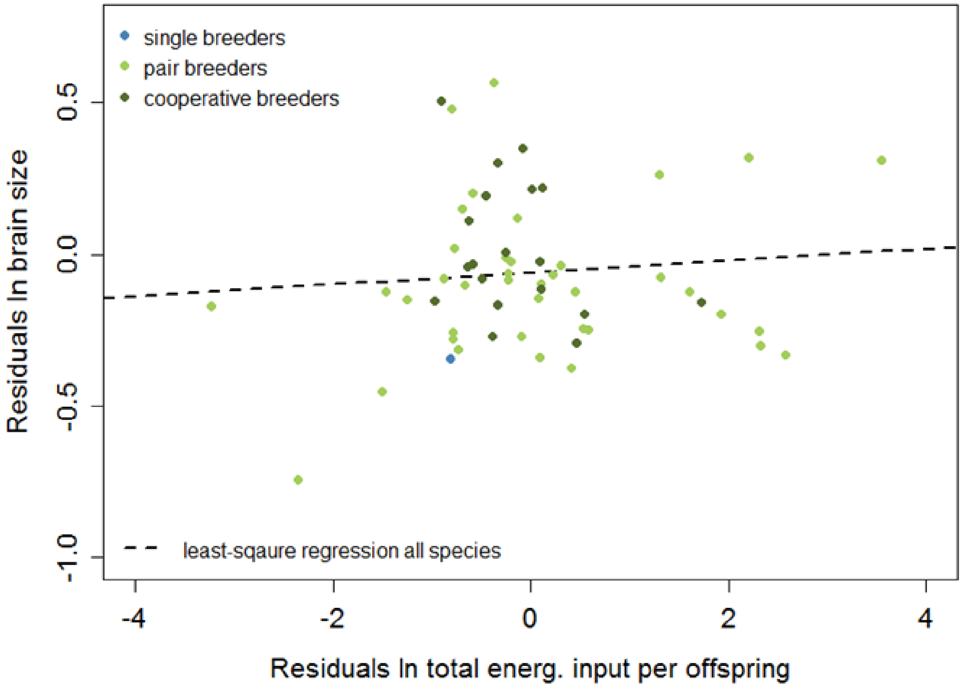


Figure 3.12: **Brain size vs. total energetic input per offspring.** Least-square regression of the residuals of ln brain mass on the residuals of ln total energetic input per offspring (PGLS: n=59, p=0.01(+)). The residuals indicate correction for body size.

## 3.5 Energy subsidies, egg mass and altriciality

**Prediction Hypothesis 4a**: Additional amount of allomaternal care in form of mate feeding during egg production, egg laying and incubation is expected to either positively correlate with egg mass or brain mass. If egg mass positively correlates with mate feeding (dummy variable): the extra energy from mate feeding is invested in egg mass. If brain mass positively correlates with mate feeding (dummy variable): the extra energy from mate feeding is rather invested in brain size. If both, egg mass and brain mass are correlated with mate feeding, the extra energy is invested in both.

**Results Hypothesis 4 a**: Over all, after correcting for the effects of body mass and development mode, I found egg mass to correlate positively with relative brain size (PGLS regression: n=1492; multiple $r^2=0.86$; brain mass: slope=0.51, p=<0.0001, corrected for body size and development mode).
I found a weak positive trend between egg mass and the factor mate feeding (dummy variable: 0 = no mate feeding; 1 = mate feeding) if brain size and duration of incubation is held constant (PGLS regression: n=258; multiple $r^2=0.87$; mate feeding: slope=0.14, p=0.12, corrected for body size and development mode, duration of incubation and brain mass). However, relative brain size shows a slight negative trend with mate feeding (PGLS regression: n=258; multiple $r^2=0.91$; mate feeding: slope=-0.12, p=0.11, corrected for body size and development mode, duration of incubation and egg mass). In other words, species with mate feeding have rather large eggs than large brains. The difference between species with mate feeding and without mate feeding concerning egg mass and brain size is shown in figure 3.13 a,b. Further, after correcting for life history pace and a few other covariates, incubation duration positively correlates with mate feeding (PGLS regression: n=139; multiple $r^2=0.39$; mate feeding: slope=0.17, p=0.009, corrected for body size, brain size, development mode, and maximum lifespan).
However, it seems strange that mate feeding shows a positive trend on relative egg size, but a negative one on brain size, because among each other, these two variables show a strong positive correlation. If including brain mass and egg mass as covariates, respectively, the effect of mate feeding on brain and egg mass probably disappears. Therefore, I ran the analyses without additionally including brain and egg mass as covariates, which reassures the findings from above. Using the exact same sample, mate feeding shows no effect on adult relative brain size, whereas with egg size a significant positive effect is observed (PGLS regression (brain mass): n=283; multiple $r^2=0.89$; mate feeding: slope=-0.02, p=0.82, corrected for body size and development mode). (PGLS regression (egg mass): n=283; multiple $r^2=0.85$; mate feeding: slope=0.19, p=0.02, corrected for body size and development mode). Among each other, relative brain and egg mass show a strong positive correlation (PGLS regression: n=283; multiple $r^2=0.91$; egg mass: slope=0.33, $p<0.0001$, corrected for body size and development mode).
Moreover, I have found that the energetic expenditures during incubation tend to be lower than during feeding the offspring (paired t-test: n=65,t=1.6, p=0.11).

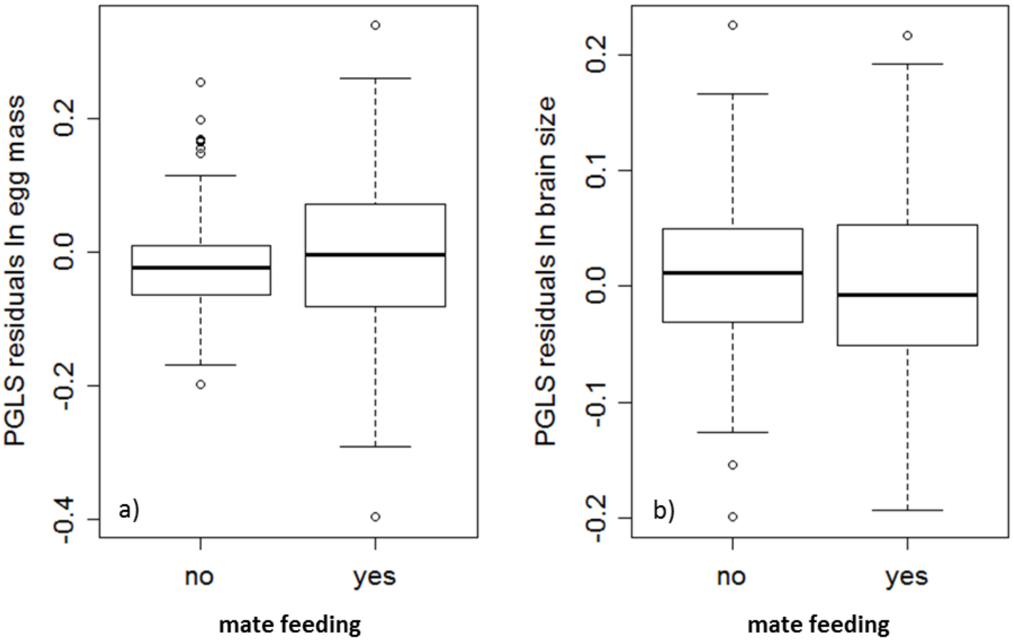


Figure 3.13: **Brain and egg size vs. mate feeding.** a) PGLS residuals of ln egg mass for species having no mate feeding (n = 43) and for species with mate feeding (n = 242) (PGLS regression: n=283, p=0.03(+)). b) PGLS residuals of ln brain mass for species with mate feeding (n = 33) and species without mate feeding (n = 224) (PGLS regression: n=283, p=0.83(-)). The horizontal lines in the boxes represents the median, the hinges represent the 25% and 75% quartiles. The whiskers indicate the 1.5*interquartile range and blank data points represent outliers.

**Prediction Hypothesis 4 b**: According to the study of Russel et al. (2007), a negative correlation between the amount of allomaternal care and egg mass is predicted on an interspecific level.

**Results Hypothesis 4 b**: According to a study of Russel et al. (2007), I expected a negative correlation between egg mass and the amount of allomaternal care at an interspecific level. I looked at the relationship between egg mass and total energetic investment per incubation/chick rearing period, number of caretakers or breeding type (using multiple PGLS regressions and GLS regression with family means): number of caretakers as well as breeding type show very slight negative trends with egg mass after correcting for body mass, development mode, brain size and incubation duration (model D and E; table 3.15), which is rather supportive of the proposed hypothesis (figure 3.14 c,d). In contrast, total energetic investment per chick rearing period ($E_{sum(chick-rearing)}$) showed to have a positive effect on egg mass using GLS regression based on family means (model A; table 3.15) (figure 3.14 b). Furthermore, the total energy invested during incubation ($E_{sum(incubation)}$) as well showed a positive trend with egg mass using PGLS regression (model B; table 3.15) (figure 3.14 a). In sum, the different measurements for the amount of allomaternal care show no consistent pattern. Number of caretakers and breeding type rather show a negative relationship with egg mass, whereas egg mass and energy input during incubation or the chick rearing period rather show positive relationships.

Moreover, I looked at whether time or energy drives the strong positive trend between egg mass and energetic effort during incubation. In fact, the positive trend can be attributed to both a positive relationship between the duration of incubation (figure 3.14 e) as well as the daily energy spent during incubation. In fact, if correcting for the duration of incubation, total energetic investment during incubation still shows a significant effect on egg mass (PGLS regression: n=54; multiple $r^2$=0.97; duration of incubation: slope=0.66, p=<0.0001; total energy incubation: slope=0.05, p=0.04, corrected for body size, brain size and development mode). Moreover, the daily energetic investment during incubation (non-estimated data) negatively correlates with duration of incubation (PGLS regression: n=27; multiple $r^2$=0.97; duration of incubation: slope=-0.71, p=0.003, corrected for body size, BMR and development mode) (figure 3.14 f).
In summary, I did not find a consistent pattern across the different quantifications of allomaternal care. The number of caretakers and breeding type show rather negative trends with egg mass, whereas the energetic measurement of the amount of allomaternal care rather shows a trend in the opposite direction.

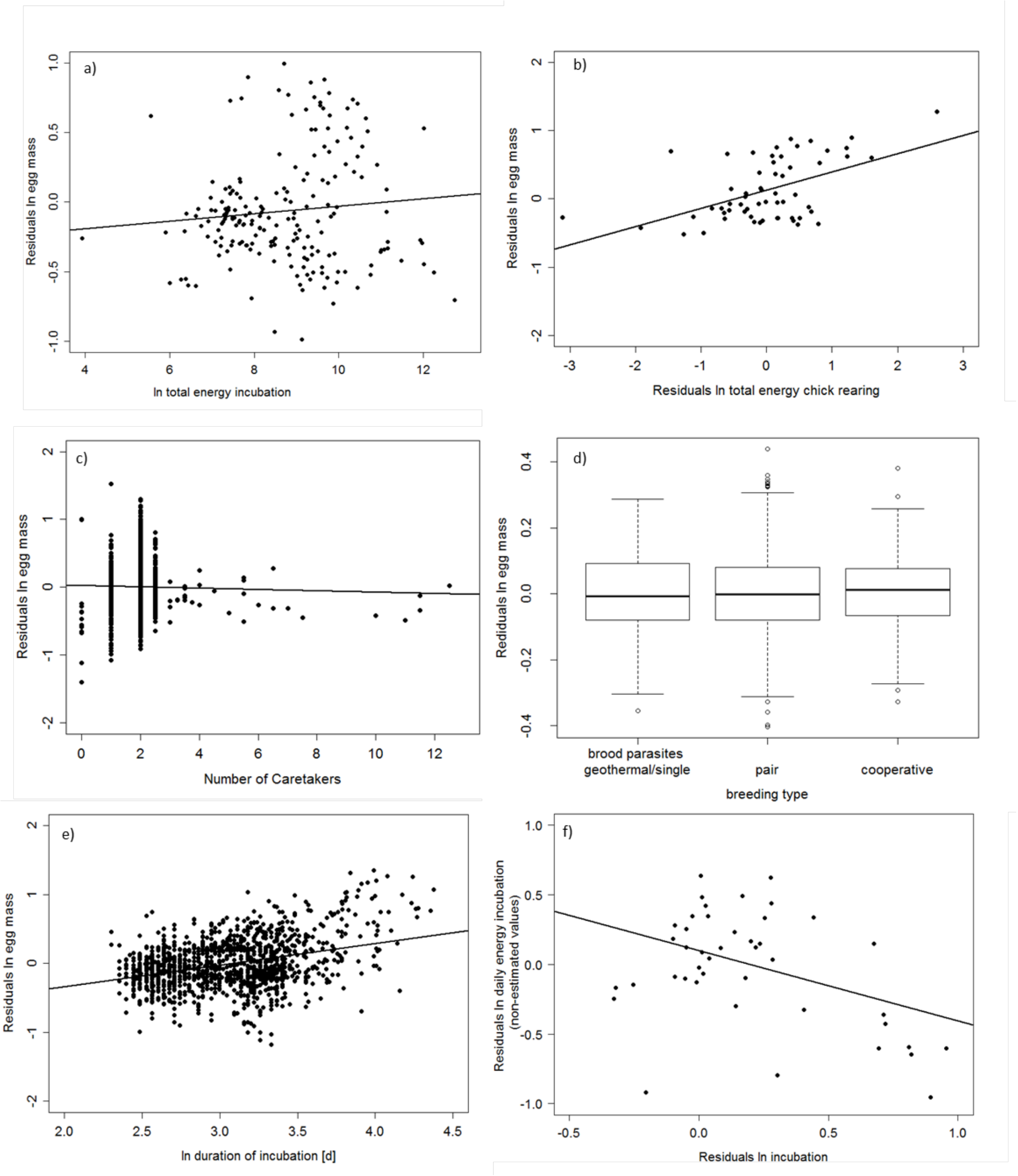


Figure 3.14: **Effects on egg size.** a) Least-square regression of the residuals of ln egg mass (non-phylogenetic, corrected for body mass) on ln total energetic input during incubation (estimated values) (PGLS: n = 197, p=0.05(+)). b) Least-square regression of the residuals of ln egg mass (non-phylogenetic, corrected for body mass) on the residuals of ln total energetic input during the chick rearing period (non-phylogenetic, corrected for body mass) (PGLS: n = 59, p=0.26(+)). c) Least-square regression of the residuals of ln egg mass (non-phylogenetic, corrected for body mass) on the absolute number of caretakers (PGLS: n = 1131, p=0.11(-)). d) Boxplots of the residuals of ln egg mass (phylogenetic residuals corrected for body mass, brain mass and development mode) for the 3 different breeding types: brood parasites, geothermal and single breeders (n = 155), pair breeders (n = 975) and cooperative breeders (n = 241) (The horizontal lines in the boxes represents the median, the hinges represent the 25% and 75% quartiles. The whiskers indicate the 1.5*interquartile range and blank data points represent outliers). (PGLS: n=1194, p=0.14(-)). e) Least-square regression of the residuals of ln egg mass (non-phylogenetic, correctied for body mass) on ln duration of incubation (PGLS: n = 54, p<0.0001(+)). f) Least-square regression of the residuals of ln daily energy invested during incubation (non-estimated values) (non-phylogenetic, corrected for body mass) on the residuals of ln duration of incubation (non-phylogenetic, corrected for body mass) (PGLS: n = 27, p=0.003(-)).

Table 3.15: Multiple PGLS regressions and GLS regressions of familiy means of ln egg mass and ln total energy input during the chick rearing period (estimated data), ln total energy input during the incubation period (estimated data), ln daily energy input during incubation (estimated data), number of caretakers and breeding type (ln egg mass as independent variable and ln total energy chick rearing, ln total energy incubation, ln daily energy input during incubation, number of caretakers, breeding type as well as ln body mass, development mode, ln brain mass and ln incubation duration as independent variables). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | **total energy chick rearing** | | **body mass** | | **development** | | **brain size** | | **incubation duration** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | method | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **model A** | PGLS | 59 | 0.96 | 1 | 0.907, NA | 0.26 | 0.04 | *0.0001* | 0.35 | *0.002* | -0.16 | *0.005* | 0.45 | *0.0001* | 0.56 |
| | GLS family means | 33 | 0.97 | | | 0.001 | 0.23 | 0.0004 | 0.53 | 0.03 | -0.15 | 0.74 | 0.08 | 0.03 | 0.27 |
| **model B** | | | | | | **total energy incubation** | | | | | | | | | |
| | | | | | | p-value | slope | | | | | | | | |
| | PGLS | 197 | 0.93 | 0.94 | 0.856, 0.983 | 0.05 | 0.05 | *0.0001* | 0.45 | *0.009* | -0.09 | *0.005* | 0.23 | *0.0001* | 0.72 |
| | GLS family means | 68 | 0.95 | | | 0.27 | 0.08 | *0.0001* | 0.53 | 0.01 | -0.15 | 0.14 | 0.26 | 0.03 | 0.23 |
| **model C** | | | | | | **daily energy incubation** | | | | | | | | | |
| | | | | | | p-value | slope | | | | | | | | |
| | PGLS | 197 | 0.93 | 0.94 | 0.856, 0.983 | 0.05 | 0.05 | *0.0001* | 0.45 | 0.009 | -0.09 | 0.005 | 0.23 | *0.0001* | 0.76 |
| | GLS family means | 68 | 0.95 | | | 0.22 | -0.08 | *<0.0001* | 0.58 | 0.007 | -0.13 | <0.0001 | 0.35 | 0.05 | 0.21 |
| **model D** | | | | | | **number of caretakers** | | | | | | | | | |
| | | | | | | p-value | slope | | | | | | | | |
| | PGLS | 1131 | 0.89 | 0.99 | 0.977, NA | 0.11 | -0.01 | *<0.0001* | 0.36 | *<0.0001* | -0.17 | *<0.0001* | 0.43 | *<0.0001* | 0.38 |
| | GLS family means | 151 | 0.96 | - | - | 0.14 | -0.04 | *<0.0001* | 0.55 | *<0.0001* | -0.17 | *0.008* | 0.31 | 0.1 | 0.11 |
| **model E** | | | | | | **breeding type** | | | | | | | | | |
| | | | | | | p-value | slope | | | | | | | | |
| | PGLS | 1194 | 0.88 | 1 | 0.990, NA | 0.14 | -0.02 | *<0.0001* | 0.35 | *<0.0001* | -0.15 | *<0.0001* | 0.45 | *<0.0001* | 0.37 |
| | GLS family means | 159 | 0.96 | - | - | 0.1 | -0.1 | *<0.0001* | 0.53 | *<0.0001* | -0.17 | *0.003* | 0.35 | 0.28 | 0.07 |

**Prediction Hypothesis 4 c**: The more additional amount of allomaternal help is available during the chick rearing period, the more precocial species are predicted to show altricial characteristics such as relatively smaller eggs and clutch sizes or shorter incubation periods (shift towards altriciality).

**Results Hypothesis 4 c**: For precocial species with high amounts of allomaternal care I expected a shift towards altriciality. Within **precocial** species, this should be reflected in negative relationships between egg mass, clutch size or incubation duration and amount of allomaternal care (total energetic investment during chick rearing period, number of caretakers or breeding type). In fact, egg mass and incubation duration correlate positively with number of helpers (figure 3.15 a) or breeding type. Using GLS family means, clutch size shows a slight negative trend with number of caretakers (table 3.16) (unfortunately, sample sizes are too small to investigate a shift towards altriciality using energetic investment as a measurement of allomaternal care). Within **altricial** species no clear pattern is found: they show no relationships between egg mass incubation duration and number of caretakers (figure 3.15 b)) or breeding type. Only when using family means in a GLS regression, egg mass shows a weak negative trend with breeding type. Clutch size positively correlates with number of caretakers and breeding type (table 3.16). However, with increasing number of caretakers, all the effects at least show the predicted direction towards stronger altriciality. In precocial species, this shows that higher amount of allomaternal care is linked to larger eggs and longer incubation durations and in altrcials, higher amount of allomaternal care results in larger clutch sizes.

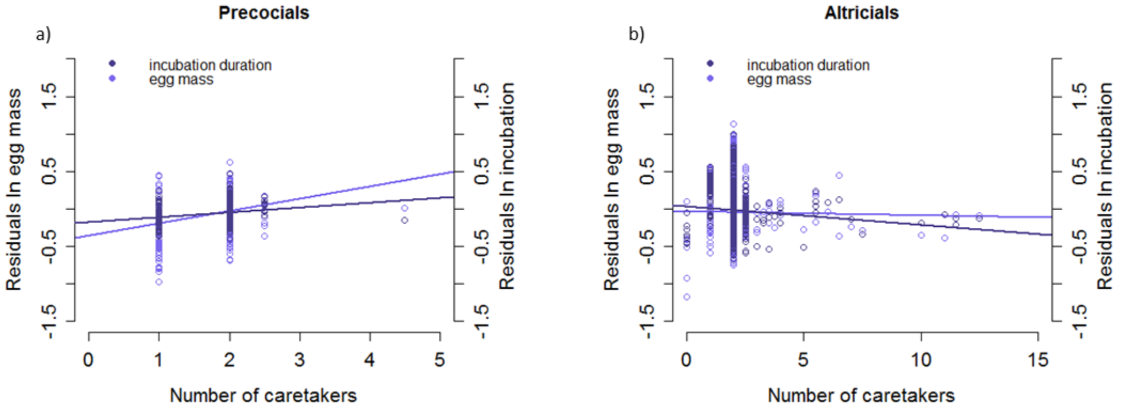


Figure 3.15: **Effect of number of caretakers on altriciality.** a) Least-square regressions of the residuals of ln egg mass and ln incubation duration on number of caretakers for precocial bird species (PGLS (incubation duration): n = 233, p=0.0003(+) ; PGLS (egg mass): n = 233, p=0.006(+)). b) Analogous to a) for altricial bird species (PGLS(incubation duration): n = 675, p=0.9(+); PGLS (egg mass): n = 678, p=0.19(-) ). All residuals indicate correction for body mass and brain mass.

Table 3.16: Multiple PGLS regressions and GLS regressions of familiy means of ln egg mass, ln clutch size, ln duration of incubation and number of caretakers or breeding type as well as ln body mass and ln brain mass separately analysed for precocials and altricials (ln egg mass, ln clutch size and ln duration of incubation as dependent variables and number of caretkaers, breeding type, ln body mass and ln brain mass as independent variables). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | | **number of caretakers** | | **breeding type** | | **body mass** | | **brain mass** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| **precocials** | **egg mass** | PGLS | 233 | 0.87 | 1 | 0.974, NA | *0.006* | 0.08 | - | - | *<0.0001* | 0.39 | *<0.0001* | 0.46 |
| | | | 233 | 0.87 | 1 | 0.973, NA | - | - | *0.009* | 0.09 | *<0.0001* | 0.4 | *<0.0001* | 0.45 |
| | | GLS fam. means | 22 | 0.31 | - | - | *0.63* | 0.07 | | | *0.27* | 0.22 | *0.02* | 0.86 |
| | | | 26 | 0.95 | - | - | - | - | *0.17* | -0.18 | *0.85* | -0.04 | *0.0005* | 1.36 |
| | **clutch size** | PGLS | 233 | 0.03 | 1 | 0.965, NA | 0.35 | -0.04 | - | - | *0.03* | 0.14 | *0.02* | -0.29 |
| | | | 233 | 0.03 | 1 | 0.966, NA | - | - | 0.19 | -0.06 | *0.03* | 0.14 | *0.02* | -0.28 |
| | | GLS fam. means | 22 | 0.55 | - | - | *0.09* | -0.35 | | | *0.01* | 0.75 | *0.03* | -1.16 |
| | | | 26 | 0.52 | - | - | | | 0.52 | -0.1 | *0.0004* | 0.96 | *0.0001* | -1.55 |
| | **duration incubation** | PGLS | 233 | 0.36 | 1 | 0.965, NA | *0.0003* | 0.06 | - | - | *0.02* | 0.06 | 0.15 | 0.06 |
| | | | 233 | 0.37 | 1 | 0.968, NA | - | - | *<0.0001* | 0.07 | *0.009* | 0.06 | 0.22 | 0.05 |
| | | GLS fam. means | 22 | 0.41 | - | - | *0.61* | -0.07 | | | *0.18* | -0.27 | 0.07 | 0.68 |
| | | | 26 | 0.2 | - | - | | | *0.94* | 0.01 | *0.84* | 0.04 | 0.8 | 0.09 |
| **altricials** | **egg mass** | PGLS | 675 | 0.87 | 1 | 0.989, NA | 0.19 | -0.009 | - | - | *<0.0001* | 0.41 | *<0.0001* | 0.41 |
| | | | 675 | 0.87 | 1 | 0.989, NA | - | - | 0.33 | -0.03 | *<0.0001* | 0.41 | *<0.0001* | 0.41 |
| | | GLS fam. means | 105 | 0.95 | - | - | *0.2* | -0.03 | | | *<0.0001* | 0.75 | *0.7* | 0.05 |
| | | | 108 | 0.95 | - | - | - | - | 0.13 | -0.11 | *<0.0001* | 0.76 | *0.85* | 0.02 |
| | **clutch size** | PGLS | 656 | 0.07 | 0.99 | 0.974, NA | *0.003* | 0.03 | - | - | 0.09 | 0.08 | *<0.0001* | -0.27 |
| | | | 656 | 0.08 | 0.99 | 0.974, NA | - | - | *<0.0001* | 0.18 | 0.14 | 0.07 | *0.0003* | -0.24 |
| | | GLS fam. means | 106 | 0.2 | - | - | *0.05* | 0.07 | | | 0.44 | -0.08 | *0.71* | -0.06 |
| | | | 109 | 0.26 | - | - | - | - | *0.0003* | 0.37 | 0.33 | -0.1 | *0.93* | -0.01 |
| | **duration incubation** | PGLS | 675 | 0.29 | 1 | 0.997, NA | 0.9 | 0.0006 | - | - | 0.71 | 0.007 | *<0.0001* | 0.16 |
| | | | 675 | 0.29 | 1 | 0.997, NA | - | - | 0.28 | -0.02 | 0.69 | 0.008 | *<0.0001* | 0.16 |
| | | GLS fam. means | 101 | 0.09 | - | - | *0.73* | -0.01 | | | 0.52 | 0.08 | *0.93* | 0.02 |
| | | | 104 | 0.1 | - | - | - | - | 0.41 | -0.09 | 0.41 | 0.09 | *0.93* | -0.02 |

## 3.6 Alternative hypotheses

Several alternative explanations exist to explain variation in relative brain size (1.2 Hypotheses explaining brain size variation).

**Prediction Development Hypothesis**: Relative brain size is expected to be bigger the more altricial the species, as there they are provisioned much more often by parents and helpers after hatching (e.g. Pagel and Harvey 1985 a,b).

- According to the energy subsidies hypothesis, including the amount of allomaternal care is predicted to yield a better statistical model than just including development mode alone.

**Results Development Hypothesis**: In general, it is known that altricial bird species have relatively larger brains than preocial bird species (Bennett and Harvey 1985a,b; Pagel and Harvey 1988; Starck and Ricklefs 1998; Iwaniuk and Nelson 2003) (PGLS regression (brain mass): n=1473 multiple $r^2$=0.86; development mode: slope=0.04, p=0.01, corrected for body size). Brain mass relative to body mass for the different development modes is shown in figure 3.16. However, assuming the energy subsidies hypothesis, I expected the amount of allomaternal care (energetic input (total input or per offspring), number of caretakers, breeding type) to have stronger effects on relative brain size than developmental aspects per se. After correcting for the effect of development mode, number of caretakers and breeding type showed no significant effect on relative brain size (model E and F; table 3.17). However, including the total energetic investment (model B: AIC = -40.79; table 3.17) and total energetic input per offspring (model C: AIC = -35.2; table 3.17) yielded better statistical models than only including development mode per se (model A: AIC = -29.99; table 3.17). In other words, if including development mode as a covariate in the PGLS model, brain size still positively correlates with total energetic input and total energetic input per offspring.

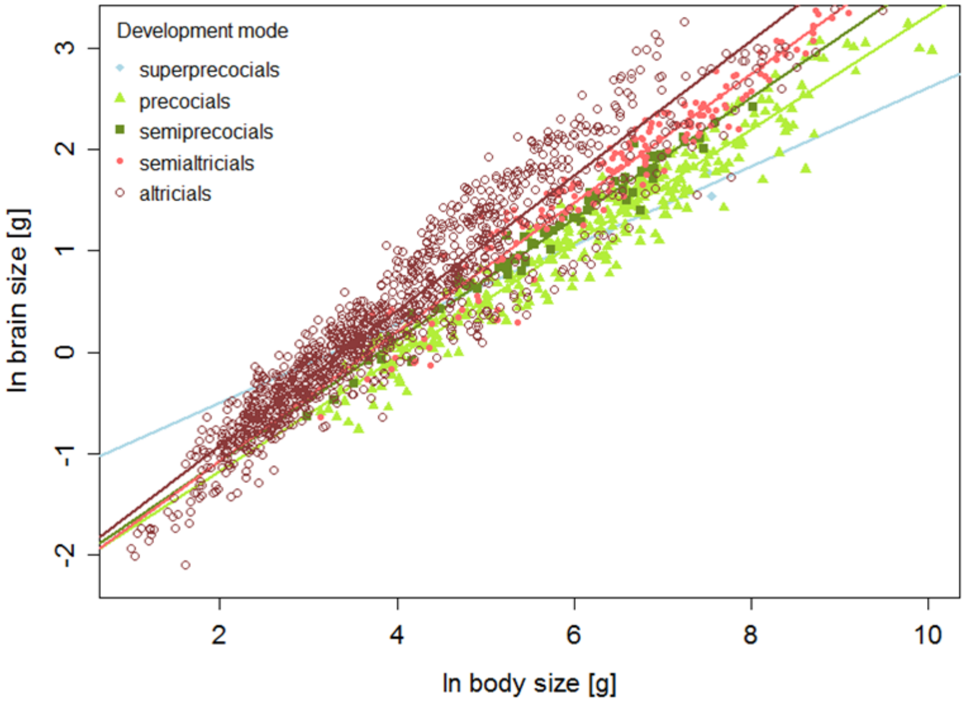


Figure 3.16: **Brain size vs. body size for different development modes.** Least-square regressions of ln brain mass on ln body size for the different development modes (superprecocials n = 4; semiprecocials n = 65; semialtricials n = 171; altricials n = 1153). PGLS regression brain mass vs. development mode, corrected for body size: n=1473, p=0.01.

Table 3.17: Multiple PGLS regressions for ln brain mass and ln total eneretic investment during the chick rearing period, ln total energetic input per offspring during the chick rearing period, number of caretakers, breeding type as well as ln body mass and development mode (ln brain mass as dependent variable; ln total energy, ln energy per offspring, number of caretakers, breeding type as well as ln body mass and development mode as independent variables). Given are the sample size (n), multiple r$^2$, Akaike information criterion (AIC), Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | **total energy** | | **development** | | **body mass** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | r$^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| **model A** | 59 | 0.95 | -29.99 | 1 | 0.923, NA | - | - | 0.01 | 0.11 | *<0.0001* | 0.61 |
| **model B** | 59 | 0.96 | -40.79 | 1 | 0.905, NA | *0.0006* | 0.09 | *0.001* | 0.13 | *<0.0001* | 0.52 |
| | | | | | | **energy per offspring** | | | | | |
| | | | | | | p-value | slope | | | | |
| **model A** | 59 | 0.95 | -29.99 | 1 | 0.923, NA | - | - | 0.01 | 0.11 | *<0.0001* | 0.61 |
| **model C** | 59 | 0.95 | -35.2 | 1 | 0.924, NA | *0.01* | 0.06 | *0.005* | 0.12 | *<0.0001* | 0.55 |
| | | | | | | **number of caretakers** | | | | | |
| | | | | | | p-value | slope | | | | |
| **model D** | 1318 | 0.87 | -917.98 | 0.96 | 0.932, 0.978 | - | - | *<0.0001* | 0.08 | *<0.0001* | 0.59 |
| **model E** | 1318 | 0.87 | -916.13 | 0.96 | 0.931, 0.978 | 0.7 | -0.002 | *<0.0001* | 0.08 | *<0.0001* | 0.59 |
| | | | | | | **breeding type** | | | | | |
| | | | | | | p-value | slope | | | | |
| **model D** | 1470 | 0.87 | -1028.88 | 0.97 | 0.949, 0.986 | - | - | *<0.0001* | 0.08 | *<0.0001* | 0.59 |
| **model F** | 1470 | 0.87 | -1032.44 | 0.97 | 0.943, 0.983 | 0.33 | -0.01 | *<0.0001* | 0.07 | *<0.0001* | 0.59 |

**Prediction Maternal Energy Hypothesis**: Assuming that the mother‘s energetic investment per offspring is strongly affecting relative brain size, a positive correlation between maternal energetic load per offspring and relative brain size of offspring would be expected (e.g. Martin 1981, 1996).

- As in most avian groups both parents (mother and father) are breeding, the total energetic input per offspring is predicted to stronger correlated with relative brain size than only the maternal energetic input per offspring.

**Results Maternal Energy Hypothesis**: Rather than the maternal investment I expected total input per offspring to have a stronger effect on relative brain size. Using the available energetic measurements (energetic maternal load, total energetic input per offspring measured as field metabolic rates in kJ) is not a proper way to differentially test for this hypothesis, because the two energetic variables are almost completely collinear (due to the calculations of these two measurements and the small sample size, see Material and Methods). Therefore, I used approximations for maternal and total energetic investment per offspring (see calculations in section 2.3.1, „Quantification of reproductive effort and allomaternal energy subsidies“). The PGLS regressions revealed that relative brain size shows no positive correlation with total or maternal input per offspring (table 3.18). The daily input per offspring even has a negative effect on relative brain size. Including both measurements, (daily) maternal and total (daily) input per offspring in the same model, does also not yield any significant effects, except for the negative effect of total daily input per offspring (table 3.19). In sum, PGLS regression models do not show a clear and consistent pattern.
However, the GLS regressions based on family means showed that relative brain size correlates more strongly with total input per offspring than with maternal input per offspring (table 3.18, figure 3.17). When including both measurements, total input as well as maternal input, in the same model, total input still positively affects relative brain size whereas maternal input per offspring shows a negative effect on relative brain size (table 3.19).

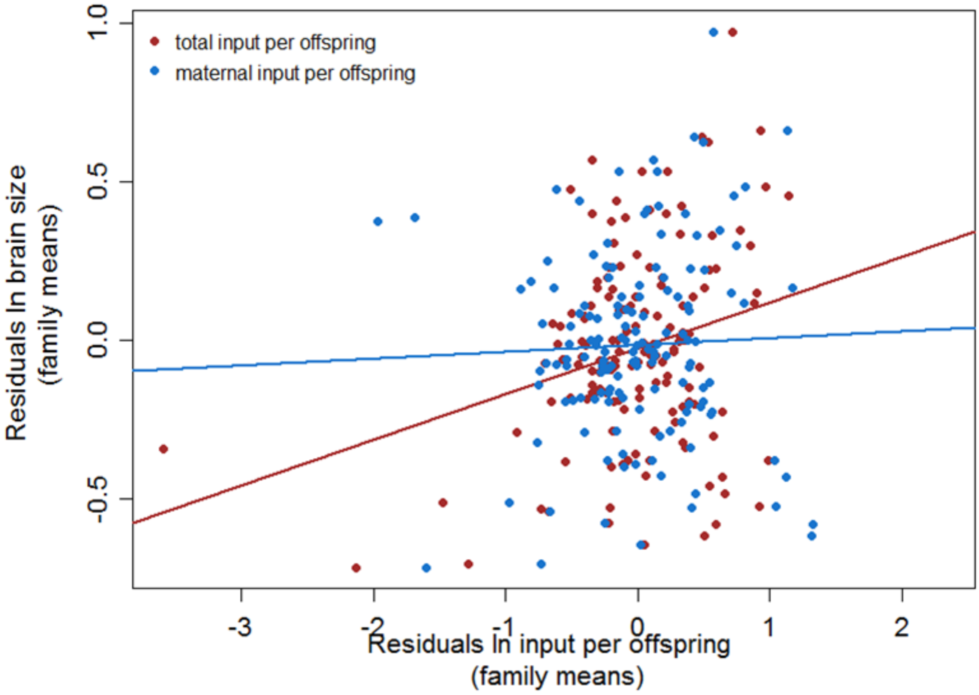


Figure 3.17: **Maternal vs. total energetic input.** Least-square regressions of the residuals of ln brain mass (family means) on the residuals of ln total (GLS family means: n=140, $p<0.0001(+)$) and maternal (GLS family means: n=140, $p=0.004(+)$) input per offspring (family means). All the residuals indicate correction for body mass.

Table 3.18: Multiple PGLS regressions and GLS regressions of family means for ln brain mass (dependent variable) and ln total input per offspring (= growth mass * TFF), ln maternal input per offspring ((growthmass * TFF)/number of caretakers), ln daily input per offspring (= growth mass), ln daily maternal input per offspring (= growthmass/number of caretakers) as well as ln body mass and development mode. Given are the sample size (n), multiple $r^2$, Akaike information criterion (AIC), Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics).

| | | | | | | **total input per offspring** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| method | n | $r^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| PGLS | 1003 | 0.87 | -693.81 | 0.97 | 0.942, 0.985 | 0.3 | 0.02 | *<0.0001* | 0.57 | *<0.0001* | 0.09 |
| GLS family means | 140 | 0.82 | 196.12 | - | - | *<0.0001* | 0.46 | 0.52 | -0.07 | 0.88 | 0.006 |
| | | | | | | **maternal input per offspring** | | | | | |
| | | | | | | p-value | slope | | | | |
| PGLS | 1003 | 0.87 | -690.63 | 0.97 | 0.942, 0.985 | 0.33 | 0.01 | *<0.0001* | 0.58 | *<0.0001* | 0.09 |
| GLS family means | 140 | 0.79 | 218.04 | - | - | *0.004* | 0.23 | *0.04* | 0.22 | 0.74 | 0.01 |
| | | | | | | **daily input per offspring** | | | | | |
| | | | | | | p-value | slope | | | | |
| PGLS | 1003 | 0.88 | -751.12 | 0.97 | 0.949, 0.990 | *<0.0001* | -1.31 | *<0.0001* | 1.95 | *<0.0001* | 0.1 |
| GLS family means | 140 | 0.89 | 127.56 | - | - | *<0.0001* | 3.27 | *<0.0001* | -2.79 | *0.023* | 0.07 |
| | | | | | | **daily maternal input per offspring** | | | | | |
| | | | | | | p-value | slope | | | | |
| PGLS | 1003 | 0.87 | -690.56 | 0.97 | 0.943, 0.986 | 0.35 | -0.02 | *<0.0001* | 0.62 | *<0.0001* | 0.09 |
| GLS family means | 140 | 0.78 | 226.61 | - | - | 0.64 | 0.06 | *0.001* | 0.46 | 0.82 | 0.01 |

Table 3.19: PGLS regressions and GLS regression of family means of ln brain mass and ln total input per offspring (= growth mass * TFF), ln maternal input per offspring ((growthmass * TFF)/number of caretakers), ln daily input per offspring (= growth mass), ln daily maternal input per offspring (= growthmass/number of caretakers) as well as ln body mass and development mode (ln brain mass as dependent variable; ln total input per offspring, ln daily input per offspring, ln maternal input per offspring, ln daily maternal input per offspring as well as body mass and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Akaike information criterion (AIC), Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics).

| | | | | | | **total input per offspring** | | **maternal input per offspring** | | **body mass** | | **development** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| method | n | $r^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| PGLS | 1003 | 0.87 | -688.93 | 0.97 | 0.942, 0.985 | 0.58 | 0.02 | 0.86 | 0.004 | *<0.0001* | 0.57 | *<0.0001* | 0.09 |
| GLS family means | 140 | 0.83 | 190.34 | - | - | *<0.0001* | 0.77 | *0.006* | -0.35 | 0.85 | -0.02 | 0.88 | -0.006 |
| | | | | | | **daily input per offspring** | | **daily maternal input per offspring** | | | | | |
| | | | | | | p-value | slope | p-value | slope | | | | |
| PGLS | 1003 | 0.88 | -749.28 | 0.97 | 0.950, 0.990 | *<0.0001* | -1.31 | 0.69 | -0.01 | *<0.0001* | 1.96 | *<0.0001* | 0.1 |
| GLS family means | 154 | 0.9 | 132.78 | - | - | *<0.0001* | 3.28 | *0.03* | -0.2 | *<0.0001* | -2.61 | *0.04* | 0.06 |

**Prediction Time vs. Energetic Constraints**: If mainly time constrains relative brain size (e.g. maturational constraint hypothesis), various time estimations in development such as incubation, pre-fledging, post-fledging parental care and time to independence are expected to correlate positively with encephalization. Time of first flight would be expected to correlate positively with relative brain size as well, as fledglings are much more dependent on help of parents and alloparental helpers in terms of feeding and protection during the time they are not able to fly. Further, time to adult size which seems to be especially important for superprecocial and precocial species leaving their nests right after hatching, is expected to be positively related to encephalization (assuming the later offspring reach adult size, the longer their brains need to grow and the longer they are provisioned by parents/helpers).

- I predict that differences in amount of allomaternal care (energetic investments per offspring, number of caretakers or breeding type) are responsible for variation in relative brain size rather than time constraints. Thus, I expect amount of allomaternal care (energetic input per offspring, number of caretakers or breeding type) to correlate stronger with relative brain size than the duration of parental care.

**Results Time vs. Energetic Constraints**: To disentangle between energetic and time constraints, I looked at the relationships between relative brain size and various time estimations in development compared to the correlation between relative brain size and energetic investment.
Relative brain size turned out to strongly correlate with almost all major time measurements in development of a young bird‘s life or at least shows a strong trend (corrected for body size and development mode) (table 3.20, figure 3.18 b)). This already suggests that time constraints are crucial to understand variation in relative brain size.

Table 3.20: Multiple PGLS regressions for ln brain mass and ln incubation, ln fledging, ln time of first flight (TFF), ln time until the young reached adult size, ln time until the young are fed from parents after they have left the nest, ln time of total parental care (fledging + feeding after nest) (ln brain mass as dependent variable; ln incubation, ln fledging, ln time of first flight (TFF), ln time to adult size, ln feeding after nest, ln total parental care as well as ln body mass and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | **brain mass** | | | | | |
|---|---|---|---|---|---|---|
| **time estimation in development** | n | $r^2$ | $\lambda$ | CI $\lambda$ | p-value | slope |
| incubation | 1389 | 0.87 | 0.96 | 0.938, 0.980 | *<0.0001* | 0.25 |
| fledging | 809 | 0.88 | 0.98 | 0.951, 0.992 | *0.002* | 0.03 |
| first flight (TFF) | 1259 | 0.87 | 0.97 | 0.944, 0.985 | 0.07 | 0.03 |
| time to adult size | 22 | 0.95 | 1 | NA, NA | 0.67 | -0.03 |
| feeding after nest | 396 | 0.89 | 0.98 | 0.955, 1 | 0.08 | 0.02 |
| total parental care | 258 | 0.9 | 0.98 | 0.950, NA | *0.003* | 0.03 |

However, what I wanted to investigate was whether duration of parental care per se is important or if rather energy is the crucial aspect for explaining the huge variation in relative brain size.
In precocial species the main brain growth occurs during embryonic development (during incubation), whereas in altricial species the main brain growth occurs after the embryonic phase, during the nestling period. Therefore, I looked at at precocial and altricial species separately, in precocial species comparing duration of incubation with energetic input during that period and in altricial species comparing nestling period (time of first flight or fledging) with energetic input during that period. According to the energy subsidies hypothesis, I expected the effect of amount of allomaternal care to be bigger than the effect of time estimations on relative brain size.

**Precocials**: A PGLS model where both, the effect of energetic input per egg per day (representing energy measurement being independent from time estimation) and the effect of the duration of incubation is included, suggests that for a constant amount of daily energy input, larger brains can be achieved by elongating the time of incubation (model B; table 3.21), and for a constant duration of incubation, a weak positive trend between daily energy input and brain size is observed. The same trends are found for total energetic input per incubation (model D, table 3.21). This would suggest, that both, energetic investment and duration of incubation, affect relative brain size. However, for a constant breeding type or number of helpers, a positive correlation or at least a trend between relative brain size and incubation duration (model F and H; table 3.21) was found, meaning that for a constant number of helpers, brain size increases with increasing duration of incubation.

**Altricials**: Including time of first flight as a covariate, daily and total energetic input per offspring during the chick rearing period show a strong trend towards a positive correlation with relative brain size (model B and F, table 3.22) (figure 3.18 a, b). This trend disappears in the smaller sample using time of fledging as a covariate (n=28) (model D and H, table 3.22). Moreover, for a constant number of helpers or breeding type, a positive correlation between relative brain size and TFF (model J and N; table 3.22) as well as a positive correlation between relative brain size and fledging (model L and P; table 3.22) were found. However, number of caretakers and breeding type do not show positive effects on relative brain size.

The models including additionally the amount of allomaternal care compared to the models including only time measurements of maternal/allomaternal care show no clear differences in the goodness of fit of the models (Akaike information criterion = AIC) (table 3.21 and 3.22). In other words, the PGLS models including the amount of allomaternal care are not better compared to models which only include time measurements of maternal/allomaternal care.

In sum, these results suggest that time as well as energetic input affects relative brain size and one might not completely exclude one or the other.

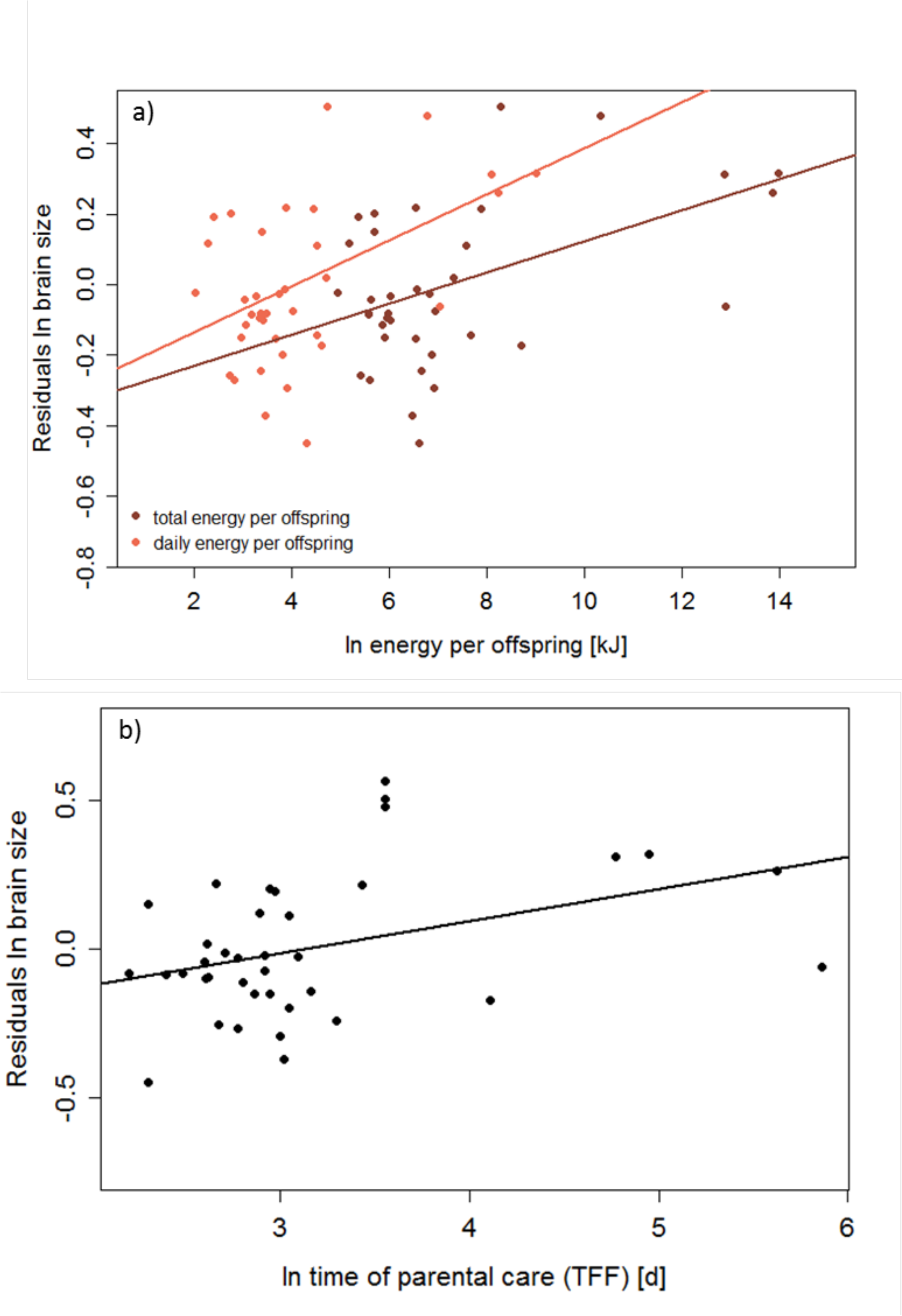


Figure 3.18: **Energetic and time constraints.** a) Least-square regressions of the residuals of ln brain mass on the residuals of ln daily energetic input per offspring during chick rearing (PGLS: n = 38, p=0.07(+)) and ln total energetic input per offspring per chick rearing period in altricials (PGLS: n = 38, p=0.07(+)). b) Least-square regression of the residuals of ln brain mass on ln time of parental care (TFF) in altricials (fort the same sample as a)) (GPLS: n = 38, p=0.16(+)). Residuals of ln brain mass indicate correction for body mass.

Table 3.21: **Time vs. energetic constraints in precocials.** Multiple PGLS regressions for ln brain mass and ln daily energy per offspring, ln total energetic investment per offspring per breeding season, ln duration of incubation, ln body mass (ln brain mass as independent variable; ln daily energy per offspring, ln total energy per offspring as well as ln duration of incubation and ln body mass as independent variables). Given are the sample size (n), multiple $r^2$, Akaike information criterion (AIC), Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

| | | | | | | **daily energy per offspring (during incubation)** | | **duration of incubation** | | **body mass** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | $r^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope |
| model A | 25 | 0.93 | -12.4 | 0.81 | 0.363, NA | - | - | 0.09 | 0.43 | *<0.0001* | 0.52 |
| model B | 25 | 0.93 | -12.74 | 0.8 | 0.347, NA | 0.17 | 0.07 | 0.08 | 0.44 | *<0.0001* | 0.52 |
| | | | | | | **total energy per offspring (during incubation)** | | | | | |
| | | | | | | p-value | slope | | | | |
| model C | 25 | 0.93 | -12.4 | 0.81 | 0.363, NA | - | - | 0.09 | 0.43 | *<0.0001* | 0.52 |
| model D | 25 | 0.93 | -12.74 | 0.8 | 0.347, NA | 0.17 | 0.07 | 0.09 | 0.41 | *<0.0001* | 0.52 |
| | | | | | | **number of caretakers** | | | | | |
| | | | | | | p-value | slope | | | | |
| model E | 247 | 0.87 | -244.15 | 0.97 | 0.892, NA | - | - | *0.06* | 0.17 | *<0.0001* | 0.5 |
| model F | 247 | 0.87 | -242.89 | 0.96 | 0.885, NA | 0.39 | 0.02 | 0.1 | 0.15 | *<0.0001* | 0.5 |
| | | | | | | **breeding type** | | | | | |
| | | | | | | p-value | slope | | | | |
| model G | 274 | 0.88 | -244.71 | 0.87 | 0.885, NA | - | - | *0.003* | 0.23 | *<0.0001* | 0.49 |
| model H | 274 | 0.88 | -244.19 | 0.96 | 0.875, NA | 0.23 | 0.03 | *0.006* | 0.22 | *<0.0001* | 0.49 |

Table 3.22: **Time vs. energetic constraints in altricials.** Multiple PGLS regressions for ln brain mass and ln daily energy per offspring, ln total energetic investment per offspring per breeding season, ln time of first flight (TFF), ln time of fledging and ln body mass (ln brain mass as independent variable; ln daily energy per offspring, ln total energy per offspring as well as ln TFF, ln fledging and ln body mass as independent variables). Given are the sample size (n), multiple $r^2$, Akaike information criterion (AIC), Pagels‘ lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

|  |  |  |  |  |  | **daily energy per offspring (during chick rearing)** |  | **TFF** |  | **fledging** |  | **body mass** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | n | $r^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| model A | 38 | 0.92 | -13.24 | 1 | 0.908, NA | - | - | 0.16 | 0.11 | - | - | *<0.0001* | 0.57 |
| model B | 38 | 0.93 | -14.84 | 1 | 0.908, NA | 0.07 | 0.07 | 0.32 | 0.08 | - | - | *<0.0001* | 0.53 |
| model C | 28 | 0.94 | -9.17 | 1 | 0.872, NA | - | - | - | - | 0.2 | 0.1 | *<0.0001* | 0.58 |
| model D | 28 | 0.94 | -7.18 | 1 | 0.873, NA | 0.95 | -0.005 | - | - | 0.23 | 0.1 | *<0.0001* | 0.59 |
|  |  |  |  |  |  | **total energy per offspring (during chick rearing)** |  |  |  |  |  |  |  |
|  |  |  |  |  |  | p-value | slope |  |  |  |  |  |  |
| model E | 38 | 0.92 | -13.24 | 1 | 0.908, NA | - | - | 0.16 | 0.11 | - | - | *<0.0001* | 0.57 |
| model F | 38 | 0.93 | -14.84 | 1 | 0.908, NA | 0.07 | 0.07 | 0.98 | 0.002 | - | - | *<0.0001* | 0.53 |
| model G | 28 | 0.93 | -9.17 | 1 | 0.872, NA | - | - | - | - | 0.2 | 0.1 | *<0.0001* | 0.58 |
| model H | 28 | 0.94 | -7.2 | 1 | 0.873, NA | 0.86 | -0.01 | - | - | 0.33 | 0.11 | *<0.0001* | 0.59 |
|  |  |  |  |  |  | **number of caretakers** |  |  |  |  |  |  |  |
|  |  |  |  |  |  | p-value | slope |  |  |  |  |  |  |
| model I | 728 | 0.87 | -503.38 | 0.98 | 0.950, 0.994 | - | - | *0.0002* | 0.09 | - | - | *<0.0001* | 0.6 |
| model J | 728 | 0.87 | -503.41 | 0.98 | 0.951, 0.995 | 0.15 | 0.009 | *0.0002* | 0.09 | - | - | *<0.0001* | 0.6 |
| model K | 418 | 0.9 | -361.43 | 0.96 | 0.925, 0.988 | - | - | - | - | *0.0002* | 0.11 | *<0.0001* | 0.63 |
| model L | 418 | 0.9 | -360.88 | 0.97 | 0.928, 0.990 | 0.23 | 0.008 | - | - | *0.0001* | 0.11 | *<0.0001* | 0.63 |
|  |  |  |  |  |  | **breeding type** |  |  |  |  |  |  |  |
|  |  |  |  |  |  | p-value | slope |  |  |  |  |  |  |
| model M | 772 | 0.88 | -553.71 | 0.97 | 0.949, 0.993 | - | - | *0.0002* | 0.08 | - | - | *<0.0001* | 0.6 |
| model N | 772 | 0.88 | -552.06 | 0.97 | 0.949, 0.993 | 0.6 | -0.009 | *0.0002* | 0.08 | - | - | *<0.0001* | 0.6 |
| model O | 439 | 0.9 | -376.2 | 0.96 | 0.925, 0.987 | - | - | - | - | *0.0001* | 0.11 | *<0.0001* | 0.63 |
| model P | 439 | 0.9 | -375.78 | 0.96 | 0.925, 0.987 | 0.21 | -0.03 | - | - | *0.0001* | 0.11 | *<0.0001* | 0.63 |

**Prediction Social Brain Hypothesis**: This hypothesis claims that larger and more complex social groups would allow for larger brains to become a selective advantage (e.g. Dunbar 1998). To test whether the effects of complex social demands or energetic constraints are behind this, I include social patterns during breeding season in the analyses, where for example a gregarious lifestyle per se does not mean additional energy.

- I expect that allomaternal care is linked to extra energy inputs and that the effects of cooperative breeding (allomaternal care) on relative brain size are stronger than the effects of a gregarious lifestyle per se.

**Results Social Brain Hypothesis**: Species with allomaternal care have relatively larger brains than species with a solitary lifestyle or a gregarious life style without allomaternal care (ANCOVA: Tukey‘s posthoc test: $p < 0.05$) (figure 3.19). In a PGLS regression model, including these factors as a continuous variable (1=solitary lifestyle without allomaternal care, 2=gregarious lifestyle without allomaternal care, 3=allomaternal care), no significant effect on relative brain size was observed (PGLS regression: n=384, $r^2$=0.89, lambda=0.96, estimate=-0.009, p=0.68).
However, after correcting for the effect of social pattern (1 = territorial solitary; 2 = territorial pair; 2.5 = territorial pair/family group; 3 = territorial family group; 4 = tolerant; 5 = colonial) in a PGLS regression model, brain size still showed a positive correlation with total energetic input per offspring (table 3.23). Number of caretakers as well as breeding type showed no positive relationships with relative brain size (table 3.23).

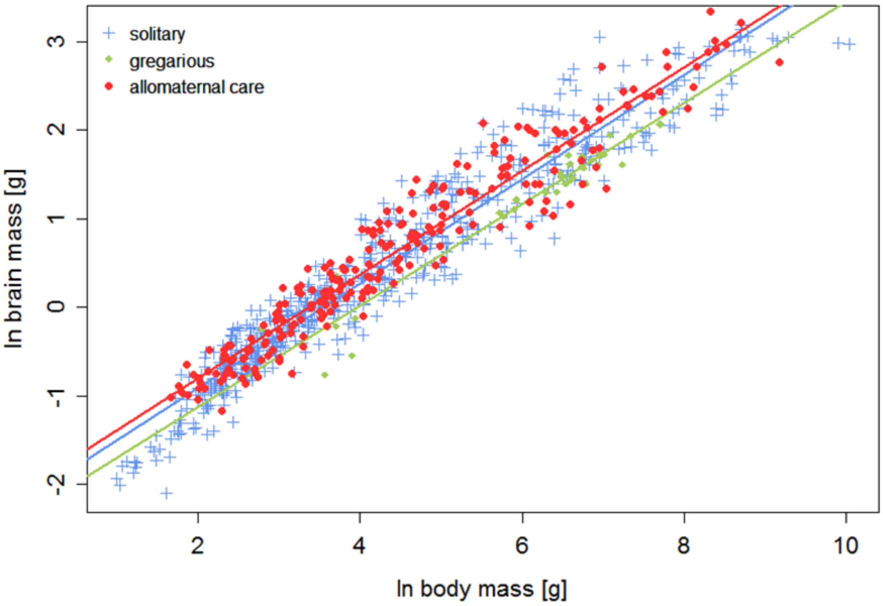


Figure 3.19: **Social pattern vs. allomaternal care.** Least-square regressions of ln brain mass on ln body mass for solitary living species (n = 604), gregarious species (without allomaternal care) (n = 42) and species with allomaternal care (n = 240). ANCOVA: Tukey‘s posthoc test: $p < 0.05$.

Table 3.23: PGLS regressions of ln brain mass and ln total energetic input per offspring during the chick rearing period, number of caretakers, breeding type as well as social pattern, ln body mass and development mode (ln brain mass as dependent variables; ln total energy per offspring, number of caretakers, breeding type as well as social pattern, ln body mass and development mode as independent variables). Given are the sample size (n), multiple $r^2$, Akaike information criterion (AIC), Pagels' lambda ($\lambda$) and the 95% confidence interval of $\lambda$ (CI $\lambda$) (significant effects are shown in italics, NA = not available = unknown value).

|  |  |  |  |  | **total energy per offspring** |  | **social pattern** |  | **body mass** |  | **development** |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| n | $r^2$ | AIC | $\lambda$ | CI $\lambda$ | p-value | slope | p-value | slope | p-value | slope | p-value | slope |
| 53 | 0.96 | -35.72 | 0.99 | 0.745, NA | - | - | 0.16 | -0.03 | *<0.0001* | 0.6 | *0.006* | 0.12 |
| 53 | 0.96 | -38.87 | 1 | 0.729, NA | *0.03* | 0.05 | *0.15* | -0.03 | *<0.0001* | 0.56 | *0.004* | 0.13 |
|  |  |  |  |  | **number of caretakers** |  |  |  |  |  |  |  |
|  |  |  |  |  | p-value | slope |  |  |  |  |  |  |
| 988 | 0.86 | -635.81 | 0.96 | 0.926, 0.978 | - | - | *0.02* | -0.01 | *<0.0001* | 0.6 | *<0.0001* | 0.11 |
| 988 | 0.86 | -633.9 | 0.96 | 0.926, 0.978 | 0.78 | -0.002 | *0.02* | -0.01 | *<0.0001* | 0.59 | *<0.0001* | 0.11 |
|  |  |  |  |  | **breeding type** |  |  |  |  |  |  |  |
|  |  |  |  |  | p-value | slope |  |  |  |  |  |  |
| 988 | 0.86 | -635.81 | 0.96 | 0.926, 0.978 | - | - | *0.02* | -0.01 | *<0.0001* | 0.6 | *<0.0001* | 0.11 |
| 988 | 0.86 | -636.63 | 0.96 | 0.929, 0.979 | 0.09 | -0.03 | *0.03* | -0.01 | *<0.0001* | 0.59 | *<0.0001* | 0.11 |

# 4 Discussion

In the broadest sense this study aimed to explain part of the huge variation in relative brain size among bird species. Why certain species have larger relative brain sizes than others seems to stay a not fully understood evolutionary phenomenon. From the energy perspective, in the context of the expensive brain framework (Isler and van Schaik 2009a; Navarrete et al. 2011), several non-exclusive ways have been proposed why certain taxa are able to grow larger brains than others. In this regard, many encouraging studies have been conducted especially across the mammalian clade. Laying the focus on one particular aspect of the expensive brain framework, the production trade-off, Isler and van Schaik (2009a,b) found that the trade-off between relative brain size and reproduction ($\mathrm{r}_{max}$) diappears in species with allomaternal care such as carnivores or altricial birds. Moreover, in mammalian as well as avian species it has been shown that in precocial species, where allomaternal help is rare, relatively large-brained species have rather low $r_{max}$. On the other hand, in altricial species, showing a lot of help during breeding, this negative relationship is strongly alleviated or even completely disappears (Isler and van Schaik 2009b). These findings indicate the importance of the breeding system and its influence on the energetic allocation problem.

As promising results have been found so far mainly across mammals, this study aims to give further insight in another major vertebrate clade - the birds.

However, former studies investigating birds used rather rough estimations of amount of allomaternal care mainly comparing altricial and precocial species. In this study I tried to find appropriate quantifications of allomaternal care in order to directly examine the effect of help on the energetic allocation between relative brain size and reproduction.

Besides the expensive brain framework, several alternative hypotheses have been proposed to explain brain size variation using either the adaptive benefit or constraint approach (e.g development or time constraint hypothesis). I aimed to show that energetic resources are more important for explaining brain size variation compared to other aspects such as development or time.

## 4.1 Metabolic constraint hypothesis

The metabolic constraint hypothesis, representing one aspect of the expensive brain framework, claims that the costs of increased brain size might be paid by an increase in energy intake, which in fact is quite a risky strategy (cf. Isler and van Schaik 2009a). Supporting evidence has been found mainly in mammals, where BMR explains about 15% (independent contrast analyses, Isler and van Schaik 2006b, Isler et al. 2008) of total brain size variation. Within mammalian orders, the correlation has been found to be significant only in marsupials and primates. However in birds, using a sample of 245 species, no evidence has been found so far that large-brained species would increase

their net energy intake (Isler and van Schaik 2006a).
These findings are confirmed by this study. Using a sample of 244 bird species, I found no positive correlation between BMR and relative brain size. Even after correcting for reproduction, which might obscure the direct metabolic constraint, BMR does still not correlate with relative brain size. According to a study of Koteja (1991, p.59), there are doubts about „the assumption that BMR is a reliable index of energy expenditure of free living animals“. Especially in reproducing birds, BMR shows only a weak correlation with FMR. Therefore, one might argue that BMR is not a representative measurement of energy expenditure of free-living birds. In this regard, I further investigated the relationship between FMR$_{non-breeding}$ and relative brain size. Interestingly, after correcting for the effect of reproduction, FMR$_{non-breeding}$ strongly negatively correlates with relative brain size. In other words, large-brained bird species have low daily energy expenditures. This might be explained by the general idea of an energetic trade-off: the more energy is used for the brain, the less can be spent for other functions, such as locomotion. However, the energtic costs of the brain are probably part of the measured FMR, and thus, this finding stays rather puzzling. Future studies need to be conducted including both, environmental and ecological aspects, such as locomotion or dietary composition, in order to gain further insight.

In sum, the metabolic constraint hypothesis could not be confirmed in bird species, as no positive relationship between the total energy turnover (BMR or FMR) and relative brain size has been found. Several authors (Koteja 1991, McNab2009, King and Farner1961, Aschoff and Pohl1970) claim that there is a basic energetic difference between mammals and birds, as in general birds show a higher resting metabolism than mammals. One and probably the most crucial factor which leads to this assumption is flight. Further, McNab (2002) found another notable difference between mammals and birds concerning BMR: faunivore and frugivore mammalian species have intermediate to high BMRs whereas faunivore and frugivore bird species have intermediate to low BMRs.
Although it might be precocious (cf. McNab 2002), all these findings would suggest a basic physiological difference between birds and mammals, which might be the reason for a missing link between brain size and energetic turvnover in avian species. In conclusion, higher total energy turnover seems not to be necessary for incrased relative brain sizes in birds, therefore an alternative explanation for brain size variation must be found.

## 4.2 Production trade-off hypothesis

### 4.2.1 Reproduction and brain size (Hypothesis 2 a)

The production trade-off hypothesis, which is part of the „expensive brain framework“ (Isler and van Schaik 2009a, Navarrete et al. 2011), predicts that the costs of relatively large brains can be paid by reducing allocation of resources to growth and reproduction. In particular, the reproduction process is energetically extremely challenging and thus, assuming an energetic trade-off between reproduction (fertility or r$_{max}$) and relative brain size is straightforward. According to Isler and van Schaik (2009a,b) there is one possible change in lifestyle which might enable to evade this trade-off. They suggest that such a change would most likely be found in the breeding system, as the energetic load of adults is highest during the breeding season. Thus, they claim that cooperative breeding or any other kind of allomaternal care during breeding alleviates the reproduction trade-off and allows for maintaining and growing larger brains and/or increased reproduction. So far, encouraging results have been found mainly in mammals (Isler and van Schaik 2009a,b). I predicted the same phenomenon for bird species, namely if controlling for the amount of allomaternal care, reproduction would negatively correlate with relative brain size. I found that both, controlling and not controlling for the amount of allomaternal care, yield a negative correlation between fertility and relative brain size, whereas relative brain size seems not to have a strong negative effect on r$_{max}$. Thus, even after controlling for the effect of „help“, $r_{max}$ does not negatively correlate with relative brain size. These results are not consistent with the predictions in hypothesis 2 a. The different findings for annual fertility and r$_{max}$ might be explained by the fact that fertility only regards number of offspring of a single generation, whereas r$_{max}$ additionally incorporates maximum reproductive lifespan, regarding reproduction across generations. Maximum reproductive lifespan is increased in large-brained species (hypothesis 2 c) which explains the missing relationship between r$_{max}$ and relative brain size (see also section 4.2.3). In other words, the short-term effect of large brains is expressed in reduced annual fertility, however, these large-brained species elongate maximum reproductive lifespan which compensate for the long-term effect of a reduced population growth rate (r$_{max}$).

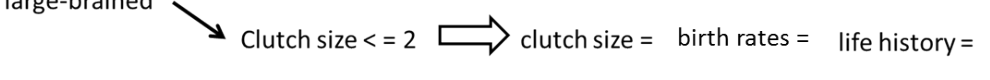
However, if investigating the reproduction trade-off separately for species with no allomaternal care (brood parasites, geothermal and single breeders) and species with allomaternal care (pair and cooperative breeders), an interesting pattern was observed. Consistent with hypothesis 2 a, species with no allomaternal care show a strong negative relationship between reproduction (fertility or r$_{max}$) and relative brain size, whereas this trade-off strongly alleviates in pair and cooperatively breeding species. This suggests that large-brained pair and cooperative breeders completely compensate the brain costs with higher amounts of allomaternal care and thus, don‘t need to pay their large brains by reducing reproduction. Furthermore, I found that the negative trade-off between r$_{max}$ and relative brain size within species having no allomaternal care is mainly driven by fertility rather than maximum reproductive lifespan.

To sum up, these findings suggests that there is a difference concerning the reproduction trade-off between species with and without allomaternal care, that is, species with allomaternal care show a strongly alleviated reproduction trade-off. Across all species, I found a negative relationship between fertility and relative brain size (but not between r$_{max}$ and relative brain size). However, including allomaternal care as a covariate in form of energetic measurements, number of caretakers of breeding type did not yield a stronger trade-off between reproduction and relative brain size. This finding does either reject the production trade-off hypothesis, or it implies that the measurements I used to quantify the amount of allomaternal care might not be appropriate ( 4.6.1).

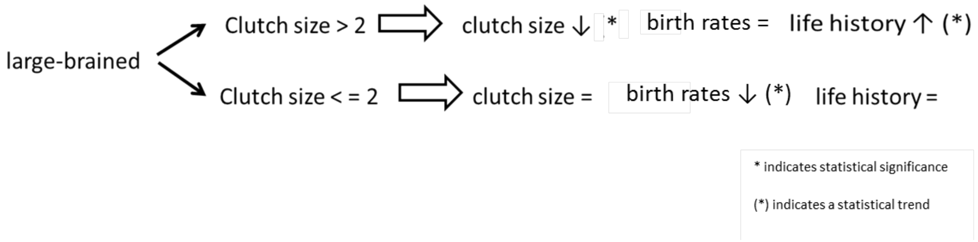
### 4.2.2 Clutch size and brain size (Hypothesis 2 b)

Looking at the reproduction trade-off in more detail with regard to litter size, Isler and van Schaik (2009a) and Isler and van Schiak (in prep.) found that in polykotous mammals (having several offspring per litter) larger brains are paid by reducing litter size, whereas in species having mostly only a single offspring per litter, bigger brains were compensated by a slower development. In birds, I expected a similar pattern. Large-brained species of taxa groups with several eggs per clutch are predicted to reduce clutch size, whereas taxa groups with only one or two eggs per clutch are expected to slow down development and decrease birth rates. Consistent with my prediction, I found species having clutch sizes larger than two show a negative correlation between clutch size and relative brain size, whereas large-brained species with only one or two eggs per clutch show not a reduced number of offspring per clutch, but instead reduced annual birth rates (trends found in large samples). This would suggest that large-brained species with only one or two offspring per breeding season are not able to change energy allocation by reducing the number of offspring per clutch, but instead they reduce annual birth rates, as expected. Further, in order to afford big brains, these taxa groups would then be expected to slow down development. However, I found no clear pattern which would support this prediction. This might indicate, that time of fledging or time of first flight is simply not a constraint in this taxa group, probably because most of the species are seasonal breeders, meaning they have only one clutch per year (Isler, personal communication). It would be interesting to test, whether taxa groups with one or two eggs per clutch and several broods per year tend to elongate development periods. Due to data set restrictions, this was not possible in this study.
In general, my findings suggest that taxa groups with several rather than only one or two eggs per clutch tend to elongate development periods (measured by time of fledging or time of first flight) with increased brain size which is the opposite of what has been predicted. Furthermore, correcting for the amount of allomaternal care did not yield differences in the results, nor did looking at species with and without allomaternal care separately. The pattern described above seems to be generally applicable across all species, which seems reasonable due to the general trade-off between annual fertility and relative brain size.

**Non-cooperative breeders** show the following pattern:



**Pair and cooperative breeders** show a similar pattern:



In conclusion, this implies that for affording larger brains, species reduce the number of offspring per breeding season if they are able to do so. However, species which are not able to do so, do not seem to elongate life history as would have been expected. Either these taxa groups use alternative ways to pay for larger brains or the sample sizes are too small to detect any clear pattern.

### 4.2.3 Longevity and brain size (Hypothesis 2 c)

With hypothesis 2 a I have found that large-brained species without allomaternal care show a strong trade-off between the reproduction ($r_{max}$ or fertility) and relative brain size. Several former studies (Isler and van Schaik 2009a,b, Sacher 1978, Deaner et al. 2003) could have shown that large-brained mammalian species increased annual adult survival and elongated their maximum reproductive lifespan in order to be nonetheless evolutionary stable. I found that taxa groups with a reproduction trade-off (brood parasites, geothermal and single breeders), large-brained species show significantly higher annual adult survival and longer maximum lifespans, which also suggests a compensation for reduced fertility. Taking pair and cooperatively breeding species together, I still found a positive correlation between longevity and relative brain size, whereas when looking at cooperatively breeding species separately, the positive correlation completely disappears. This would suggest that species with large amounts of allomaternal care (cooperative breeders with at least 3 caretakers), showing no trade-off between reproduction and relative brain size, do not need to elongate their maximum reproductive lifespan in order to be nonetheless evolutionary stable. Correcting for the effects of allomaternal care including all species does never yield a stronger postive correlation between longevity and relative brain size. This might suggest that the measures of allomaternal care are not adequate, otherwise one would find an effect if controlling for the amount of help (section 4.6.1).

In summary, **across all avian species**, annual fertility correlates negatively with relative brain size which seems to be compensated by an elongated maximum lifespan. The maximum rate of population increase ($r_{max}$) which incorporates annual fertility as well as maximum reproductive lifespan shows a very slight negative trend with relative brain size (figure 4.1). This suggests that in large-brained taxa the compensation by reduced mortality rates and prolonged longevity is almost fully complete. Contrary to my findings in birds, Isler and van Schaik (2009a) found a very strong negative correlation between $r_{max}$ and relative brain size across a wide range of mammalian species (figure 4.2). My results suggest that birds, in contrast to mammals, are largely able

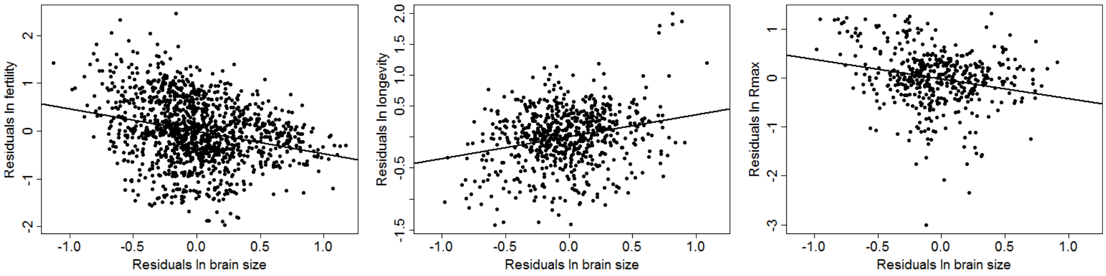


Figure 4.1: **Reproduction trade-off in birds.** Least-square regressions of (a) residuals of ln annual fertility (PGLS: $n = 447$, p=0.01(-)), (b) residuals ln longevity (PGLS: $n = 447$, p=0.06(+)), (c) residuals ln $r_{max}$ (PGLS: $n = 447$,p=0.12(-)) on the residuals of ln relative brain size in birds.

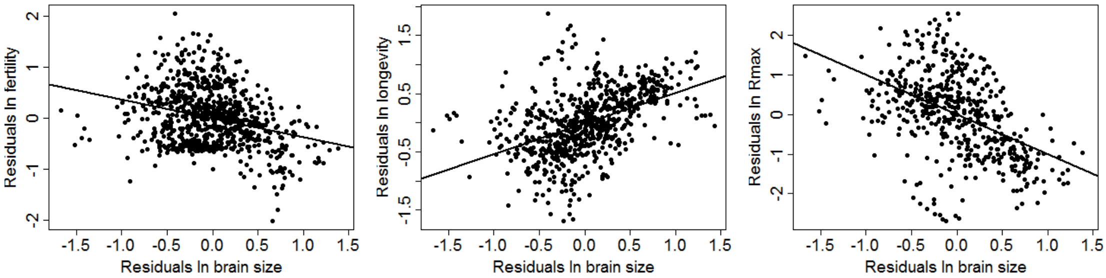


Figure 4.2: **Reproduction trade-off in mammals.**Least-square regressions of (a) residuals of ln annual fertility, (b) residuals ln longevity, (c) residuals ln $r_{max}$ (Independent contrast analysis: n=535, p<0.0001(-), Isler and van Schaik 2009b) on the residuals of ln relative brain size in mammals (data provided by Karin Isler).

to evade the reproduction trade-off. In birds over 90% of all species are pair or cooperative breeders which probably is the crucial change in lifestyle allowing them to largely evade the trade-off between brain size and reproductive rate. Further, one might ask then why most birds breed in pairs or cooperatively and why in mammals these forms of parental care are rather rare? Birds, in contrast to mammals, do not have lactating mothers, so the hatchlings are not exclusively dependent on the mother, but may also be cared for by others than the mother (allomothers). In mammals on the other hand, offspring are mainly dependent on lactation and helpers are not able to replace the function of the lactating mother (Clutton-Brock et al. 1998).

### 4.2.4 „Grey ceiling“ (Hypothesis 2 d)

Large-brained species which compensate the costs with lowering $r_{max}$ might result in a so called „grey ceiling“ (Isler and van Schaik 2009b). In other words, these lineages reach a maximum viable brain size as compensation by prolonged longevity and reduced mortality rate is incomplete. Species cannot evolve too large brains, otherwise they may not be able to recover from population collapses which makes them much more vulnerable to extinction. Therefore, I expected large-brained species with reduced reproduction to be classified rather as vulnerable or endangered on the worldwide scale. Across all species, I found no relationship between the reproduction and the classification on the worldwide scale, and also no relationship between relative brain size and the classification on the worldwide scale. Nevertheless, endangered or vulnerable bird species predominantly seem to have rather low reproductive rates (residuals $< 0$) and large relative brain size (residuals $> 0$) (figure 3.7), which might be an indication of these species having reached their „grey ceiling“. The lack of data of very rare and endangered species might explain the absent significance in the PGLS regression models. For future studies, therefore, more data of threatened species need to be collected to further test this hypothesis. Contrarily, one might argue that birds have not reached their maximum viable brain size, as I have found that the trade-off between $r_{max}$ and relative brain size is strongly alleviated across all birds in contrast to mammals.

Furthermore, it would be interesting to test this hypothesis only within species with no allomaternal care, showing a very strong reproduction trade-off, which requires more data on the status on the worldwide scale.

## 4.3 Energy subsidies hypothesis

### 4.3.1 Brain size or reproduction (Hypothesis 3 a)

The main aim of this study was to investigate whether energy subsidies during breeding (allowing for an alleviated reproduction trade-off) are related to the evolution of large brains in birds or/and an increase in reproduction. Investigating the reproduction trade-off per se does not allow to distinguish between the one or the other (figure 4.3). Therefore, I tested the effect of three alternative quantifications of allomaternal care (energetic measurement, number of caretakers, breeding type) on relative

brain size and reproduction ($r_{max}$, annual fertility, clutch size and egg mass). Interestingly, I found that that **total energetic expenditure** during the chick rearing period ($E_{sum(chick-rearing)}$, see Material and Methods) positively correlates with relative brain size, whereas reproduction ($r_{max}$ and annual fertility) shows a negative relationship. This would suggest that the total circulating energy is invested in brain size rather than in reproductive quantity. Additionally, total energy shows a significant positive effect on egg mass suggesting that higher energetic investment during chick rearing allows for larger hatchlings. In sum, this proposes that extra energetic input is put in size of brains and eggs rather than in the number of offspring - quality before quantity (figure 4.4). Regrettably, as data on $FMR_{chick-rearing}$ is scarce, the sample used for this analysis includes only one singly breeding species, whereas all the other species are pair or cooperative breeders. Furthermore, comparing the three alternative quantifications of allomaternal care, one needs to consider that the total energy shows no positive correlation with number of caretakers or breeding type (which is not surprising as the variation in number of caretakers/breeding type is very low in that particular sample)(further discussed in section 4.6.1).
However, these results suggest a positive relationship between energy resources and relative brain size within species with amount of allomaternal care which have been found to show an alleviated reproduction trade-off.
Furthermore, regarding the trade-off between fertility and relative brain size (figure 4.5), species with no allomaternal care (brood parasites, geothermal and single breeders) are largely found in the upper left corner, meaning that they have rather many offspring and small brains. For species with allomaternal care (pair and cooperative breeders), which are predominantly found in the bottom right corner, this would suggest that an increase in brain size allows for an alleviated reproduction trade-off, which in the end reassures the finding that „help“ during breeding rather affects reproductive quality than reproductive quantity.
However, using **number of caretakers** or **breeding type** as quantifications of the amount of allomaternal care, no clear pattern has been found. This implies either that these two quantifications do not truly represent allomaternal care, or that the number of caretakers or breeding type per se might be not enough to explain brain size variation, because also the duration of how long these caretakers are caring for offspring probably plays an important role (see also sections 4.5.3 and 4.6.1).
Further, using another approach for investigating the effect of breeding type on relative brain size, independently of the reproduction trade-off, I looked at possible grade shifts in relative brain size between the different breeding types. Ignoring the phylogenetic relationships, I found that cooperative breeders have relatively larger brains than pair breeders and pair breeders again have relatively larger brains than single breeders. However, applying multiple PGLS regressions or GLS regressions with family means testing for the effect of breeding type on relative brain size, these effects disappear (section 4.6.1).

In conclusion, energy subsidies really seems to have en effect on the link between brain size and reproduction, as the reproduction trade-off is strongly alleviated in taxa groups with allomaternal care (section 4.2.1). From this results per se it is

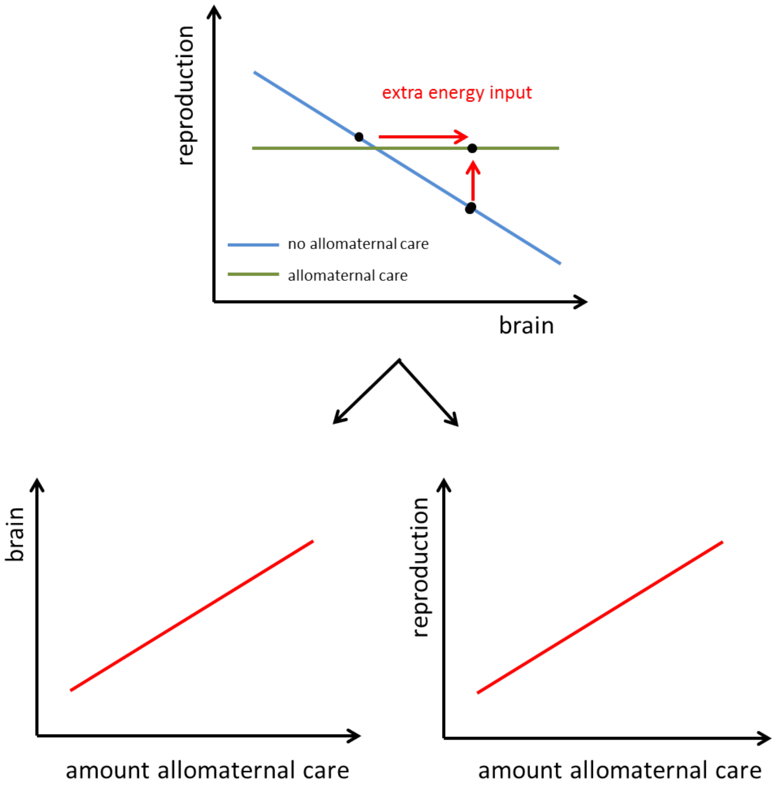


Figure 4.3: **Brain or reproduction.** Both, an increase in brain size as well an increase in reproduction may lead to an alleviated reproduction trade-off. The amount of allomaternal care either positively correlates with brain size or with reproduction, or both. The blue line indicates the reproduction trade-off for taxa groups with no allomaternal care. The green line indicates the alleviated reproduction trade-off for taxa groups with allomaternal care. The black dots indicate single species.

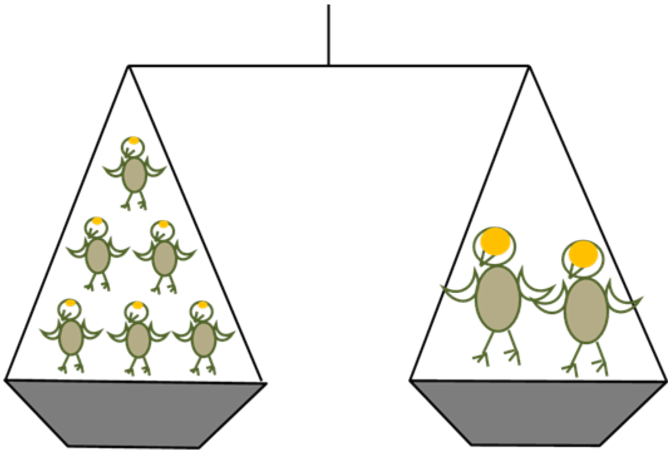


Figure 4.4: **Trade-off between reproductive quality and quantity.** Species either invest in many small offspring with small brains (brains are indicated by the yellow dot) or in few large offspring with large brains.

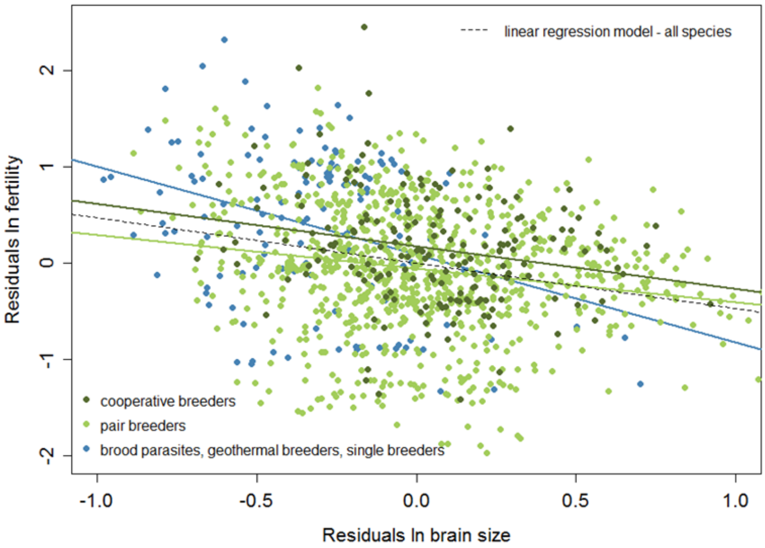


Figure 4.5: **Reproduction trade-off.** Least-square regression of the residuals of ln fertility on the residuals of ln brain mass, shown for brood parasites/geothermal breeders/single breeders, pair and cooperative breeders seperately (n(brood parasites, geothermal/single breeders)=131; n(pair breeders)=874; n(cooperative breeders)=181). The dashed lines indicate the least-square regressions of all species. All residuals indicate correction for body size.

hard to detect whether the extra energy inputs from allomaternal helpers affects brain size or reproduction (figure 4.3). In this respect, using the energetic measurement during chick rearing as a quantification of the amount of allomaternal allows to draw a first conclusion. Extra energetic resources seem to be invested in brain and egg size rather than number of offspring. In other words, it is rather reproductive quality than reproductive quantity which is affected by higher energetic resources.

### 4.3.2 Energetic load per caretaker (Hypothesis 3 b)

Contrarily to my prediction, I found that the higher the energetic load per caretaker, the larger the relative brain size. This suggests that the more energy each caretaker invests during the chick rearing period, the larger the adult brain size rather than an energetic trade-off between these two. From the perspective of the caretaker, this might be indicating that large-brained species need to increase their total energy turnover during breeding even more compared to their small-brained relatives. In contrast, $r_{max}$, annual fertility and clutch size show rather negative relationships with energetic investment per caretaker, suggesting again that extra energetic resources are invested in brain size rather than number of offspring. Interestingly, across the same sample, $FMR_{non-breeding}$ shows no effect on relative brain size. This might be indicating that mainly the energy balance during the breeding period affects the energetic allocation with brain. These results are again restricted to a data set mainly including species with allomaternal care.

Furthermore, regarding the positive link between energetic load and brain size, one could argue that the time effect is the driving force of this positive correlation, because the duration of chick rearing is as well included in the calculations of the total energetic load per caretaker and might have a positive effect on relative brain size. However, additionally controlling for the duration of the chick rearing period shows that energetic load per caretakers still shows a significant positive effect on relative brain size. Therefore, the positive relationship is not exclusively time dependent.

However, future studies including a wider range of species with and without allomaternal care may provide a pattern in another direction and thus, it would be premature to reject the prediction about the energetic trade-off between maintenance of the brain and reproductive effort.

### 4.3.3 Energetic input per offspring (Hypothesis 3 c)

In concordance with hypothesis 3 c, I found species with an increased total energetic investment per offspring to have larger relative brain sizes. Due to lack of data, this analysis is also based on sample including only one singly breeding species, which again would constrict my findig to species with allomaternal care. Nevertheless, from the perspective of the offspring, this might be suggesting that higher energetic resources received during the nestling period allow for growing larger brains.

## 4.4 Energy subsidies, egg mass and altriciality

### 4.4.1 Mate feeding (Hypothesis 4 a)

Mate feeding as a form of allomaternal care might either affect egg size or enable energetic load-lightening of the incubating parent allowing for maintaining large adult brains.

I found that species with mate feeding have rather large eggs than large adult brains. This would suggest that species with mate feeding during egg production, egg laying and incubation invest this extra energetic input in egg mass rather than compensate the energy for maintaining large adult brain sizes. Therefore, mate feeding as a form of allomaternal care seems not to affect energetic alleviation allowing for larger relative brain sizes. The finding is consistent with an earlier study by Nisbet (1973) who found that courtship feeding is associated with higher clutch and egg size. Furthermore, Pearse et al. (2004) found that females being supported by their mates show higher nest attentiveness, which in the end may allow for larger eggs. Several other studies have shown that mate feeding (mainly the female) contributes quite a lot to her daily energy intake (Nisbet 19973, Taske and Mils 1981, Avery et al. 1988, Donazar et al. 1992, Hatupka 1994). Unfortunately, I was not able to reassure these findings due to data set restrictions.

However, contradictionary to my prediction, mate feeding as a form of allomaternal care seems not to affect energetic alleviation allowing for larger relative brain sizes. Consistent with other studies (Drent and Daan 1980, Oftedal 1985), I have found a trend that the energetic costs during incubation are lower than during feeding the offspring. Therefore, probably the costs during chick rearing rather than during incubation are more crucial regarding the energetic allocation with brain.

### 4.4.2 Allomaternal care and egg mass (Hypothesis 4 b)

A study of Russel et al. (2007) found that within a species (*Malurus cyaneus*), mothers in presence of helpers produce smaller eggs. They claim that this premature state of hatchling is compensated by the support of helpers later in development.

Using the three alternative quantifications of the amount of allomaternal care, no clear pattern occurs whether higher amount of allomaternal care during chick rearing is linked to a smaller egg size across species. Whereas number of caretakers and breeding type show rather weak negative trends with egg mass, energetic expenditure during the chick rearing period shows rather a positive relationship. This positive relationship between egg mass and energy spent during the chick rearing period might be explained by that larger energetic expenditures during chick rearing are needed for larger hatchlings to be nourished.

Further investigating what might influence the size of eggs, I found a strong positive trend between the total energetic investment during incubation and relative egg mass. This positive trend can be attributed to an increase in both, duration of incubation and daily energetic investment, whereas among each other they show a negative relationship. This suggests that higher daily energetic investment during incubation allows for shorter incubation durations and an increase in egg mass is achieved if duration of incubation as well as daily energetic investment is increased (figure 4.6).

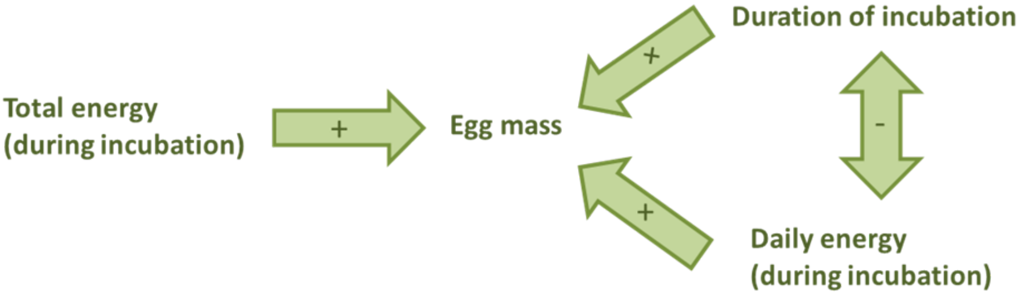


Figure 4.6: **Relationship between energetic measurements, duration of incubation and egg mass.** Duration of incubation (PGLS: n=54, p<0.0001(+)), total (PGLS: n=197,p=0.05(+)) and daily (PGLS: n=197,p=0.05(+)) energy during incubation show positive effects on egg mass, whereas among each other they show a negative relationship (PGLS: n=27, p=0.003(-)). Total energy invested during incubation again has a positive effect on egg mass.

In conclusion, it might be premature the reject the hypothesis of Russel et al. (2007) as no consistent pattern has been found. However, it seems as if higher energetic resources are linked to larger eggs. In this regard, it is important to keep in mind that patterns occuring at an intraspecific level are not necessarily observed at an interspecific level.

### 4.4.3 Altriciality (Hypothesis 4 c)

For precocial species with high amounts of allomaternal care I expected a shift towards altriciality, because help is most effective during the post-hatching period acting directly on offspring. However, within precocial species I found rather a shift towards extreme precociality than altriciality. The more help available, the bigger the eggs and the longer the duration of incubation. In fact, within mammals, rodents show a similar pattern, and only precocial primates show a shift towards altriciality. This might have something to do with the ability to shelter the offspring if they are very helpless (Isler, personal communication). Precocial birds cannot be sheltered, even worse than in rodents. Within altricials, however, at least weak trends were observed in the predicted directions. In fact, egg mass and duration of incubation tend to decrease with an increasing number of helpers.

## 4.5 Alternative hypotheses explaining brain size variation

Several alternative explanations extist to explain the variation in relative brain size. I tried to show that energetic aspects explain higher portions of the variation than other aspects such as development mode or time.

### 4.5.1 Development hypothesis (Hypothesis 5)

Altricial species having larger relative brain sizes than precocial ones is a well-known phenomenon across birds (Bennett and Harvey 1985a,b, Pagel and Harvey 1988, Starck and Ricklefs 1998, Iwaniuk and Nelson 2003). This has been explained by the difference in parental care, namely that altricial avian hatchlings are provisioned and protected by parents and sometimes helpers after birth in contrast to precocial species, and thus have more time and energy to invest in brain growth and maintenance (Bennett and Harvey 1985a,b, Iwaniuk and Nelson 2003). However, although many precocial species do not feed their offspring in the nest, most of them protect them in and also after they have left the nest. This would probably allow precocial species to grow large brains as well and therefore, does not properly explain the difference in relative brain size between altricial and precocial species. Moreover, above all, this hypothesis does not ultimately explain why precocials, in contrast to altricials, do not provision their offspring after hatching.

I aimed to show that energetic aspects play a more significant role in explaining brain size variation than development mode per se. In fact, my results show that if including development mode as a covariate in the model, brain size still positively correlates with total energetic investment, supporting my prediction. Using number of caretakers and breeding type no such pattern is observed. Either increased number of caretakers is not associated with larger brains or the two quantifications do not truly represent the amount of allomaternal care.

In conclusion, the differences in developmental modes are not sufficiently and ultimately explaining the variation in relative brain size. Why do precocial bird species not provision their offspring after hatching to grow larger brains as well but precocial mammals do ? The development hypothesis rather represents a mechanical than an ultimate explanation. Moreover, the developmental differences do not explain brain size variation in mammals (e.g. marsupials are highly altricial but are not very large-brained (Isler, personal communication)). With the results of this study, I have demonstrated that development modes per se are not sufficient for explaining relative brain size variation and that energetic resources are linked to the relative size of the brain.

### 4.5.2 Maternal energy hypothesis (Hypothesis 6)

The maternal energy hypothesis claims that brain size is constrained either by the mothers‘ energy budget and the amount she is able to invest into the offspring or by the length of gestation and postnatal growth, or a combination of the two. So far, supporting evidence has mainly been found in mammals (Martin 1996, Jones and MacLarnon 2004, Isler et al. 2008, Isler 2011). As in mammals mainly the mother lactating the offspring is the crucial provisioning source, in birds often also helpers assist in feeding the hatchlings at the nest. Therefore, I expected that in birds not only the energetic provisioning by the mother is important, but rather the total energetic input by all caretakers mainly affects relative brain size. Using PGLS regression models, I found no consistent pattern which would support my prediction. However, the GLS regression models based on family averages show that total input per offspring stronger correlates with relative brain size than maternal input per offspring. This is a first hint into the direction that in birds total investment of all caretakers is more important than only the maternal investment. Nevertheless, the chosen approximations for the total energy input per offspring and maternal energy input per offspring might be not precise enough to properly test the maternal energy hypothesis. To better disentangle between maternal and total input per offspring one would need true energetic measurements not only representing the energetic investment per caretaker, but as well representing the energetic input per offspring (e.g. by measuring the daily caloric food intake).

### 4.5.3 Time vs. energetic constraints (Hypothesis 7)

In context of the development hyothesis, Iwaniuk and Nelson (2003) found that several developmental traits (incubation, age of fledging, postfledging parental care and total period of parental care) correlate positively with relative brain size across a wide range of avian species. Basically, they claim that due to high costs of brain growth and maintenance, brain size increases with increasing development periods (increased periods of neuronal growth). This argumentation is quite reasonable. However, I predicted that energetic constraints rather than time constraints per se are crucial for explaining brain size variation. Simply regarding the correlations between relative brain size and different developmental traits, I found the same pattern as Iwaniuk and Nelson (2003). Namely, incubation duration, time of fledging, duration of postfleding parental care and total parental care show significant positive effects on relative brain size, whereas time of first flight shows only a trend.

Due to differences in main brain growth, I looked at at precocial and altricial species separately. For **precocials**, I found that both, duration of incubation and energetic input tend to increase with increasing brain size. This suggests that for evolving larger brains, not only the daily amount of energy input is increased, but also the duration of incubation needs to be elongated.

In **altricials**, on the other hand, after correcting for the time of parental care (only in the sample including TFF), still a strong positive trend between relative brain size and energetic input during the chick rearing period is observed. However, in the same model, the positive trend between relative brain size and duration of parental care found in precocial species, completely disappears in altrcial species. Although, the effects are not significant and rather represent trends, this might suggest that adding energetic variation explains variation in relative brain size slightly better than variation in time estimations per se and thus, would support the energy subsidies hypothesis. Using time of fledging as an estimate of the posthatching period, no such pattern occurs which might be explained the smaller sample size ($n = 38$). As in many other analyses, number of caretakers and breeding type do not show positive effects on relative brain size.

In summary, probably both factors are needed to explain brain size variation. Thus, to evolve larger brains in birds, on the one hand, the time of parental care needs to be elongated and on the other hand, energetic inputs must be increased. In contrast, carnivores with allomaternal care show no elongation in lactation, meaning that large-brained species raise their offspring in the same time compared to their small-brained relatives (Isler and van Schaik 2009a; Isler, personal communication).

Nevertheless, only further data on energetic measurements as well as on developmental traits (e.g. time of fledging) allow to fully disentangle between energetic and time contraints. Until then, my assumptions remain rather speculative.

### 4.5.4 Social brain hypothesis (Hypothesis 8)

The social brain hypothesis claims that higher social complexity acts as a selective force towards the evolution of large brains (Byrne and Whiten, 1988, 1997). Group living requires good cognitive skills in terms of recognising conspecifics‘ sex, rank etc. In birds, Shultz and Dunbar (2010) claim that social relationships (e.g. in form of strong pair-bonds) allowed for the evolution of relatively large-brained taxa groups.

In contrast, I expected rather the amount of allomaternal care to be the crucial issue allowing for larger brains. I found that species with allomaternal care have larger relative brain sizes than species with a gregarious life style without allomaternal care. Further, after correcting for the effect of social pattern, relative brain size still shows a positive correlation with total energetic input. These results support the energy subsidies hypothesis as they claim that only allomaternal care but not a gregarious life style per se means additional amount of energy leading to larger relative brain sizes. For future studies, it would be interesting to additionally disentangle between energetic measurements and long-term pair bonds in birds.

## 4.6 General discussion

In this part of the discussion, I will bring all the results of the different hypotheses together and discuss the findings as a whole. The hypotheses with the predictions and corresponding results are summarized in table 4.1.

Table 4.1: **Summary hypotheses.** All the the tested hyotheses with the predictions and corresponding results. Whether a prediction is supported or not is indicated by ✓or by a ✗. A checkmark in brackets (✓) indicates that the hypothesis has partly been supported.

| **Hypothesis** | **Prediction** | **Results** | |
|---|---|---|---|
| 1. Metabolic Constraint Hypothesis | Relative brain size correlates positively with BMR or FMR. | After correcting for reproduction, relative brain size shows a negative correlation with FMR. | ✗ |
| 2. Production Trade-off Hypothesis | a) If controlling for the amount of allomaternal care, reproduction negatively correlates with relative brain size. From another prespective, species without allomaternal care show a reproduction trade-off, whereas species with allomaternal care do not. | After controlling for the amount of allomaternal care, reproduction does not correlate more negatively with relative brain size. However, a strong trade-off has been found within non-cooperatively breeding species, whereas in cooperatively breeding species this trade-off is alleviated or even completely disappears. | (✓) |
| | b) Taxa groups with clutch size $> 2$: lare-brained species reduce clutch size. Taxa groups with clutch size $< = 2$: large-brained species reduce birth rates and elongate development periods. | Clutch $> 2$: large-brained species reduce clutch size. Clutch $< = 2$: large-brained species tend to reduce birth rates. However, development periods are not elongated. | (✓) |
| | c) If controlling for the amount of allomaternal care, longevity positively correlates with relative brain size. From another prespective, species without allomaternal care show a positive correlation between longevity and relative brain size, whereas species with allomaternal care do not. | After controlling for the amount of allomaternal care, longevity does not correlate more positively with relative brain size. However, a positive correlation has been found within non-cooperatively breeding species, whereas in coopeartively breeding species this relationship is alleviated or even completely disappears. | (✓) |
| | d) Large-brained species with reduced reproduction are more endangered. | No correlation between relative brain size or reproduction and status on the worldwide scale has been observed. However, the probabilty of being endangered is highest for species with rather large brains and low reproduction. | ? |

(to be continued)

| | | | |
|---|---|---|---|
| 3. Energy Subsidies Hypothesis | a) Either a positive correlation between relative brain size and amount of allomaternal care or reproduction and amount of allomaternal care is expected. | **Energetic measurements** show a positive correlation with relative brain size and a negative one with reproduction. **Number of caretakers** and **breeding type** show neither a correlation with relative brain size nor with reproduction. | (✓) |
| | b) Energetic load per caretaker is predicted to correlate negatively with relative brain size. | Energetic load per caretaker positively correlates with relative brain size. | ✗ |
| | c) Energetic input per offspring is expected to correlate positively with adult relative brain size. | Energetic input per offspring strongly positively correlates with relative brain size. | ✓ |
| 4. Energy Subsidies, Egg mass and Altriciality | a) Mate feeding shows either a positive correlation with relative brain size or egg size. | It seems as if mate feeding rather correlates with relative egg size than brain size, however it is hard to distinguish between these two, as they show a strong positive correlation among each other. | (✓) |
| | b) Amount of allomaternal care correlates negatively with relative egg mass. | No clear pattern has been found. Number of caretakers and breeding type show rather weak negative trends with relative egg mass, whereas total energetic input shows a positive relationship. | ? |
| | c) Species with higher amounts of allomaternal care are expected to show a shift towards altriciality. | In precocial species, rather a shift towards extreme precociality than altriciality has been found. | ✗ |
| 5. Development Hypothesis | Amount of allomaternal care shows a stronger effect on relative brain size than development mode per se. | After including development mode as covariate, total energetic input still shows a positive correlation with relative brain size. | ✓ |
| 6. Maternal Energy Hypothesis | Total input per offspring correlates stronger with relative brain size than maternal input per offspring. | Total input per offspring tends to correlate stronger with relative brain size than maternal input per offspring. | ✓ |

(to be continued)

| | | | |
|---|---|---|---|
| 7. Time vs. Energetic Contraints | The amount of allomaternal care is expected to correlate stronger with relative brain size than duration of parental care. | After correcting for the duration of parental care, energetic expenditure shows still a trend towards a positive correlation with relative brian size. However, also time shows a positive correlation with relative brain size. Thus, both, energetic and time aspects affect relative brain size. | (✓) |
| 8. Social Brain Hypothesis | Amount of allomaternal care is expected to affect relative brain size rather than a gregarious lifestyle per se. | After correcting for social pattern, total energetic input still shows a positive correlation with relative brain size. | ✓ |

### 4.6.1 Inconsistent findings using the three alternative measurements of allomaternal care

Comparing the three alternative measurements of allomaternal care (total energetic input during the chick rearing period, number of caretakers and breeding type), no consistent pattern has been found. There are several explanations for that.

Regarding the difference between breeding types in hypothesis 2 a, a very clear pattern has been observed. Species without allomaternal care show a strong trade-off between reproduction and relative brain size, whereas in species with allomaternal care this negative relationship diappears. However, contradictionary to my prediction, additionally including one of the three alternative measurements of allomaternal care as a covariate, does not yield a stronger negative relationship between reproduction and relative brain size. These results imply that the quantifications of allomaternal care are not adequate. Using simply the number of caretakers as a measurement of allomaternal care might not accurately enough represent the differences within cooperative breeders. In fact, taxa groups with two or more caretakers during breeding represent alomst 90% of all species and most of them are pair breeders (ca. 70%). Thus, the number of caretakers mostly equals two and rather rarely three or more, so the variation is very low resulting in non-significant results. Moreover, although total energetic input during chick rearing probably represents an accurate measurement of the amount of allomaternal care, the sample size is rather small (n=59) including only pair and cooperatively breeding species. Therefore, correcting for the energetic input does also not yield a stronger negative relationship between reproduction and relative brain size. Regarding the analyses with family means, also no clear pattern has been observed, probably because the sample size is still quite high, (up to 180) swamping the contrasts which would account for the predicted effects.
Additionally, in birds there is a high flexibility in breeding systems and high variability in parental care which makes it very difficult to appropriately measure the amount of allomaternal care. In some groups, there is no parental care at all, such as in brood parasites, or geothermal breeders, and others are obligate cooperative breeders which need the help of others to at least rear one offspring (e.g. certain honeyeaters). Taxa

groups with parental care show a huge variety of how caring for young. Either the food is only shown to offspring and they mainly feed on their own, or in other species the offspring is actively fed by caretakers and in others again the offspring are only guarded (Clutton-Brock 1991 b). Further, the assignment of breeding functions among caretakers is probably often uneven, and how much each helper contributes to total energy resources is difficult to quantify, so the simple number of caretakers or breeding type are probably not accurately representing the amount of allomaternal care.

With the results of hypothesis 3, I have shown that total energetic input during chick rearing shows a strong positive effect on relative brain size and a rather negative effect on reproduction. However, using the alternative measurements of allomaternal care (number of caretakers or breeding type), no such pattern has been observed.
First, this might be explained by the fact that all analyses are corrected for development modes in order to avoid pseudo correlations. One might argue that due to this correction in the large samples, including number of caretakers and breeding type with a high variation in development modes, exactly these contrasts disappear which would actually account for the predicted effects, because the differences in the amount of care frequently coincides with the difference in development mode (Isler, personal communication). The small sample, including the energetic measurements, shows a very low variation in development mode and thus, the effects do not disappear.
Second, the missing link between number of caretakers and relative brain size and reproduction might be explained by a possible inaccurate representation of the amount of allomaternal care as discussed in the previous paragraph, or third, the energetic quantification and number of caretakers cannot be used as alternative measurements, representing not the same issue. In fact, total energetic input shows no positive correlation with number of caretakers, as I would have expected. Actually, according to the model estimating $\text{FMR}_{chick-rearing}$ (table 2.2), the energetic expenditure per caretaker tends to decrease with an increasing number of caretakers, suggesting a load-lightening effect. This would imply that an increasing number of caretakers does not mean higher total energetic input during breeding, and that the results of energetic measurements and number of caretakers need to be regarded separately. Thus, other unknown factors (e.g. ecology), not examined in this study, rather than number of caretakers are needed to explain the variation in total energetic resources during breeding.

### 4.6.2 How do cooperative breeders evade the reproduction trade-off?

In summary, the main aim of this study, including hypothesis 2 and 3, was to investigate the cascade between allomaternal care, load lightening effect of parents, increased brain size and/or reproduction and thus, the reproduction trade-off. I found that species with allomaternal care show an alleviated reproduction trade-off (arrow 1, figure 4.7). There exist several ways for achieving such an alleviated trade-off.
First, cooperative breeding might be linked to an increased total energetic input which might be invested in either brain size or reproduction, or both and eventually allowing for an alleviated reproduction trade-off (arrows 8, 11, 12, 13 and 14, figure 4.7). How-

ever, for now, I did neither find a positive relationship between number of caretakers and total energetic input (arrow 8, figure 4.7) nor between number of caretakers and relative brain size (arrow 7, figure 4.7). However, for testing the link between number of caretakers and total energetic input per breeding season (arrow 8, figure 4.7) more data is needed especially including non-cooperatively breeding species. Furthermore, no relationship between number of caretakers and reproduction (arrow 9, figure 4.7) has been observed and rather a negative one between total energetic input and reproduction (arrow 12, figure 4.7). Based on these results I would reject the original prediction that additional caretakers during breeding allow either for an increase in relative brain size or in reproduction leading to an alleviated reproduction trade-off (arrows 7, 8, 9, 12, 13 and 14, figure 4.7).

Second, having additional help during breeding (cooperative breeding) might allow for an energetic load-lightening of the parents, resulting in higher adult survival (arrows 2 and 4 in figure 4.7). I found that with an increasing number of caretakers the energetic load per caretaker tends to decrease, supporting that part of the cascade. Moreover, in concordance with other studies (Reyer 1984, Hodge 2005, Cockburn et al. 2008), I found a positive relationship between annual adult survival and number of caretakers (arrow 3, figure 4.7). One might think that an energetic load-lightening during breeding allows for maintaining larger brains, which in the end would lead to the alleviated reproduction trade-off. However, I found neither a positive link between number of caretakers and brain size (arrow 7, figure 4.7) nor a negative relationship between energetic load per caretaker and relative brain size (arrow 6, figure 4.7). Therefore, an increase in relative brain size seems not to be the explanation for the alleviated reproduction trade-off within cooperative breeders. The found results supporting the cascade between number of caretakers, load-lightening and higher survival (incorporated in $r_{max}$) rather suggest that the alleviated reproduction trade-off (between $r_{max}$ and relative brain size) in coopearatively breeding species is possible because of higher adult survival due to help during breeding. Moreover, the higher rates of survival enable to have rather few offspring, but of high qualitative, in other words, large offspring with large brains (reproductive quality > reproductive quantity), which as well explains the positive link between survival and relative brain size and the strong negative correlation between annual fertility and relative brain size across species.

To sum up, additional helpers during breeding lead to load-lightened parents and higher rates of survival which in the end allows for an alleviated reproduction trade-off.

Variation in the energetic input during the chick rearing period seems not to arise from variation in number of caretakers but rather from other factors such as ecology, which are not yet understood. However, the energy during breeding, which seems to be independent from the breeding system, and duration of development periods positively affect relative brain and egg size. In other words, higher energetic resources during breeding are invested in brain and egg size.

For future studies, it is crucial to collect further data on energetic expenditures during breeding including species with and especially without allomaternal care, including small- and large-brained species, in order to draw more general and reliable conclusions about the framework of energetic expenditures during breeding, allomaternal care and relative brain size. Especially the link between cooperative breeding and total energetic input during breeding needs to be further investigated. Moreover, directly comparing FMR data of a breeding pair with and a breeding pair without helpers in an occasional cooperative breeding species would give further important insights regarding energy subsidies.

Finally, to explain variation in total energetic resources during breeding, other factors such as ecology and further aspects of avian metabolism need to be considered.

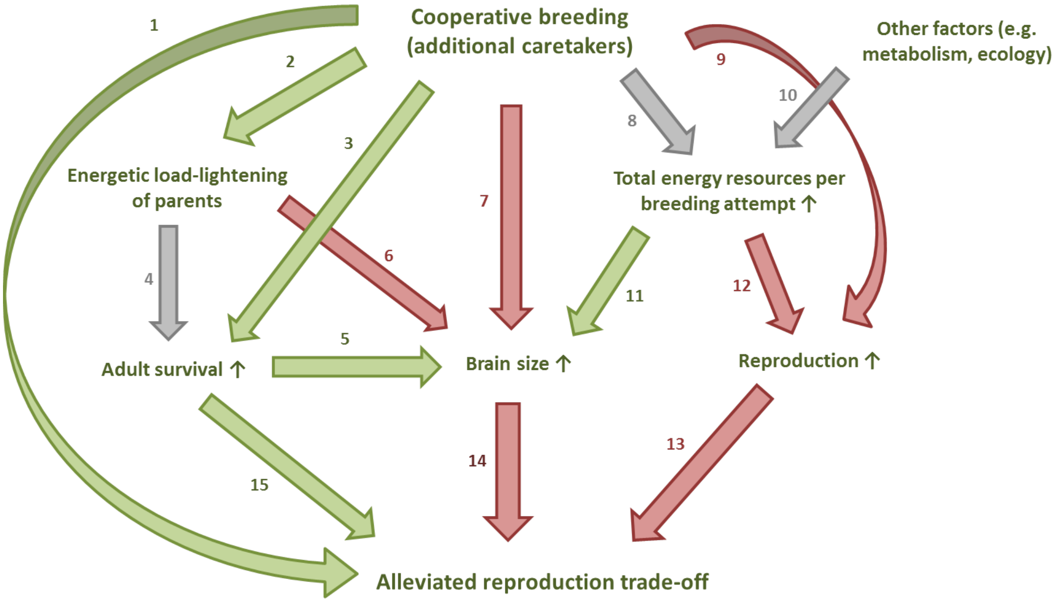


Figure 4.7: **Cooperative breeding and the alleviated reproduction trade-off.** There are several possible ways how cooperative breeders evaded the reproduction trade-off. 1. Consistent with part of hypothesis 2a, I have shown that the reproduction trade-off is strongly alleviated in species with allomaternal care (pair and cooperative breeders). 2. I have found that species with more caretakers tend to reduce the energetic expenditures during breeding, suggesting a load-lightening effect (table 2.2). 3. Number of caretakers and breeding type show positive correlations with annual adult survival and longevity (hypothesis 2c). 4. Energetic load-ligthening during breeding probably allows for higher annual adult survival. 5. Longevity, in contrast to annual adult survival, shows a positive correlation with relative brain size (Hypotesis 2c). 6. According to the findings from hypothesis 3b, energetic load-lightening does not allow for larger relative brain sizes. 7. Relative brain size also shows no correlation with number of caretakers (hypothesis 3a). 8. Cooperative breeding may be linked to higher total energetic input during breeding (although I have found a trend rather indicating a load-lightening effect, this relationship needs to be tested using a much larger sample size). 9. Number of caretakers showed no correlation with reproduction (hypothesis 3a). 10. Other factors, such as ecology or differences in metabolism, and not number of caretakers, might explain variation in total energetic resources (this relationship was not tested in this study). 11. I found an increase in total energetic input per chick rearing period to correlate positively with relative brain size (hypothesis 3a). 12. Reproduction ($r_{max}$ and annual fertility) shows a negative correlation with total energetic input during the chick rearing period (hypothesis 3a). 13. As an increase in reproduction linked to number of caretkakers or energetic input has not been found, this is probably not the way how cooperative breeders alleviate the reproduction trade-off. 14. As no relationship between relative brain size and numer of caretakers has been observed, it is probably not an increase in relative brain size which allows cooperative breeders to alleviate the reproduction trade-off. 15. Higher adult survival, regarding recovery after breeding, probably enables species with higher amounts of allomaternal care to alleviate the reproduction trade-off. Confirmed relationships are coloured in green, unconfirmed relationships in red, and grey arrows represent relationship which were not (fully) tested in this study.

# 5 Conclusions

In the context of the expensive brain framework, this study aimed to explain variation in relative brain size. My results reassured former findings that the total energetic turnover is not correlated with relative brain size, rejecting the metabolic constraint hypothesis in birds, in contrast to mammals. As mainly evidence has been found in mammals so far, the main focus of this study laid on cooperative breeding and a possible link to the evolution of larger brains in birds.

I have shown that species without allomaternal care show a strong trade-off between reproduction and relative brain size. Large-brained species with several eggs per clutch reduce clutch size, whereas species with only one or two eggs per clutch reduce annual birth rates. On the other hand, species which breed cooperatively show no reproduction trade-off.

My results indicate that additional helpers during breeding are linked to a load-lightening effect rather than an increase in total energetic resources. Further, this then leads to increased annual adult survival, a link which has not been found in mammals, and in the end allows for evading the reproduction trade-off (higher rates of survival regarded as the ability to fully recover after the breeding season). Contrarily to my predictions, neither an increase in relative brain size nor in reproduction seems to allow cooperative breeders to evade the reproduction trade-off. Moreover, the higher rates of survival result in the production of few offspring of high quality (originally known as the „K-strategy“ by MacArthur and Wilson (1967)).

Variation in total energetic input during breeding, being independent of number of caretakers, and durations of development periods are linked to the variation in relative brain size. Other, yet unkown factors (e.g ecology) and not the number of caretakers seem to determine the amount of energetic resources during breeding.

Furthermore, alternative theories (e.g. development hypothesis, maternal energy hypothesis or social brain hypothesis) could have been shown not to sufficiently and ultimately explain the huge variation in relative brain size.

Although, not every single link could have been fully examined and understood, there are many indications that energy plays a crucial role in the framework of allomaternal care and relative brain size (figure 4.7). The framework as a whole enlightens important aspects of cooperative breeding and brain size evolution in birds. These findings support the cooperative breeding hypothesis (Hrdy 2009) which claims that the evolution of cooperative breeding enabled the human lineage to be large-brained. Thus, these findings are important for the further study of brain size evolution in mammals, especially in the lineage of *Homo*.

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