Die Reproduktion von Dinosauriern, speziell der Sauropoden und deren Bedeutung für ihren Gigantismus

Dissertation zur Erlangung des Grades
Doktor der Naturwissenschaften

Am Fachbereich Biologie
der
Johannes Gutenberg-Universität Mainz

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Mainz im August 2010

Dekan:

1. Berichterstatter:

2. Berichterstatter:

Tag der mündlichen Prüfung: 15.12.2010

Danksagung

Ich möchte allen danken, die mich bei der Durchführung meiner Dissertation in irgendeiner Weise unterstützt haben.

Diese Dissertation war eingegliedert in der DFG Forschergruppe 533, “Biology of the Sauropod Dinosaurs: The Evolution of Gigantism” und wäre ohne die finanzielle Hilfe der deutschen Forschungsgemeinschaft (DFG) nicht zustande gekommen (Förderungsnummer: GR 2625/2-1).

Danke an meine Familie und Freunde.

“Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relationship to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring.”

- Charles Darwin -

Kapitel 2 wurde zur Publikation bei Indian University Press akzeptiert und befindet sich im Druck:
Griebeler, E.-M., and J. Werner. in press. The life-cycle of sauropods *in* N. Klein, C. Remes, C. T. Gee, and P. M. Sander, eds. Biology of the Sauropod Dinosaurs: Understanding the life of giants. Indian University Press, Bloomington.

Kapitel 4 wurde zur Publikation beim Journal of Evolutionary Biology eingereicht und befindet sich im Review:
Werner, J., and E. M. Griebeler. in review. Reproductive biology and its impact on body size: Comparative analysis of mammalian, avian and dinosaurian reproduction. Journal of Evolutionary Biology.

Inhaltsverzeichnis

1 Allgemeine Einleitung

Die Rekonstruktion von kompletten life-histories (Lebenszyklusstrategien) ausgestorbener Organismen oder auch nur Teilen davon ist schwierig, scheint teilweise unmöglich und birgt immer die Gefahr fehlerhaft zu sein, da viele ihrer life-history Merkmale nur indirekt aus Fossilfunden, meist aber auch nur durch Ableitung von rezenten Verwandten, rekonstruiert werden können (Case 1978b; Dunham et al. 1989; Deeming 2006; Erickson et al. 2007; Ricklefs 2007; Jackson et al. 2008; Lee und Werning 2008; Varricchio et al. 2008; Griebeler und Werner im Druck, Kapitel 2). Aber gerade Erkenntnisse über die life-history ausgestorbener Organismen können einen wichtigen Beitrag zum Verständnis bestimmter life-history Merkmale (z.B. Wachstum oder Reproduktion) und deren Evolution (z.B. hin zu schnellerem Wachstum oder Änderung von Reproduktionsmerkmalen) liefern (Sander et al. 2004; Zelenitsky 2006; Varricchio et al. 2008; Zelenitsky und Therrien 2008a, b; Zelenitsky et al. 2008). Daher ist die Rekonstruktion der life-history ausgestorbener Organismen oder auch nur Teile von ihr, wie z.B. die Reproduktion, eine Herausforderung für jeden Paläontologen oder Evolutionsbiologen.

So soll unter anderem die hohe Reproduktionskapazität der oviparen Dinosaurier es diesen ermöglicht haben, im Vergleich zu terrestrischen viviparen Säugetieren sehr viel größer zu werden (Kurtén 1953; Janis und Carrano 1992). Bei den rezenten Säugetieren nimmt die jährliche Anzahl der Nachkommen mit zunehmender Körpergröße ab, während sie bei den heutigen Vögeln unabhängig von der Körpergröße ist (Janis und Carrano 1992) und bei den rezenten Reptilen sogar zunimmt (Blueweiss et al. 1978). Ohne abgesicherte Erkenntnisse über die Reproduktionsstrategie von Dinosauriern lässt sich diese Hypothese zur Reproduktionskapazität aber nur schwer bestätigen oder widerlegen.

Bei der Rekonstruktion von life-history Merkmalen, die nicht direkt aus Fossilien ableitbar sind, ist eine Zusammenarbeit von Paläontologen und Biologen notwendig. Dies ermöglicht die Nutzung der neusten Forschungserkenntnisse aus beiden Fachrichtungen und minimiert fehlerhafte Interpretationen. Insgesamt ist ein Zusammenführen verschiedener Fachdiszipline vor allem immer dann sinnvoll, wenn komplexe Themen bearbeitet werden sollen. So habe ich diese Dissertation im Rahmen eines Projekts angefertigt, in dem Wissenschaftler aus verschiedensten

Disziplinen zusammenarbeiten, um den Gigantismus der Sauropoden (langhalsige herbivore Dinosaurier mit langem Schwanz, z.B. Apatosaurus; jüngeres Synonym: Brontosaurus; größte bekannte landlebende Wirbeltiere) zu erforschen.

1.1 life-history und Reproduktion

Lebewesen sind nicht nur durch ihr Genom, ihre Physiologie und ihre Morphologie charakterisiert, sondern auch durch ihre life-history (Lebenszyklusstrategie). Sie steht im Mittelpunkt der Forschung eines Teilbereiches der Ökologie und auch der Evolutionsbiologie. Eine stark vereinfachte und verallgemeinerte life-history umfasst die Geburt, eine präreproduktive Phase, eine Fortpflanzungsphase, eine postreproduktive Phase und den Tod als Folge der einsetzenden Seneszenz. Mortalitäten können aufgrund externer Ursachen in jeder Phase des Lebens auftreten. Die life-histories aller unitaren Organismen können als Variationen dieses einfachen Musters angesehen werden, obwohl eine postreproduktive Phase aufgrund der extern verursachten Mortalitäten wahrscheinlich eher die Ausnahme ist (Townsend et al. 2002). So wird die life-history eines Dinosauriers auch durch obiges Muster beschrieben werden können.

Histologische Analysen von fossilen Knochen können Informationen über das Wachstum und das Alter der Dinosaurier liefern, was wiederum Rückschlüsse über das Eintreten und die Dauer der aufgezeigten Phasen ihrer Lebenszyklen erlaubt (Sander et al. 2004; Sander et al. 2006; Erickson et al. 2007; Ricklefs 2007; Klein und Sander 2008; Lee und Werning 2008; Klein et al. 2009). Fossilfunde von Eiern und Gelegen können Erkenntnisse über die Reproduktion von Dinosauriern liefern (Carpenter et al. 1994; Chiappe et al. 1998; Carpenter 1999; Chiappe et al. 1999; Horner 1999; Reisz et al. 2005; Deeming 2006; Jackson et al. 2008; Sander et al. 2008; Varricchio et al. 2008). Wissenschaftler versuchen sogar demographische Verteilungen von Populationen, die Aussagen über altersabhängige Mortalitäten ermöglichen, aus fossilen Knochenansammlungen (Erickson et al. 2006) oder Fußspuren abzuleiten (Lockley 1994), so dass zumindest ansatzweise eine life-history für bestimmte Dinosaurier skizziert werden kann. Wie genau diese aber ausgesehen hat bleibt weitestgehend spekulativ. Trotzdem ist es sinnvoll anhand aller bekannten Fakten eine mögliche life-history zu skizzieren, da so neue

Hypothesen abgeleitet werden können, die für die Vervollständigung unseres Wissens über die Dinosaurier erforderlich sind.

Ein wichtiger Teil jeder life-history ist die Reproduktion. Um wenigstens diesen Teil der life-history, in den größten jemals existierenden Landlebewesen, den Sauropoden, besser zu verstehen, untersuchte ich in meiner Arbeit hauptsächlich diese. Unterschiedlichste Reproduktionsstrategien (z.B. annuelle oder perenne Arten, iteropare oder semelpare Arten) sind im Laufe der Zeit in Wechselwirkung mit verschiedenen Umweltbedingungen (z.B. konstante gegen variable Umwelt) in Organismen unterschiedlichster Größe entstanden (Stearns 1976, 1977; Townsend et al. 2002). Trotz der vielen existierenden unterschiedlichen Körpergrößen und Reproduktionsstrategien von Organismen gibt es bei vielen von ihnen, wenn nicht gar bei allen, generelle Zusammenhänge zwischen bestimmten Reproduktionsmerkmalen und der Körpergröße, besser gesagt dem Körpergewicht (Blueweiss et al. 1978; Western und Ssemakula 1982; Ernest et al. 2003). Aus diesen Zusammenhängen ergeben sich direkt Fragen wie: Sind große unitare Organismen durch bestimmte life-histories und/oder Reproduktionsstrategien gekennzeichnet? Wenn ja, wie sah die Reproduktion in den größten bekannten Landlebewesen, den Sauropoden aus? Welche Konsequenzen ergeben sich für extreme Körpergrößen daraus?

1.2 Die Reproduktion in eierlegenden Amnioten

Um die Frage zu beantworten, wie die Reproduktion in den größten bekannten Landlebewesen den Dinosauriern aussah, kann man einerseits auf Fossilfunde zurückgreifen. Fossilfunde, wie Gelege mit Embryonen (Norell et al. 1994; Chiappe et al. 1998; Horner 1999; Horner 2000; Varricchio et al. 2002; Reisz et al. 2005), auf Gelegen „sitzende“ Dinosaurier (Norell et al. 1995; Dong und Currie 1996; Varricchio et al. 1997; Clark et al. 1999) aber auch neue Forschungsmethoden wie der CRT-Scan (hilft beim Auffinden von Embryonen in fossilen Eiern) machen es Paläontologen möglich bisher nicht oder nur unsichere Zuweisungen von fossilen Gelegen zu Dinosauriertaxa zu belegen. Somit können Eier und Gelege bestimmten Dinosauriern zugeordnet werden und man kann direkt anhand der Fossilien Aussagen über die Größe der Eier und Gelege oder das Verhältnis Körpergewicht zu

Ei- oder Gelegegewicht (anhand von Schätzungen) treffen. Andererseits sagen die Fossilfunde nichts darüber aus, wie viele Gelege pro Jahr oder pro Reproduktionsereignis von den Tieren gelegt wurden. Auch sind Angaben in Bezug zur Gelegegröße oft sehr unsicher, da häufig unklar ist, ob die Gelege vollständig sind und manchmal nicht klar ist, ob einzelne Eier tatsächlich zu einem Gelege gehören (Cousin et al. 1994; Moratalla und Powell 1994; Carpenter 1999; Sander et al. 2008). Um eine Aussage zu den nicht aus Fossilfunden direkt ableitbaren Reproduktionsmerkmalen machen zu können oder um die unsicheren Ergebnisse besser abzusichern, muss man sich die Reproduktion bei den heute noch existierenden nächsten phylogenetisch verwandten Taxa der Dinosaurier anschauen. Dabei kommen einem die oben erwähnten Zusammenhänge zwischen Körpergröße und Reproduktion möglicherweise zu gute.

Die Korrelationen zwischen dem Körpergewicht und den verschiedenen Reproduktionsmerkmalen von Organismen lassen sich meist recht gut durch eine Potenzfunktion der Form $R = c \times BM^{b}$ beschreiben (Rahn et al. 1975; Blueweiss et al. 1978; Ernest et al. 2003, Hendriks und Mulder 2008). Dabei ist R ein Reproduktionsmerkmal, c eine Konstante, BM das Körpergewicht und b ein Exponent. Da der Exponent normalerweise von eins verschieden ist, werden diese Potenzfunktionen auch als allometrische Gleichungen oder einfach nur Allometrien bezeichnet. So sind z.B. das Eigewicht oder das Neugeborenengewicht, das Gelege- oder Wurfgewicht und das jährliche Gelege- oder Wurfgewicht in allen rezenten Amnioten mit dem Körpergewicht positiv korreliert (Blueweiss et al. 1978; Western und Ssemakula 1982; Ernest et al. 2003; Hendriks und Mulder 2008). Diese Zusammenhänge lassen sich mit allometrischen Gleichungen beschreiben, wobei der Exponent in Abhängigkeit des Reproduktionsmerkmals und Taxons häufig zwischen 0.25 und 1 liegt (Blueweiss et al. 1978; Western und Ssemakula 1982; Ernest et al. 2003; Hendriks und Mulder 2008). Da diese Zusammenhänge zwischen Körpergröße und Reproduktionsmerkmalen in allen rezenten Amnioten zu beobachten sind, kann man davon ausgehen, dass sie auch in ausgestorbenen Amnioten, wie den Dinosauriern existiert haben. Um die Frage zu beantworten, wie die Reproduktion in Dinosauriern vermutlich aussah, kann man allometrische Gleichungen für deren phylogenetische Verwandte, wie Vögel und Reptilen, bestimmen und diese als Modelle für die Dinosaurier verwenden.

1.3 Gigantismus und Reproduktion

Die Körpergröße ist wohl eines der auffälligsten und wesentlichsten Merkmale jedes Lebewesens. Sie beeinflusst beinahe jeden biologischen Aspekt eines Organismus (Bonner 2006; Hunt und Roy 2006). Daher beschäftigen sich eine riesige Anzahl an Studien mit „scaling“, den Zusammenhängen zwischen Körpergröße und anderen Eigenschaften von Individuen, wie z.B. die Reproduktion (Blueweiss et al. 1978; Western und Ssemakula 1982; Allaine et al. 1987; Thompson 1987; Brown und West 2000; Ernest et al. 2003; Brown et al. 2004 und Referenzen darin; Dol’nik 2000; Hendriks 2007 und Referenzen darin; Hendriks und Mulder 2008; Birchard und Deeming 2009). Fast so zahlreich wie die Lebewesen auf unserem Planeten, ist die Variabilität in der Körpergröße, die man an rezenten, aber auch an ausgestorbenen Lebewesen beobachten kann. So reicht das Größenspektrum bereits bei Säugetieren über mehrere Zehnerpotenzen von 2 g (Schweinsnasenfledermaus, Etruskerspitzmaus) bis 120 t (Blauwal). Besonders interessant ist es extreme Körpergrößen zu untersuchen, da dies unter anderem Aufschluss darüber geben kann, welche Merkmale und Eigenschaften limitierend bzw. begünstigend auf extreme Körpergrößen wirken können. Wie sind Körpergewicht und andere Merkmale in besonders großen (oder kleinen) Organismen korreliert? Welche Merkmale sind das und warum genau diese?

Maximale Körpergröße, auch Gigantismus genannt, kann man direkt an rezenten Organismen, wie z.B. dem schwersten marinen Lebewesen, dem Blauwal, oder dem größten bekannten Baum, dem Mammutbaum, beobachten und studieren. Andere Gigantismen kennen wir nur aus erdgeschichtlich vergangenen Epochen. Sie können deshalb nur anhand von Fossilfunden erforscht werden, wie z.B. das größte bekannte Insekt, eine Libelle aus dem Karbon (Protodonata, Dudley 1998) oder das größte bekannte landlebende Tier, ein Sauropode (*Argentinosaurus*, Mazzetta et al. 2004) aus der Gruppe der Dinosaurier, der in der Kreidezeit gelebt hat. Will man den Gigantismus in terrestrischen Wirbeltieren erforschen und der Frage nachgehen, warum z.B. Säugetiere nicht so groß wurden wie manche Dinosaurier, muss man die größten Dinosaurier, das sind die Sauropoden, und deren rezente Verwandte untersuchen. Was hat aber der Gigantismus der Dinosaurier mit deren Reproduktion zu tun?

Die Fortpflanzung oder Reproduktion ist eine grundlegende Eigenschaft jedes Lebewesens (Ruiz-Mirazo et al. 2004; Purves et al. 2006). Ohne Reproduktion, die die Vermehrung von Individuen gewährleistet, würde es langfristig kein Leben auf der Erde geben. Auch auf molekularer Ebene, der DNA jedes Organismus, findet man die Fähigkeit zur Replikation und sogar Grenzformen des Lebens, wie Viren, können sich reproduzieren (auch wenn sie dazu einen Wirt brauchen). Somit ist die Reproduktion ein Merkmal von Lebewesen das mindestens seit Anbeginn des Lebens unter natürlicher Selektion steht (Joyce 2002; Manapat et al. 2010). Trotz oder gerade weil die Reproduktion Milliarden von Jahren Zeit hatte in unterschiedlichsten Organismen zu evolvieren (Hedges et al. 2004; Schopf et al. 2007), kann man heute eine große Anzahl verschiedener Reproduktionsstrategien bei Organismen als Anpassungen an die von ihnen bewohnten Umwelten beobachten (Cole 1954; Giesel 1976; Stearns 1977; Townsend et al. 2002).

Manche Reproduktionsmerkmale, wie das jährliche Gelege/Wurfgewicht sind anscheinend, unabhängig von dem betrachteten Organismus, immer ähnlich mit dem Körpergewicht korreliert (Blueweiss et al. 1978; Western und Ssemakula 1982; Ernest et al. 2003), während andere Merkmale, wie die Gelege/Wurfgröße, in manchen Organismengruppen mit der Körpergröße positiv (z. B. Reptilien, Blueweiss et al. 1978; Thorbjarnarson 1996; King 2000), gar nicht (z.B. Vögel, Kulesza 1990; Janis und Carrano 1992; Figuerola und Green 2006) oder sogar negativ (z.B. Säugetiere, Tuomi 1980; Millar und Zammuto 1983; Janis und Carrano 1992) korreliert sein können. Daher wies schon Kurtén (1953) darauf hin, dass Körpergröße in einem Taxon nicht nur durch mechanische oder physiologische Beschränkungen limitiert sein kann, sondern auch durch die Korrelation mit bestimmten Reproduktionsmerkmalen. Dies wirft natürlich die Frage auf, ob die Reproduktionsstrategie der Dinosaurier, insbesondere der Sauropoden, etwas mit ihrem Gigantismus zu tun haben könnte.

1.4 Ziele der Arbeit

Inhalt dieser Arbeit war es einen Teil der life-history, die Reproduktion, von Dinosauriern, speziell der Sauropoden, zu untersuchen, um unter anderem den Zusammenhang zwischen Gigantismus und Reproduktion zu erforschen.

Sauropoden eignen sich besonders um diese Fragestellungen anzugehen, da sie die größten bekannten Landlebewesen sind. Weiterhin sind sie eine gut untersuchte Dinosauriergruppe mit vergleichsweise vielen Fossilbelegen. So existieren fossile Eier und Nester, sowie in einem Fall sogar Eier mit Embryonen, die deren sichere Zuordnung zu einem Sauropodentaxon (Titanosaurier) ermöglicht.

Mein erstes Ziel war es eine mögliche life-history für Sauropoden, auf Grundlage des heutigen Forschungsstands in der Biologie und der Paläontologie, zu erstellen. Mein zweites Ziel war die Etablierung eines Modells zur Analyse der Reproduktion bei ausgestorbenen eierlegenden Wirbeltieren, um der Frage nachzugehen, wie einige Merkmale der Reproduktion bei Dinosauriern wahrscheinlich ausgesehen haben. Mein drittes Ziel war die Überprüfung der Hypothese, dass Dinosaurier, insbesondere Sauropoden, eine höhere Reproduktionskapazität hatten als gleich große landlebende Säugetiere, was ersteren im Vergleich zu letzteren ermöglicht haben soll viel größer zu werden (Janis und Carrano 1992).

Alle drei Studien dieser Arbeit beruhen auf Literaturrecherche, mit dem Ziel der Erhebung von Daten zu Reproduktionsmerkmalen von phylogenetisch mit den Dinosauriern verwandten Wirbeltiergruppen. Während die erste Studie ein reines Review ist, beschäftigen sich die beiden anderen hauptsächlich mit Vergleichen allometrischer Zusammenhänge zwischen Körpergewicht und verschiedensten Reproduktionsmerkmalen bei unterschiedlichen rezenten und ausgestorbenen Wirbeltiergruppen. Um die große Menge an aufgenommen Daten zu sichern, zu verwalten und analysieren zu können, habe ich für diese eine Datenbank mit Microsoft Access 2003 (11.8166.8221, ServicePack 3) erstellt. Insgesamt habe ich für über 300 Arten, 7 Merkmale pro Art und meistens mindestens zwei unterschiedliche Literaturquellen pro Merkmal gesammelt, und damit insgesamt weit über 4000 Datensätze in die Datenbank aufgenommen.

Meine Dissertation beinhaltet drei Hauptkapitel, die jeweils wie Publikationen in Büchern oder Fachzeitschriften verfasst sind. Kapitel 2 (Griebeler und Werner, im Druck) fasst das gegenwärtige Wissen über Dinosaurier, speziell der Sauropoden, in Hinblick auf deren life-history und Reproduktion zusammen und erläutert, wie die life-history eines Sauropoden aufgrund von Erkenntnissen aus Fossilfunden, aus life-history Studien an rezenten nahen Verwandten der Dinosaurier und aus der Ökologie ausgesehen haben könnte. Kapitel 3 befasst sich mit der Etablierung von Modellen zur Prognose von Reproduktionsmerkmalen von ausgestorbenen eierlegenden Wirbeltieren. Wie sieht die Reproduktion in rezenten, eierlegenden Wirbeltieren aus, die nahe mit den ausgestorbenen verwandt sind? Hierzu werden von mir die Zusammenhänge zwischen Körpergröße und verschiedenen Reproduktionsmerkmalen, wie Eigewicht, Gelegegewicht und Gesamtgewicht aller Gelege pro Jahr, untersucht. Die Validierung dieser allometrischen Modelle erfolgt durch Daten zu ausgestorbenen Vögeln. Die erstellten Modelle werden dann von mir auf verschiedene Dinosaurier angewendet. Kapitel 4 beschäftigt sich mit dem Vergleich der Zusammenhänge zwischen der Körpergröße und der Gelegegröße und der Anzahl der Nachkommen pro Jahr von rezenten nahen Verwandten der Dinosaurier (Vögel) und Säugetieren. Des Weiteren werden diese Ergebnisse in Bezug zu den bekannten Gelegegrößen von Sauropoden und anderen Dinosauriern gesetzt. Ich bearbeite die Hypothese, ob Dinosaurier, insbesondere Sauropoden, eine höhere Reproduktionskapazität hatten als gleich große ebenfalls landlebende Säugetiere und ob dies etwas mit dem Gigantismus in ersteren zu tun haben kann (Janis und Carrano 1992). Ist diese bereits ältere Hypothese unter neusten Erkenntnissen aus der Paläontologie und Biologie auch bei Anwendung neuerer statistischer Auswerteverfahren noch haltbar?

2 The life-cycle of sauropod dinosaurs

2.1 Abstract

As sauropod dinosaurs are extinct, it might seem impossible to fully reconstruct their life-cycles. Nevertheless, information on reproduction, reproductive behavior, growth in body size and sexual maturity can be directly derived from the fossil record. In addition, we can also use living phylogenetically related taxa as models for these extinct animals in order to support and expand our knowledge on sauropod life-cycles. Predictions from life-history theory on the relationship between reproductive traits and body size as well as the analyses of life-cycle characteristics of extant reptiles, birds, and mammals are also appropriate. In the present chapter, we utilize this complex approach for the reconstruction of sauropod life-cycles. We summarize the information on eggs, clutches, nests, hatching, adolescence and growth in body size that had been derived from the fossil record. In addition, we try to fill the gaps in our knowledge concerning the reproductive behavior, the total reproductive output of animals, and the mortality during the life-cycle using information from extant phylogenetic brackets or predictions of life-history theory. Finally, we discuss hypotheses explaining gigantism of sauropods based on their life-cycles.

2.2 Geographic distribution of egg shells, intact eggs, and eggs with embryonic bone or integument

As in all extant archosaurs (birds, crocodilians) the life of a sauropod began in an egg. Dinosaur eggshell fragments were first reported in 1859 by Jean-Jacques Pouech from the egg-rich rugged foothills of the French Pyrenees (Buffetaut and Le Loeuff 1994). Matheron (1869) attributed similar eggshells to the sauropod *Hypselosaurus,* based on the thickness of the eggshell and the presence of this species in the same formation. These large, round eggs are distributed nearly worldwide, occur exclusively in the Late Cretaceous, and belong to the Megaloolithidae (Figure 2.1). Identical eggs to those first found in France are also known from the Tremp Basin of northeastern Spain (López-Martinéz 2000; Sander et al. 1998, 2008). During the Late Cretaceous period and prior to the uplift of the Pyrenees, a continuous facies belt existed between the Spanish and French egg sites. Eggs from the Tremp Formation in northern Spain are preserved in paleosols that were developed on alluvial to marginal marine deposits (Sander et al. 2008). The oofamily Megaloolithidae includes over 20 oospecies, and the most thoroughly documented localities occur in Argentina, northern Spain, southern France, and India; however, other occurrences are known from Romania, Korea and Africa (Sander et al. 2008).

Figure 2.1. Eggs of the oogenus *Megaloolithus* from southern Europe. Eggs on the left are from Catalonia, northern Spain; eggs on the right are from southern France. The eggs are in the collections of the Institute of Paleontology of the University of Bonn, Germany. Scale bar is 5 cm.

Substantial diversity within the oofamily Megaloolithidae is also documented from the Lameta Formation in north-central India (Mohabey 2001, 2005). The egg bearing strata occur in the Deccan Traps, a rugged landscape containing lava flows that record immense volcanism during Late Cretaceous (Maastrichtian) time. The sauropods used this region between periods of volcanic eruptions. Thousands of eggshells and unhatched eggs have been found in this region, but none preserve embryonic remains. Although most of the egg material from the Lameta Formation is assigned to the oofamily Megaloolithidae (Sahni et al. 1994), detailed observations on egg occurrence have not been published (Sander et al. 2008).

In contrast to these Indian and European sites, the Auca Mahuevo locality in Argentina produced the first eggs containing sauropod embryonic bones and integument in 1997. Cranial characters of the in ovo embryos allowed the identification of the eggs as those of titanosaur sauropods (Chiappe et al. 1998; 2001; Salgado et al. 2005). This spectacular nesting site is located about 120 km north of the city Neuquén in Neuquén province. Egg-bearing layers occur in uniform mudstones representing overbank deposits on a fluvial plain. Several egg-beds are also reported from Barreales Norte and Barreales Escondido, two adjacent nesting sites 15 and 22 km south of Auca Mahuevo, respectively. Auca Mahuevo nesting sites include thousands of in situ titanosaur fossil eggs referable to the *Megaloolithus patagonicus* (Calvo et al. 1997). Jackson et al. (2004) also documented clutches containing abnormal eggs from this locality.

Reisz et al. (2005) reported the oldest eggs referable to the Sauropoda that contain embryos. This cluster of six subspherical eggs assigned to the prosauropod *Massospondylus carinatus* came from the Lower Jurassic Elliot Formation of South Africa. Since the eggshell structure of these eggs is unidentifiable, most likely due to recrystalization (F. D. Jackson, pers. comm.), eggs are not assignable to any oofamily. Grigorescu et al. (1994) described megaloolithid eggs from a site near the Romanian village of Tustea. They assigned them to the hadrosaur *Telmatosaurus* based on embryonic or hatchling bones found in the mudstone that contained the eggs. These taxonomic assignments, however, are controversial (Carpenter 1999), because assignments of an egg to a taxon on any evidence other than embryonic remains within an egg have been proven fallacious (Norell et al. 1994; Horner and Weishampel 1988).

2.3 Morphology and parataxonomy of eggs

Assigning the fossil eggs and eggshells to a specific dinosaur species is difficult and often speculative. Positive identifications rely on the presence of an embryo inside an egg, but even this does not necessarily guarantee a correct assignment. There can be a considerable morphological difference between an embryo and the adult animal. Individuals can change characteristics during ontogeny and various embryos can look very similar to one another, even across broad categories of taxa. Bones from embryos or hatchlings are rare. Small bones are less likely to be preserved because they are more easily destroyed by environmental and geological forces or even trampling by other animals. Nevertheless the classification of dinosaur eggs and eggshells based on macrostructural (e.g. size, shape, shell thickness and ornamentation) and microstructural characteristics (e.g. shell units, pores) can reveal important insights in the reproductive biology of dinosaurs and their taxonomy.

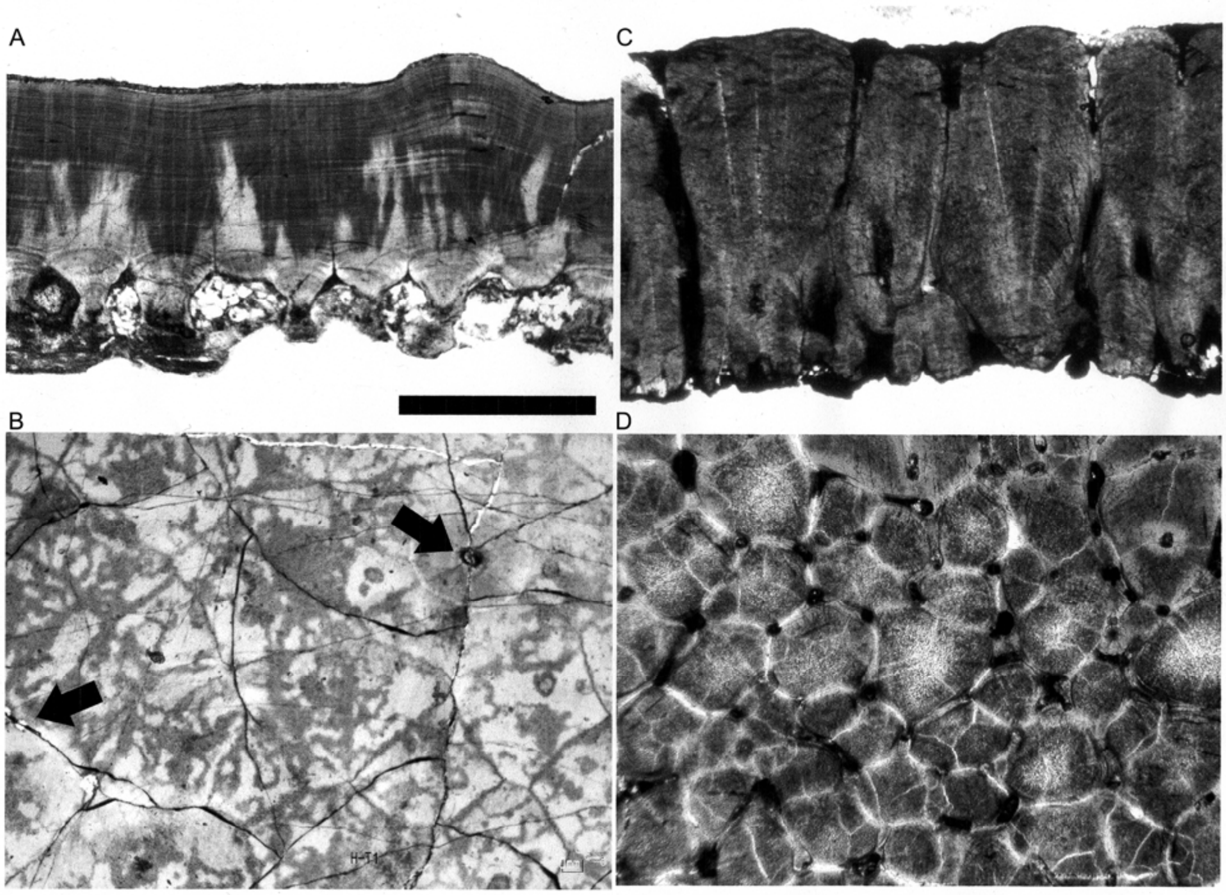


Figure 2.2. Comparison of shell microstructure and porosity. **A**. *Megaloolithus patagonicus* from Auca Mahuevo, Argentina: radial cross section, specimen PVPH 113, an egg containing an embryo, and **B** tangential section of an uncatalogued egg. Note that there are only two pores visible in this section (arrows), with a third one possibly located between the arrows. **C**. *Megaloolithus mammilare* from Coll de Nargó, Spain: radial cross section and **D** tangential section of egg XXII/4. Note the numerous pores located at the junction of the shell units. The shell samples figured in A and B are catalogued at the Museo Carmen Funes, Plaza Huincul, Argentina, and those figured in C and D at the Institute of Paleontology of the University of Bonn, Germany. Scale bar is 1 mm and applies to all images.

As all living archosaurs (birds, crocodilians) have hard-shelled eggs, it is assumed that the eggs laid by all sauropodomorph dinosaurs had been hard-shelled.

This was corroborated by the basal sauropodomorph *Massospondylus* from the Early Jurassic of South Africa for which hard-shelled eggs had been discovered (Reisz et al. 2005).

Eggs and eggs with embryos from the Auca Mahuevo locality are similar in size, shape, microstructure (Figure 2.2), and surface ornamentation. They are spherical to subspherical, with a diameter between 13 cm and 15 cm and an average volume of 1.5 l (Chiappe et al. 1998; Jackson et al. 2008). Shell thickness of eggs ranges from 1.00 mm to 1.78 mm with a mean of 1.40 mm (Chiappe et al. 1998). Surface ornamentation consists of domed tubercles with an average diameter of 0.45 mm (Chiappe et al. 1998). Pore canals enabling gas exchange are unevenly distributed between the tubercles. Shell units exhibit a radial-tubular ultrastructure.

Eggs from southern Europe are round to slightly oval, ranging in size from about 14 x 27 cm to 18 x 22 cm (Figure 2.1; Peitz 2000; Sander et al. 2008). Eggshell thickness is rather variable between localities and between clutches; however, the average thickness among the eggs of a single clutch is rather constant (Peitz 2000; Sander et al. 2008). Average thickness of eggs studied by Peitz (2000) at two Catalan localities ranged from 1.3 to about 4.5 mm. In the egg with the thinnest shell, it ranges from 1.6 mm to 2.4 mm, while in the egg with the thickest shell it ranges from 3.0 mm to 4.5 mm. The European eggs have a much higher number of pores than the Auca Mahuevo eggs (Figure 2.2; Sander et al. 2008) and higher water vapor conductance rates (Jackson et al. 2008). The diameter of shell units ranges from 0.25 mm to 1.31 mm with a high variability within a single egg (0.48 – 0.81 mm). Despite the observed high variability in egg attributes Peitz (1999, 2000) and Sander et al. (2008) assign these eggs to a single oospecies, *Megaloolithus mammilare* and assume that they were produced by *Ampelosaurus atacis* (Sander et al. 2008; Figure 2.3). The conclusion of Peitz (1999, 2000) and Sander et al. (2008) about the parataxonomy of eggs from southern Europe differs from those of French and Spanish paleontologists who assign them to numerous oospecies (Vianey-Liaud and López-Martinéz 1997; Bravo et al 2000; López-Martinéz 2000; López-Martinéz et al. 2000; Panadés I Blas 2002, 2005).

Indian eggs of the oofamily Megaloolithidae vary in their diameter between 12 cm and 20 cm (Vianey-Liaud et al. 2003). They are spherical and shell thickness ranges from 1.17 mm up to 3.60 mm. Shell units show high morphologic variation, ranging from cylindrical to fan-shaped. As in the European eggs, the Indian eggs have a much higher number of pores than the Argentinian eggs. Based on their different shell microstructure, eggs from India are assigned to numerous oospecies (Khosla and Sahni 1995; Mohabey 1998; Vianey-Liaud et al. 1987; Mohabey 2001).

Figure 2.3. Reconstructed skeleton of *Ampelosaurus atacis,* the possible producer of the eggs from southern France (Figure 2.1). The mounted skeleton and original bones of this Late Cretaceous titanosaur are exhibited in the Musée des Dinosaures Espéraza, France. Photograph with kind regards from Jean Le Loeuff.

2.4 Egg clutches, nests and pre-hatching parental care

2.4.1 Egg clutches and nests

Clutch size at Auca Mahuevo ranges from about 15 to nearly 40 eggs (Chiappe et al. 2004; Jackson et al. 2004). Eggs are in direct contact with one another or loosely packed with a random distribution in single or multiple layers (up to three layers have been observed so far; Jackson et al. 2004). While most of the clutches are preserved in red mudstone, a few are contained in large, subcircular to subelliptical to kidney-shaped depressions in sandstone. The interstitial spaces between eggs in these clutches are filled with mudstone. These clutches preserve evidence of nest architecture because the eggs truncate cross bedding and an elevated rim of structureless sandstone surrounds the clutch. The fact that the eggs in these nests are entombed by mudstone resulting from the flooding events in this alluvial system suggests that these titanosaurs did not bury their eggs (Chiappe et al. 2004). The low porosity of eggshells limited gas conductance, thus providing further support for the absence of substrate burial in the Auca Mahuevo eggs (Jackson et al. 2008; Sander et al. 2008).

Clutches from Europe and India are much smaller than those at the Argentinian site. For example, clutches discovered at the Spanish and French localities did not exceed eight eggs and some contained as few as three eggs (Sander et al. 2008). Clutches found in the Indian Lameta Formation show a higher variability in size (Mohabey 1990, 1996, 2000, 2001; Sahni et al. 1994), but the maximum number of eggs per clutch (8 eggs) appears to be similar to that of the European clutches (Sander et al. 2008). European and Indian eggs occur in a single layer and are more closely spaced than at the Argentinian site, with no apparent egg arrangement. Based on extant amniote eggs, the high eggshell porosity documented for European and Indian eggs indicates that incubation occurred in a vegetation mound or the eggs were buried in a substrate (Seymour 1979; Deeming 2006). The eggs were most likely deposited in a shallow depression and covered with soil and/or vegetation (Sander et al. 2008).

2.4.2 Nesting behavior and site fidelity

Maps showing the spatial distribution of eggs and clutches, the stratigraphic distribution of egg-layers, and the sedimentological context in which they are preserved allow inferences about the nesting behavior and site fidelity of sauropods. The close spacing of clutches (ca. 3m), their high density and the continuity of clutches observed at Auca Mahuevo suggest a gregarious nesting behavior of this titanosaur species (Chiappe et al. 2000). However, it remains unclear whether the clutches were laid at precisely the same time. Among the European and Indian sites, clutch spacing can only be estimated with confidence at the Spanish locality of Coll de Nargó, Tremp Formation (Sander et al. 2008). Here, but also at the other European and Indian sites, spacing is wide and irregular. It differs from the Argentinian site and thus, gregarious nesting of these titanosaurs seems unlikely. In contrast, this arrangement suggests that a small number of females have deposited clutches in this area at any one time. Nevertheless, a high occupation time of over 10,000 years estimated for the Bastur locality in this geographic region documents a repeated use of this nesting site by titanosaurs (Sander et al. 1998).

2.4.3 Pre-hatching parental care?

Many extant birds and reptiles show nest-guarding behavior that reduces the risk of nest predation. The titanosaurs of Auca Mahuevo, however, might have shown little or no parental care of their clutches for several reasons. The eggs from Argentina most likely were not buried. Although this argues for nest guarding or attendance, the large size of adults and the close proximity of clutches contradict this conclusion. Inadvertent trampling of eggs by adults would result in eggshell fragments around the clutches; the absence of eggshells between clutches, therefore, suggests that movement within the area was limited once the eggs were laid. Nest guarding may have been limited to the periphery of the nesting ground (Chiappe and Dingus 2001). That clutches from Europe and India were most probably deposited in a shallow depression and covered with soil and/or vegetation does not completely contradict nest guarding or attendance because just this kind of parental care is observed in modern crocodilians (Figure 2.4) and a few turtles (Somma 2003) which both bury their eggs. However, potential differences in the parental care for eggs between the Auca Mahuevo titanosaurs and those from Europe and India can also be the result of intra-species variation as observed in living animal species.

Figure 2.4. A breeding female American alligator that defends her nest.

2.4.4 Egg development

The amount of time necessary for a dinosaur embryo to mature to the hatching stage may never be known with certainty, but at least may be roughly estimated using a model that was developed by Rahn and Ar (1974) for birds. Based on the comparison with extant birds that have an incubation temperature of about 40°C, a dinosaur egg of 1.5 kg (the size of an ostrich egg) would require an incubation time of about 60 days to hatch. Temperature, however, can greatly prolong or accelerate incubation time in extant species: (i) The incubation temperature depends on the body temperature of the breeding species. (ii) The temperature in a nest that is not incubated by parents (e.g. depression filled with sand or vegetation, mound) varies within the environment at the local scale. The female optimizes incubation temperature by nest site selection and the way of nest construction.

2.5 Hatching, adolescence, growth in body size and sexual maturity

2.5.1 Hatching

Fossil eggs are considered to be hatched when the upper proportion of the egg is missing, and the inside is filled with the sediment that surrounds the egg (Carpenter 1999). Carpenter (1999) hypothesized that the dinosaur hatchling starts to crack the eggshell by pecking with an egg tooth (a small, sharp, cranial protuberance present in most birds and reptiles) and push their legs and shoulders against the shell. Although hatched eggs are not documented for Auca Mahuevo, García (2007) has identified an 'egg-tooth'-like structure for in ovo embryos of these titanosaurs, the presence of which had been predicted by Mueller-Töwe et al. (2002). Hatched eggs of the oofamily Megaloolithidae are frequent in clutches from Europe (Sander et al. 1998) and India (Mohabey 2001), but absent in Auca Mahuevo.

2.5.2 Precocial versus altricial

Extant reptiles and many ground-nesting birds are precocial. They hatch fully developed and are able to care for themselves immediately after hatching. In modern altricial birds (e.g. passerines) parents provide their nestlings with food and guard their nest to reduce the risk of predation of young. A synchronization of hatching is a strategy that is applied by many precocial species to significantly reduce the predation risk of hatchlings, because predators are unable to eat the oversupply of prey (predator satiation). Whether sauropods were precocial or altricial or whether they showed synchronization in hatching is unclear. The possibly low or absent parental care in the nest phase, however, favors that they might have been precocial as observed for modern turtles, reptiles, and some birds. The low fracturing of the hatched eggs observed for the Indian oospecies suggests that these hatchlings immediately left the nests after hatching, providing further support that at least these oospecies might have been precocial (Mohabey 2005). The lack of hatched material from Auca Mahuevo and from the European sites does not allow any conclusion on whether these sauropods were also precocial. Studies of hatchling and adult skeletons (Horner and Weishampel 1988) or in the structure of the eggshell (Bond et al. 1988) are currently applied by paleontologists to test the hypothesis that sauropods were precocial (Horner 2000). These refer to differences in skeletons and eggshells that exist in extant precocial and altricial species. Contrary to altricial species, the hatchlings of precocial species are fully developed and their skeleton shows a high level of ossification (Lack 1968). In extant birds, eggs yielding altricial young are usually smaller and are more quickly formed than eggs of precocial hatchlings (Lack 1968). Precocial birds have eggs which do not lose water rapidly (due to a low porosity) and are insulated against temperature change (due to a high eggshell thickness) resulting in a large incubation time (Rahn and Ar 1974).

2.5.3 Adolescence and growth in body size

Sauropod hatchlings may have been much less than a meter long from head to tail (Chiappe et al. 1998, 2001) and weighed much less than 10 kg (the maximum volume is 4.5 l in the southern European eggs and about 1.5 l in the Argentinian eggs; Breton et al. 1986; Weishampel and Horner 1994; Jackson et al. 2008). As adults, their estimated lengths reached more than 30 m and their weight ranged between 30 t (t = metric tons) and 80 t (Table 1 in the appendix of Klein et al. (in press) and the references cited therein).

Growth patterns in dinosaurs have been assessed by bone histology. Growth-lines comparable to annual rings seen in cross-sections of trees are counted in vertebrate long bones and are used to estimate the longevity of individuals of the same species (summarized in Erickson 2005). Growth rates have been difficult to quantify in sauropods because histologic growth marks are rare and at best appear late in ontogeny (Sander 2000; Klein and Sander 2008). The few growth mark records that are available suggest that longevity was more than four decades (Curry 1999; Sander 1999, 2000; Sander and Tückmantel 2003; Wings et al. 2007; Sander et al., in press). Juvenile growth was very rapid in sauropods because bones of juveniles consist of highly vascularized bone (Sander 2000; Klein and Sander 2008). The lower limit in this exponential phase of growth was about 2 t per year Wings et al. 2007; Sander et al., in press; but see Lehman and Woodward 2008 for lower estimates). The qualitative growth record also suggests that sauropods reached sexual maturity well before maximum body size (Sander 2000; Klein and Sander 2008) and that this pattern is consistent with other non-avian dinosaurs (Erickson et al. 2007; Klein and Sander 2007; Lee and Werning 2008; Ricqle`s et al. 2008). Sauropods seem to have reached the age at sexual maturity in the second decade of life (Sander 2000; Sander and Tückmantel 2003). This observation coincides with the upper theoretical limit for the age at sexual maturity derived by Dunham et al. (1989).

After a series of simulation studies of demographically imposed constraints to the life-cycle they showed that life-histories with an age of first reproduction larger than 20 years are very unlikely. As such high ages at sexual maturity would require juvenile and adult survival rates that have not been reported in populations of extant birds and reptiles the authors concluded that such life-cycles probably did not exist, even in any dinosaur.

Dinosaur behavior during adolescence and the adult stage is highly speculative. Sauropod tracksites indicate that they sometimes traveled in groups (Wright 2005). It has been suggested that hatchlings and juveniles did not stay with the adults due to their exceptional differences in body size and mass (Paul 1994). Juveniles could be overlooked by adults and trampled; in addition, juveniles required food plants of smaller height than adults did. Trackway and bone-bed evidence of sauropods indicates that only juveniles of at least one third of adult size join adults (Paul 1994). Meyers (unpublished master thesis 2003) found for the Mother's Day Quarry a clear age partitioning of a diplodocid herd in only juvenile and subadult individuals. Martin (1994), however, describes *Phuwiangosaurus* material from northern Thailand which includes both juveniles ("less than two meters long") and adults. The latter observation suggests that at least in this species parents might have attended or guarded their young as observed in many extant herd living herbivores. Living in herds had also been discussed for other sauropods (Martin 1994; Wright 2005) and is a simple form of defense to predators.

2.6 Mortality during adolescence and the adult stage

Ecologists distinguish between three basic, idealized curves to describe the age-dependency of survival of animal species (Pearl and Minor 1935; examples in Figure 2.5). Many survivorship curves of species show components of these three generalized types at different times in a specie's life-history. The curve of type 1 is convex and assumes a very high survival before individuals reach sexual maturity, followed by a period of increasing rates of mortality caused by senescence-driven die-offs. This survivorship curve is characteristic for species that are extremely safe from predation and that experience a low neonate mortality as observed in humans living in highly industrialized countries (Figure 2.5), or as observed in captive animal populations.

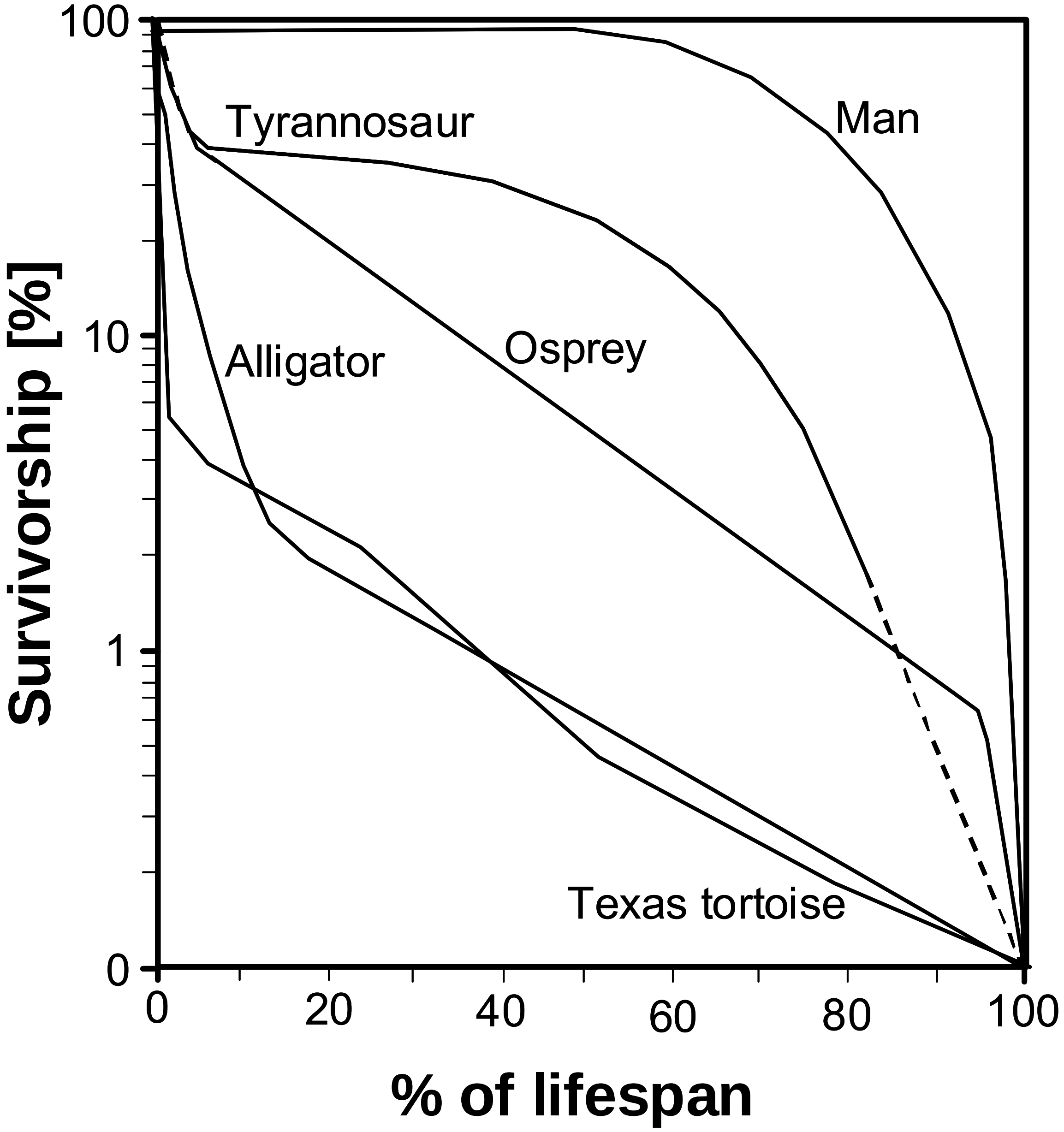


Figure 2.5. Survivorship curves. Curves for man (industrialized country, representing a typical type 1 species with high juvenile survival), tyrannosaur (*Albertosaurus sarcophagus*), osprey (a type 2 species with a constant mortality) and alligator (a typical type 3 species with a high mortality in the early juvenile stage) are adapted from Erickson et al. (2006); the curve for the Texas tortoise (a type 3 species with a very high mortality after hatching) is based on survival estimates obtained in a field study of Hellgren et al. (2000).

In contrast, the survival of species showing a linear survivorship curve (type 2) is characterized by a constant mortality risk throughout their life, which is dominated by predation (including cannibalism). Small short-lived birds, mammals and lizards have a linear survivorship curve. Species showing a concave curve (type 3) experience high mortalities in the beginning of their life that is mainly caused by predation, followed by low mortalities before reaching their maximal life span. Large, long-lived reptiles show this concave pattern in survival (Figure 2.5, alligator and Texas tortoise). Erickson et al. (2006) reported a sigmoidal survivorship curve based on type 1 survival for tyrannosaurs (Figure 2.5) which suggests that these non-avian dinosaurs were minimally susceptible to predation throughout their life with the exception of a higher mortality during the first two years. These authors derived their curves from an analysis of the age structure of four tyrannosaur populations (*Albertosaurus sarcophagus*, N= 22; *Daspletosaurus* sp., N=14; *Gorgosaurus libratus*, N=39; *Tyrannosaurus rex*, N=30) and used growth lines in fibulae and metatarsals to estimate the age of individuals. Ages of individuals included in their analyses ranged from two years to a maximal age that differed between species. The observed survival pattern of tyrannosaurs severely differs from curves found for birds (Figure 2.5, osprey), crocodiles (Figure 2.5, alligator) and turtles (Figure 2.5, Texas tortoise), but conforms much better to long-lived large mammals showing a long period of parental care to increase juvenile survival (Erickson et al. 2006).

Predation and competition for resources are the main agents of mortality in populations. Sinclair et al. (2003) analyzed the patterns of predation and competition for resources of a highly diverse mammal community of the Serengeti ecosystem. They found that smaller-bodied ungulates suffered predation from many predators and their predation rate was higher than in large ungulates that were predated by fewer species. Very large herbivores (elephant, rhinoceros, hippopotamus) almost never suffered predation as adults and only rarely as juveniles. The relationship between ungulate body size and predation rate was not linear. The proportion of annual adult mortality caused by predators declined rapidly as body size increased above a threshold body size. After having passed this size resource limitation strongly controlled herbivore populations. When transferring their results to sauropod communities, we can expect that small-bodied sauropod species and small juveniles of sauropods might have experienced a strong predation pressure, while the predation pressure on large-bodied adult sauropods was probably very low as observed in modern megaherbivores (Sinclair et al. 2003; Owen-Smith and Mills 2008).

Growth rates in body size had been exceptional fast in sauropods (Sander 2000; Klein and Sander 2008). Rapid growth is advantageous when survival rate increases with body size (Arendt 1997) as found for the ungulates in the Serengeti ecosystem. Rapid growth minimizes the amount of time spent in stages in which individuals are vulnerable to predation. A model of Case (1978a) predicted this benefit of rapid growth. In his model growth rate was fastest in species with a high ratio of juvenile to adult mortality (large adult sauropods are nearly safe from predation). Cooper et al. (2008) found evidence for a relation between predation and growth rate for the hadrosaur *Hypacrosaurus stebingeri*. After analyzing sequences of lines of arrested growth in tibias and femurs of this prey species and its predators, they showed that the hadrosaur was able to partly avoid predators by growing. For sauropods, in general, the high juvenile mortality resulting from predation might be reflected by the fact that small and even larger juveniles had been so far rarely found in the fossil record.

However, the tyrannosaur species studied by Erickson et al. (2006) show stronger relative increases in body size than do sauropods (defined as ratio of growth rate in the exponential phase and adult body mass; growth rates estimates in the exponential phase: *Tyrannosaurus rex* ca. 0.6 t/yr, Erickson et al. 2006; sauropods ca. 2 t/yr, Wings et al. 2007; Sander et al., in press; estimated adult body mass: *Tyrannosaurus rex* ca. 6 t, Erickson et al. 2006; sauropods ca. 30-80 t; Table 1 in the appendix of Klein et al. (in press) and the references cited therein). This corroborates the conclusion of Erickson et al. (2006) that these tyrannosaurs had a long period of parental care, which increased juvenile survival, while sauropods were at least most probably precocial and experienced a higher predation risk. Altricial and semi-altrical young of extant species that are attended or guarded and fed by parents are able to allocate the saved energy (they do not have to expend energy to acquire food or protect themselves) to grow more rapidly than precocial species that have to care for themselves after hatching (Case 1978a).

In total, we conclude that the survivorship curve of sauropods was most probably characterized by a phase in which predation dominated survival as observed in modern birds (Figure 2.5, osprey; because sauropods had been most probably precocial and the high growth rates in body size suggest a significant predation risk for juveniles), followed by a phase were sauropods were more or less safe to predation (due to their large body size) as observed for turtles (Figure 2.5, Texas tortoise), crocodiles (Figure 2.5, alligator) and large mammals (Figure 2.5, humans and tyrannosaurs). Our interpretation of growth curves with respect to survivorship curves contradicts Lockley (1994), who derived convex survivorship curves from fossil footprints of sauropod herds. This may be explained by the fact that herds did not cover all age-classes of animals ranging from hatchlings to adults (Paul 1994).

2.7 Reproductive output of sauropod females

The deaths of the individuals in a population always have to be compensated by the births of new individuals to enable long-term population survival. Thus, high reproductive outputs of females are needed to compensate the high mortality before reaching sexual maturity.

Table 2.1. Life-cycles of extant turtles, crocodiles and birds versus sauropods.

	Tortoises(1)	Crocodiles(2)	Ratites(3)	Sauropods
Clutch/nest	Buried	Buried	Open nest	Buried/open nest
Clutch size	Medium	Large	Small	Small/Medium
Multiple broods per year	Yes	Yes	Yes	Probable
Nest guarding before hatching	Rare(4)	All species	All species	Unlikely to limited
Parental care after hatching	Precocial	Precocial	Precocial	Most probable precocial
Juvenile mortality	High	High	High	High
Adult mortality	Low	Low	Low	Low
Sexual maturity	After full-grown	After full-grown	After full-grown	Considerable before full-grown
Longevity	Large	Large	Small to medium	Medium

We only include tortoises (Family Testudinidae) among turtles because of their exclusively terrestrial life style. Ratites were chosen as representatives for birds because they are unable to fly. Both taxa are closely phylogenetically related to sauropods. 1) Ernst and Barbour (1989), 2) del Hoyo et al. (1992), 3) Thorbjarnarson (1996), 4) Somma (2003)

The reproductive output of females is manifested in two variables: the frequency of reproduction and clutch size/litter size. In extant reptiles, both variables increase with increasing body size (Thorbjarnarson 1996). However, body size also affects egg and offspring size. Mammals and birds increase neonate size to a much larger extent than reptiles for an increasing body size. Modern species showing high juvenile mortalities have therefore high clutch sizes (most crocodiles, Thorbjarnarson 1996) and/or multiple clutches per breeding season (most turtles, Ernst and Barbour 1989;

passerine birds, Ricklefs 2000). Since the clutch size of sauropods (≤8 for European and Indian sauropods, <40 for Argentinian sauropods) is low in comparison to most extant reptiles (Table 2.1), their eggs are very small in relation to adult size, and because of the physiological limitation of clutch size that is imposed by respiration of embryos if eggs are buried (Seymour 1979), multiple clutches per breeding season are a very likely option (Sander et al. 2008). Multiple clutches, allow a female to spread the predations risks over multiple nests and thus increases the hatching rate of eggs. If sauropods had multiple clutches, hatchlings must have been very abundant in their populations (Sander et al. 2008).

2.8 Hypotheses explaining gigantism of sauropods based on their life-cycle

One of the most obvious features of the living world is that organisms strongly differ in their life-cycles. Species traits such as adult body size, longevity, age at sexual maturity, mortality and fecundity show a wide variation, and are the result of evolutionary adaptation; these processes are not mutually exclusive.

2.8.1 Gigantism and increased fecundity

Classical life-history theory approaches body size from the age at sexual maturity: age at sexual maturity increases with adult body size, because “one must grow for a longer time to get larger” (Stearns 1992). Most models making predictions on age at sexual maturity rest on assumptions about trade-offs between reproductive benefits and costs of long growth periods (e.g. through mortality). They predict that either fecundity increases or offspring mortality decreases with increasing age at maturity (Stearns 1992). Thus, since the offspring of sauropod dinosaurs must have suffered from significant mortality and these animals do not show particularly early sexual maturity (reproduction starts presumably in the second decade of life, Sander 2000; Sander and Tückmantel 2003), an increase in fecundity seems to be the most probable benefit of their increased body size.

This conclusion coincides with predictions from allometric scaling. The amount of space inside the body cavity available for eggs increases as the cube of the length of the species, and thus the body mass of the species, presuming that egg size is constant and there is no change in shape of animals with changing body sizes (Roff 2002). This positive relationship between clutch size and body size is well documented for many ectotherms, in particular for Crustacea, Mollusca, Annelida, Arachnida, Insecta, Tunicata, fish, amphibians, and reptiles (reviewed in Roff 2002). Endothermic birds and mammals, however, do not comply with the predictions from allometric scaling (Janis and Carrano 1992). Janis and Carrano (1992) found no correlation between body size and clutch size (or annual fecundity) for birds (see below). Positive allometric relationships between litter size and body size are rare in mammalian taxa (Millar and Hickling 1991; Roff 2002). By contrast, large mammals tend to have one to two young per year whereas small mammals such as cricitine rodents are frequently quite fecund (Roff 2002). This bimodal distribution of litter size leads to an overall decrease in litter size and number of offspring per year with increasing body size for mammalian vertebrates (as noted by Janis and Carrano 1992, see below).

Whether the hypothesis of increased fecundity resulting from an increased age at sexual maturity (body size) is valid for sauropods is unclear and difficult to prove. Reptiles and birds show no consistent pattern in both fecundity and clutch size depending on body mass. Reptiles point to an increase in sauropod fecundity and clutch size with increasing body mass whereas birds show no relationship between fecundity or clutch size and body mass. While clutch size can be determined from the fossil record, the frequency of reproduction determining fecundity cannot be.

2.8.2 Gigantism and the risk of population extinction

The body size and the density of a population reflect whether the energy available in the inhabited area is allocated either to many small-bodied or to fewer large-bodied individuals. Body size and density also strongly influence the chance of long-term survival of populations (Blackburn and Gaston 2001). Crucial factors limiting body size and the number of supported individuals are the bauplan, which reflects the evolutionary history of the species, its physiology including mechanisms enabling energy efficiency as well as the herbivorous or carnivorous mode of nutrition, the resource availability, and ecological interactions of the species with other species (Blackburn and Gaston 2001).

Janis and Carrano (1992) suggested a hypothesis that links the life-cycle of dinosaurs to ecological processes. They hypothesized that the oviparous mode of reproduction was the most important contributing factor to gigantism in dinosaurs after analyzing large datasets for number of offspring versus body mass for mammals (> 1kg) and for terrestrial non-passerine birds. The authors found no significant change with respect to adult body mass in the number of offspring per clutch, number of clutches per year, and total number of offspring per year for oviparous birds. In contrast, viviparous mammals showed a significant decrease of all this life-cycle characteristics with increasing body mass. They proposed that the oviparous reproduction strategy of dinosaurs (having a greater number of offspring, but experiencing higher juvenile mortality than mammals) is a great advantage over evolutionary time. This is because dinosaurs have a greater potential for reproductive turnover than similar sized mammals, making them less vulnerable to population extinction under environmental perturbations. High intrinsic growth rates allow species to rebuild populations more rapidly after severe declines in individual numbers than species with lower rates (e.g. mammals). This improves their chance of long-term survival and enables populations with on average fewer large-bodied individuals. The Janis and Carrano (1992) hypothesis was supported by Paul (1994, 1997) based on a statistical analysis of annual fecundity and body size of reptiles, birds, monotremes, marsupials and placentals.

Macroecological analyses of oviparous taxa reveal further support for the success of the reproduction mode of dinosaurs. Increasing clutch sizes with increasing body sizes are documented for turtle species (Frazer and Richardson 1986; Hailey and Loumbourdis 1988; Iverson 1992), for crocodiles (Thorbjarnarson 1996), for snakes (Ford and Seigel 1989), and for reptiles in general (Blueweiss et al. 1978; King 2000). No correlation between body size and clutch size was found for galliform birds (Kolm et al. 2007) in accordance with the results obtained by Janis and Carrano (1992). The difference between extant reptiles and birds may be explained by their internal thermal conditions (Shine 2005) and the different mode of incubation of eggs in the taxa.

The hypothesis of Janis and Carrano (1992) assumes a selective advantage of an oviparous reproduction mode in comparison to the viviparous mode of mammals, which enables larger body sizes including gigantism. Consequently, Farlow et al. (1995) had stated that this hypothesis would predict gigantism in Tertiary birds in the form of multi-ton ground birds, which did not evolve. Since the evolution of any life-history trait of an organism is always constrained, other factors may have prevented birds and other oviparous taxa from becoming multi-ton animals. These may be any ecological, morphological or physiological factor in general or in the case of the Tertiary birds competition from mammals, or their evolutionary history, including their obligatory bipedalism. Large bipedal, flightless birds evolved from birds that were able to fly, which definitely influenced their bauplan. In contrast, large mammals evolved from nonvolant animals adapted to a terrestrial life. Nevertheless, relative gigantism seems to be well represented by island birds from New Zealand, the moa, and Madagascar, the elephant birds (although elephant birds and moa had low clutch sizes, most probably because they inhabited islands), and by predatory birds in mainland ecosystems that lacked efficient mammalian predators, i.e. in the Early Tertiary of the northern hemisphere and throughout the Tertiary of South America (Mazzetta et al. 2004). It is also known from extant tortoises inhabiting several islands (genus *Dipsochelys* from the Seychelles, *Chelonoidis nigra* from Galápagos). Fossils of the giant crocodyliform *Sarcosuchus imperator* from the Cretaceous of Africa (Sereno et al. 2001) also corroborate the hypothesis of Janis and Carrano (1992).

2.9 Summary

The life of a sauropod started from an egg with a hard shell. After hatching, it grew very fast in body size and reached sexual maturity in the second decade of life. Parental care in the juvenile stage was most likely absent or low, and juvenile mortality must have been significant as suggested by the high growth rates of juveniles and observed in extant small herbivores. Clutches from Europe and India were buried in the substrate, whereas those from Argentina were deposited in an open nest structure and remained uncovered by sediment or plant material. Gregarious nesting behavior is likely for the Argentinian titanosaurs whereas repeated use of the nesting sites over a long period is likely for those from Europe and India. The clutch size of females was low (≤8 eggs in Europe and India, <40 eggs in Argentina) in comparison to extant large reptiles (Table 2.1) and eggs are very small in comparison to adult size, suggesting together with absent or low parental care during incubation that sauropods had multiple clutches per season. The oviparous reproductive strategy might have contributed to gigantism of dinosaurs in general because it enabled them to rapidly recover populations after crashes in population size and prevent population extinction (Janis and Carrano 1992). The exceptional gigantism in (herbivorous) sauropods in comparison to (carnivorous) theropods reflects the energy loss between an herbivorous and carnivorous mode of nutrition. The life-cycle of sauropods shows several characteristics that have evolved in birds but also such found in extant turtles and crocodiles (Table 2.1).

3 Reproductive models for large extinct birds (moa, elephant bird) and dinosaurs: linking information from the fossil record and from the allometries of extant close relatives

3.1 Abstract

In this study, we establish allometries on body mass and different reproductive traits (egg mass, clutch mass, annual clutch mass) for extant close relatives (birds or birds and reptiles) of extinct large flightless birds (moa, elephant bird) and of dinosaurs to infer information on the reproduction of both extinct species groups. Body mass and reproductive traits were highly correlated in birds and reptiles. At the level of egg mass, relations between egg and body mass differed for birds and reptiles, but differences disappeared for clutch mass or annual clutch mass (sometimes even statistically equal) versus body mass. The established allometries were applied to different extinct large birds and dinosaurs for which information on body mass, egg mass and clutch mass is preserved in the fossil record. In general, the results corroborated our hypotheses that reproductive traits of extinct birds coincided with those of extant birds. For dinosaurs that are phylogenetically close to birds (e.g. theropods), traits coincided with those of birds whereas traits of more basal dinosaurs (e.g. prosauropods) coincided with those of reptiles. Moa and the elephant bird had egg mass to body mass relations as observed in other extant birds but had not high clutch sizes (clutch masses). Whether they had extremely low (only one to two eggs) or rather moderate clutch sizes (four to seven) is unclear. One (moderate clutch size) or two to three (low clutch size) clutches per year and female are realistic based on the established allometries. Dinosaurs had egg mass to body mass relations that ranged between those of reptiles and birds. Dinosaur clutch masses (sizes) mostly fitted to clutch masses (sizes) predicted from allometries of extant taxa. Dinosaurs, such as theropods, had probably one clutch per year. Dinosaurs, such as prosauropods, moderate sized sauropods and hadrosaurids, had probably 2 up to 4 clutches per year. Large sauropods probably had laid 6 - 7 clutches per year. In how many clutches the eggs were exactly distributed depends on clutch size.

3.2 Introduction

Our information on organisms that have lived in the past is limited to fossils. Fossils, however, do not allow to fully reconstruct life-cycles of organisms, because traits can be either inaccurately or even not preserved in the fossil record. For example, clutches can be incomplete and breeding frequency is simply not documented in the fossil record. To infer knowledge on extinct species paleontologist apply both the "extant phylogenetic brackets" approach (EPB, Case 1978b; Witmer 1994; Farlow et al. 1995; Horner 2000; Tsuihiji and Parrish 2006; Varricchio et al. 2008) and the allometric approach (Case 1978b; Farlow 1993; Farlow et al. 1995; Varricchio et al. 2008). EPB's are the two most-proximal living outgroups of the fossil taxon of interest and "bracket" the fossil taxon by constraining all inferences (Witmer 1997). Allometries are mathematical functions that predict one trait of a species from another trait.

In amniotes (and other organisms), mass specific reproductive traits such as egg mass, clutch mass and annual reproduction mass (clutch mass × number of clutches per year) are highly correlated with body mass (Rahn et al.1975; Blueweiss et al. 1978; Rohwer 1988; Iverson 1992; Thorbjarnarson 1996; Dol'nik 2000; Ernest et al. 2003; Figuerola and Green 2006). The relationships follow a power function $Y = c \times BM^b$, where c is a normalization constant, BM is body mass and b is an exponent. Allometric functions are usually log-log plotted. In this presentation, the normalization constant c is the intercept and the exponent b the slope of a straight line. The exponent b differs between different amniotic groups when egg mass is regressed against body mass (Blueweiss et al. 1978; Hendriks and Mulder 2008). Conversely, b is often very similar in different amniotic groups, when clutch mass or annual reproductive mass is plotted against body mass (Blueweiss et al. 1978; Ernest et al. 2003; Hendriks and Mulder 2008).

Especially, for endothermic vertebrates when annual reproductive mass is regressed against body mass, the observed values of b are close to ⅔ or ¾ or they range in between (Ernest et al. 2003; Brown et al. 2004). Analogously, basal metabolic rate (MR) scales with body mass as $MR = c \times BM^b$, where b is again ⅔ or ¾ or is inbetween (Kleiber 1932; Heusner 1991; West et al. 1997; Dodds et al. 2001; White and Seymour 2003; Savage et al. 2004; Packard and Birchard 2008). To explain the identity of exponents b in these two allometries, the metabolic theory of ecology (MTE, Brown et al. 2004) assumes that many rate processes of organisms scale with body size and temperature in the same or reciprocal way as the metabolic rate itself (Ernest et al. 2003; Brown et al. 2004).

In mammals and birds, the annual rate of biomass production can be expressed as annual litter or clutch mass (because sexually mature individuals allocate no biomass to their own growth in body mass), and hence from the two above mentioned allometries, i) similar slopes for the metabolic rate and annual reproduction mass result, and ii) similar slopes for different vertebrate groups (birds, mammals) for annual reproduction mass result. While the slopes *b* are often statistically equal, the normalization constants significantly vary among taxa even when for internal temperature conditions of organisms influencing metabolic rate was corrected (Ernest et al. 2003) or species with similar internal temperature conditions were studied (Sibly and Brown 2007). We expect that similar dependencies for reproductive traits exist within close relatives of moa, elephant bird and dinosaurs, and that allometries observed in extant species are applicable to these extinct amniotes.

In our study, we take an extant phylogenetic bracket approach (EPB). We chose phylogenetically close relatives with similar reproductive traits (e.g. ground breeding bird species from the orders: Struthioniformes, Tinamiformes, Anseriformes, Galliformes; reptile species with calciferous mostly hard eggshells: crocodiles and tortoises) as an extant “bracket” for dinosaurs. In particular, we chose a combination of phylogenetic inferences and extrapolatory analysis similar to the approach of Bryant and Russell (1992). We establish allometries between body mass and different reproductive traits (egg mass, clutch mass, annual clutch mass) for extant birds and reptiles. Allometries are then applied to different extinct large birds and dinosaurs for which information on body mass, egg mass and clutch mass is preserved in the fossil record. We expect that the values estimated for reproductive traits of extinct birds will fit to those of extant birds and that dinosaurs, which were more “bird-like” in their reproductive mode (e.g. theropods), will fit to extant birds, whereas dinosaurs, which are more “reptile-like” in their reproductive mode, will fit to reptiles (e.g. prosauropods, sauropods). Additionally the allometries between body mass and annual clutch mass derived in this study allow a further independent test of the predictions of Ernest et al. (2003) on biomass production and body mass which are highly controversially discussed with respect to the metabolic theory of ecology (see Brown et al. 2004; but see Clarke 2006).

3.3 Material and methods

3.3.1 Extinct birds

We applied the established allometries between body mass and different reproductive traits to large extinct flightless birds for which body mass estimates and assignments to fossil eggs/clutches were available (Table 1 in appendix A). These were birds from the order Dinornithiformes (moa: *Euryapteryx curtus*, *Megalapteryx didinus*, *Anomalopteryx didiformis*, *Emeus crassus*, *Euryapteryx geranoides*, *Pachyornis elephantopus*, *Dinornis robustus*) and from the order Aepyornithiformes (elephant birds: *Aepyornis* sp.). Note that the Dinornithiformes and Aepyornithiformes are sometimes considered as a family (mainly in older literature) and are denoted Dinornithidae and Aepyornithidae, respectively.

3.3.2 Close relatives of extinct birds

Since all studied extinct bird species belong to the Paleognathae (Harshman et al. 2008) we choose extant Paleognathae and relatives to establish allometries. The extant orders Struthioniformes and Tinamiformes are also members of the Paleognathae (Cooper et al. 2001; Haddrath and Baker 2001). For Struthioniformes, however, only data of seven species (two kiwi species and five other ratites) were available. The two kiwi species (~ 1-3 kg, cave breeding) strongly differ from the other ratites (~ 20-90 kg, open breeding) in terms of their body masses and their reproductive strategies. It has been shown that cavity-breeding species (e.g. kiwi) differ profoundly in breeding ecology and life-history from open breeding species (Martin and Li 1992; Jetz et al. 2008). Because of the low sample size and the inhomogeneity of species traits we excluded Struthioniformes in our allometric analyses, but included their data in the plots for comparison (see results). For the Tinamiformes, we found no single species for which body mass and all studied reproductive traits were available.

However, since phylogenetic analyses had revealed a close relationship of the orders Galliformes and Anseriformes to the Paleognathae (Sibley and Ahlquist 1990; Clarke et al. 2005; Pereira and Baker 2006b; Livezey and Zusi 2007) we chose these two orders in our analyses as close relatives. Because the studied extinct birds were terrestrial and ground breeding (Worthy and Holdaway 1999; Worthy and Holdaway 2002), we restricted our allometric analyses to ground breeding, terrestrial avian species as far as possible. In the regression analyses for Galliformes we did not consider the megapode because of the very different breeding ecology of megapodes in comparison to other birds, but included the data in the plots for comparison (see results).

3.3.3 Dinosaurs

We tested our allometries established on all dinosaurs for which body mass estimates and assignments to fossil eggs or clutches are currently available (Table 1 in appendix A, Varricchio et al. 2008). In particular, these assignments only exist for three theropods (*Troodon formosus*, *Oviraptor philoceratops*, *and Citipati osmolskae*), two hadrosaurs (*Maiasaura peeblesorum*, lambeosaurine dinosaur), two sauropods (*Megaloolithus patagonicus*, *Megaloolithus siruguei*) and one prosauropod (*Massospondylus*). For the sauropods, only oospecies are defined. Whereas the *Megaloolithus patagonicus* oospecies is assigned to a titanosaurian sauropod based on embryonic remains in eggs (Chiappe et al. 1998; Chiappe et. al. 1999, 2001; Grellet-Tinner et al. 2004; García and Cerda 2010), the *Megaloolithus siruguei* egg type (with a highly porous shell) is commonly assigned to titanosaurian sauropod dinosaurs, because titanosaur bones had been found in the same horizon or formation. Note that *Megaloolithus siruguei* combined with other oospecies of the *Megaloolithus* type from Spain and from southern France are also regarded as only one oospecies *Megaloolithus mammilare* (Sander et al. 2008)*.* For our analyses we used the *Megaloolithus siruguei/mammilare* egg volume from Jackson et al. (2008). Because Jackson et al. (2008) denominated the eggs as *Megaloolithus siruguei* we preferred this denotation to clarify that we mean these eggs with the egg volume as Jackson et al. (2008) assumed. Although taxonomic identification of the eggs and their producers are more or less uncertain, sauropod species with a mass of at least 5 t (t = metric tons) were assigned to *Megaloolithus* oospecies (Sander et al. 2008; Varricchio et al. 2008).

3.3.4 Close relatives of dinosaurs

Birds, crocodiles and dinosaurs are members of Archosauria (Weishampel et al. 2004). Thus, as EPB of dinosaurs, we selected birds and crocodiles that are presumed to be close phylogenetic relatives of ancient dinosaurs (Padian et al. 2001;

Turner et al. 2007). Since extant birds and crocodiles differ in their reproductive strategies, we established a bird model and a reptile model for allometries of body mass and reproductive traits. Given that dinosaurs were most probably terrestrial and ground breeding (Paul 1994; Horner 2000; Sander et al. 2008), we restricted our dataset to ground breeding, terrestrial avian and reptilian species if possible. For birds, we chose only species from phylogenetic old avian orders, because birds are descendants of dinosaurs (Gauthier 1986; Padian et al. 2001; Barrett and Rayfield 2006; Turner et al. 2007). Galliformes and Anseriformes were selected as EPB for the reasons already mentioned above. Body masses and reproductive traits of Struthioniformes were again only included in the plots (see results). For the reptile model and in accordance with the EPB approach we primarily selected extant crocodilian species (Table 1 in appendix A) although these live semi-aquatic to aquatic rather than terrestrial. To enlarge our dataset for the reptile model, we also included turtles in our analyses, because turtles could be a sister taxon of archosaurs (Iwabe et al. 2005). For turtles, we selected only species of the family Testudinidae (tortoises, Table 1 in appendix A) because they are well adapted to terrestrial life and thus should be better model organisms for terrestrial dinosaurs than their aquatic or semi-aquatic relatives.

3.3.5 Life-history traits

We gathered data on adult body mass, egg mass, clutch size and number of clutches per year. For body mass we preferred estimates of the mass of females, because mass is more strongly linked to reproductive traits in females than in males. In some cases (e.g. all dinosaurs), however, it was not possible to distinguish between male and female body masses because only averages of both sexes were available or the sex was unknown (dinosaurs) or not denoted in the source. To maximize our sample size while minimizing any bias introduced by male body masses, we used female body masses wherever possible and averaged body masses otherwise. Egg mass for dinosaurs was calculated from egg volume using an avian/crocodilian egg density of 1.13 g/cm³ (Rahn and Paganelli 1989, mean egg density of the six bird orders in Table 3; Ferguson 1985, Table 3). Egg volume was calculated from fossil egg dimensions from equations $V = 0.51\ L*D^2$ (asymmetrical, bird-like) or $V = 0.524\ L*D^2$ (ellipse, crocodile-like), where V gives the egg volume, L the egg length and D the egg diameter (Hoyt 1979; Ferguson 1985). Egg mass of extinct birds was taken from

Dickison (2007). As a first conservative approximation of the unknown annual breeding frequency, we assumed one clutch per year for extinct birds and for dinosaurs, because all studied extant birds and reptiles lay at least one clutch per year. Clutch mass was calculated as egg mass multiplied by clutch size. Annual clutch mass was calculated as clutch mass multiplied by the number of clutches per year.

3.3.6 Data sources

Data on body mass and reproductive characteristics of species were mainly collected from the literature (Table 1 in appendix A). A few complete datasets of bird species were taken from the AnAge database (AnAge, Build 11, release date: 07/05/2009, provided by the Human Ageing Genomic Resources project, de Magalhaes 2005). Only extant species for which all required life-history data were available, were used in our allometric analyses. Data on body mass and reproductive biology of dinosaurs and extinct birds were exclusively collected from the literature (Table 1 in appendix A). Suitable literature was identified through keyword searches in databases of original publications (Web of Science), internet search engines (Google, Google scholar), as well as individual scanning of references in books and in original publications.

3.3.7 Statistical analyses

Establishment of allometries for birds and reptiles. In a first step, we separately analysed the allometries of extant Anseriformes, Galliformes, tortoises and crocodiles. We calculated for each of these taxa and each of the three reproductive traits regression slopes and normalization constants, using standardised major axis regressions (SMA) on log-log-transformed data. We first performed an overall comparison of calculated regression slopes and normalization constants of all taxa groups. When the overall analyses showed that normalization constants and/or slopes differed, we additional pairwise compared the normalization constants and/or slopes to identify differences or similarities in normalization constants and/or slopes of groups. We applied SMA for two reasons. First, SMA estimates the line best describing the bivariate scatter of two traits; second if the statistics of the slope is of primary interest then SMA is more appropriate than ordinary linear least square regression (Warton et al. 2006).

In a second step, we calculated common regression slopes and common normalization constants for each of the reproductive traits and each of the different taxonomic groups (birds: Anseriformes and Galliformes, reptiles: crocodiles and tortoises). These common regressions establish our allometries on body mass and reproductive traits for birds and reptiles and are hereafter called bird model and reptile model. We preferred the common regression approach over a regression of pooled data of avian and reptilian species, respectively. Regressions are prone to variations in the lower and upper end of the plotted data points. For allometries of amniotes, when relating body mass to other traits, normalization constants often differ between taxa groups, but equal or very similar slopes are observed between (Hemmingsen 1960; Linstedt and Calder 1981; Ernest et al. 2003; Hendriks and Mulder 2008) or within groups (Rahn et al. 1975; Heusner 1991; Sibly and Brown 2007). In addition, we did not control for phylogenetic effects in traits and the different groups of birds (Anseriformes, Galliformes) and reptiles (tortoises, crocodiles) differing in body mass range. To our knowledge no consistent phylogenetic tree for any of the groups is currently available that is required for controlling for phylogeny in the regression analyses.

Finally, as a measure of variability in residuals and in the deviation of single species from the expected average, we calculated for each common regression line two parallel lines, one above and one below the common line. The normalization constants of these borderlines were i±rs, where i is the normalization constant of the common regression line and rs is the maximal observed residual value. To calculate rs we used all available data points from an extant taxon also including those that were omitted in the regression analyses (see above).

Application of allometries to extinct birds and dinosaurs. For each of the trait pairs (body mass vs. reproductive trait) of extinct birds and dinosaurs, we calculated the residual(s) to the common regression line(s) for the bird and reptile model. These residuals were then compared to the maximal residual value of the extant species with either comparable observed (if the extinct species falls within the body mass range of the extant species with the maximal residual value) or extrapolated body masses. For a better comparison between models, we computed so-called relative fits. Relative fits to the regression model (rF) were calculated as

$$rF = 1 - resV_{extinct}/max\_resV_{extant},$$

where $resV_{extinct}$ is the residual value of the tested extinct species and max_resV_{extant} is the residual value of the extant species which is found on the same side of the common regression line as the extinct species and which had the maximum residual value. A relative fit of one corresponds to a perfect fit (100%) to the common regression line (residual value of the extinct species = 0) and a relative fit of zero means that the residual value of the tested extinct species equals the observed maximum residual value of the extant species. A negative relative fit indicates that the residual value of the tested extinct species is outside the observed range of residual values of the extant taxa. Its absolute value gives the degree of deviation from the maximum residual value of the extant species.

Estimation of clutch sizes, annual egg numbers and clutches per year. Furthermore, we estimated, for each extinct bird and dinosaur species, clutch sizes and numbers of eggs per year applying the common regression lines derived for birds and reptiles (mean value) and the respective parallel lines below (lower boundary) and above (upper boundary) the common regression line. Therefore, we used gathered data on body mass and egg mass for extinct birds and dinosaurs. Clutch size was calculated from fossil egg mass and the clutch mass estimated from each of the common regression line of birds and reptiles. Analogously, the total number of eggs per year was calculated from annual clutch mass estimated from the common regression lines of birds and reptiles and the mass of fossil eggs. Clutches per year were calculated from annual egg numbers and from estimated clutch sizes respectively fossil clutch sizes.

Software used. The calculations of clutch sizes, numbers of eggs per year and clutches per year from the bird and reptile model were done with Excel 2003. All other analyses were carried out in R (Version 2.9.2). For calculations and comparisons of SMA regressions, common regressions slopes and common normalization constants, we used the “smart” package for R (Warton et al. 2006). The calculations of the residual values and relative fits were coded by hand.

3.4 Results

3.4.1 Establishment of allometries for birds and reptiles

Egg mass. The adjusted R^2 for egg mass versus body mass ranged from 0.67 (crocodiles) to 0.87 (Anseriformes, Table 3.1). Only several slopes and normalization constants of regression lines calculated for each of the taxa groups (Anseriformes, Galliformes, tortoises, crocodiles) significantly differed pairwise (Table 3.2). Slopes of Anseriformes and Galliformes and of tortoises and crocodiles were statistically equal. While for the reptile groups the normalization constants did also not statistically differ, the normalization constants differed between the two bird groups (Table 3.2). Comparing body mass vs. egg mass of birds and of reptiles revealed significantly steeper slopes for birds than for reptiles (Table 3.1 and 3.2). Nevertheless, the normalization constant for Galliformes differed not significantly from the reptilian ones, whereas the normalization constant of the Anseriformes significantly differed (Table 3.2).

Clutch mass. The range of adjusted R^2 for clutch mass versus body mass varied between 0.69 (Galliformes) and 0.84 (tortoises, Table 3.1). However, in contrast to the regressions for egg mass versus body mass, the regression slopes did not significantly differ between all groups (Table 3.2). By contrast, normalization constants significantly differed between groups, except for crocodiles and Galliformes (Table 3.2).

Table 3.1. Results of the SMA regression analyses carried out for body mass against several reproductive traits for different extant amniotic groups. Allometric functions are log-log plotted. In this presentation, the normalization constant *c* is the intercept and the exponent *b* the slope of a straight line. N = sample size. 95% CI = 95% confidence interval of the intercept or slope of the regression line

		N	intercept	95% CI	slope	95% CI	adjusted R²
Egg mass vs. body mass							
	Anseriformes	93	0.050	[0.047; 0.052]	0.95	[0.88; 1.03]	0.87
	Galliformes	11	0.022	[0.017; 0.028]	0.8	[0.58; 1.11]	0.79
	Tortoises	20	0.018	[0.014; 0.022]	0.4	[0.31; 0.5]	0.75
	Crocodiles	22	0.025	[0.017; 0.035]	0.36	[0.28; 0.47]	0.67
Clutch mass vs. body mass							
	Anseriformes	93	0.389	[0.355; 0.417]	0.8	[0.71; 0.89]	0.7
	Galliformes	11	0.209	[0.151; 0.288]	0.87	[0.59; 1.28]	0.69
	Tortoises	20	0.058	[0.042; 0.081]	0.78	[0.65; 0.95]	0.84
	Crocodiles	22	0.170	[0.091; 0.324]	0.73	[0.58; 0.92]	0.74
Annual clutch mass vs. body mass							
	Anseriformes	93	0.398	[0.363; 0.417]	0.8	[0.71; 0.90]	0.65
	Galliformes	11	0.224	[0.158; 0.309]	0.83	[0.55; 1.26]	0.65
	Tortoises	20	0.158	[0.112; 0.219]	0.78	[0.64; 0.94]	0.84
	Crocodiles	22	0.166	[0.085; 0.324]	0.74	[0.59; 0.95]	0.72

Annual clutch mass. The adjusted R^2 ranged from 0.65 (Anseriformes) to 0.84 (tortoises) for annual clutch mass versus body mass. Regression slopes did not significantly differ between all groups. Normalization constants did not significantly pairwise differ (Table 3.2), except for Anseriformes that significantly differed from all other groups.

Common regression functions. The common regression functions derived on body mass against egg mass, clutch mass or annual clutch mass differed between birds and reptiles. Functions are given in Table 2 in appendix A.

Table 3.2. Summary of results of tests for significant pairwise differences between regression intercepts and slopes of different species groups. For sample sizes refer to Table 3.1.

	intercepts			slopes		
	Galliformes	Tortoises	Crocodiles	Galliformes	Tortoises	Crocodiles
Egg mass vs. body mass						
Anseriformes	p<0.0001	p<0.0001	p<0.0001	p=0.28	p<0.0001	p<0.0001
Galliformes		p=0.23	p=0.53		p=0.0011	p=0.0005
Tortoises			p=0.06			p=0.63
Clutch mass vs. body mass						
Anseriformes	p<0.0001	p<0.0001	p<0.0001	overall analyses revealed no differences between slopes (p= 0.85)		
Galliformes		p<0.0001	p=0.33			
Tortoises			p<0.0001			
Annual clutch mass vs. body mass						
Anseriformes	p<0.0001	p<0.0001	p<0.0001	overall analyses revealed no differences between slopes (p= 0.94)		
Galliformes		p=0.11	p=0.29			
Tortoises			p=0.93			

3.4.2 Application of allometries to extinct birds and dinosaurs

Extinct birds - Egg mass. Body mass to egg mass relations of all extinct flightless birds fitted into the interval that was defined by the common regression line and the upper and lower boundaries that were derived from extant birds (Figure 3.1A). Accordingly, relative fits were greater than zero and ranged from 0.71 to 0.95 (Table 3 in appendix A).

Extinct birds - clutch mass and annual clutch mass. In contrast, the clutch masses and annual clutch masses of extinct birds were outside the respective intervals of birds (Figure 3.2A and 3.3A) and the relative fits of species were negative. The relative fits ranged from -0.51 (*Euryapteryx curtus*) to -0.05 (*Pachyornis elephantopus*) for clutch mass and from -0.48 (*Euryapteryx curtus*) to -0.01 (*Pachyornis elephantopus*) for annual clutch mass (Table 3 in appendix A).

Dinosaurs - egg mass. Except for the prosauropod *Massospondylus* that fitted very well to the reptile model (relative fit rF = 0.98), dinosaur egg masses fitted neither to egg masses of similar sized birds nor to those of reptiles (Figure 3.1). In particular, the theropods (*Troodon formosus*, *Oviraptor philoceratops*, *and Citipati osmolskae*), the lambeosaurine dinosaur (hadrosaur) and sauropod *Megaloolithus siruguei* from Spain had egg masses more similar to birds than to reptiles whereas the egg masses of the hadrosaur *Maiasaura peeblesorum* and the sauropod *Megaloolithus patagonicus* were closer to those of reptiles (Figure 3.1). The relative fits of all dinosaurs studied ranged from -0.62 (*Maiasaura peeblesorum*) to -3.14 (lambeosaurine dinosaur) for the reptile model and from -0.16 (*Troodon formosus*) to -2.35 (*Megaloolithus patagonicus*) for the bird model (Table 4 in appendix A).

Dinosaurs - clutch mass. Except for *Massospondylus* and the lambeosaurine dinosaur, the clutch masses of dinosaurs fitted either best to clutch masses of similar sized reptiles (*Maiasaura peeblesorum, Megaloolithus siruguei, and Megaloolithus patagonicus*) or to those of birds (*Troodon formosus*, *Oviraptor philoceratops*, *Citipati osmolskae*, Figure 3.2). The clutch mass of *Massospondylus* was lower than masses of extant reptiles and birds. The lambeosaurine dinosaur clutch mass did not coincide well with each of the two groups but it had a higher relative fit to the bird model than to the reptile model (Figure 3.2). The relative fits ranged from 0.96 (*Megaloolithus siruguei*) to -0.33 (*Troodon formosus*) for the reptile model and from 0.96 (*Troodon formosus*) to -0.99 (*Megaloolithus patagonicus*) for the bird model (Table 4 in appendix A) for all dinosaurs studied.

Dinosaurs - annual clutch mass. The annual clutch masses of theropods fitted well to the bird model. Nevertheless, annual clutch masses of *Troodon formosus* and *Citipati osmolskae* were also consistent with the reptile model although the relative fit values were much lower than under the bird model (Figure 3.3). The annual clutch mass of the lambeosaurine dinosaur was between the mass expected under the bird model and the mass derived from the reptile model (Figure 3.3). Annual clutch masses of both sauropods coincided with the reptile model. Annual clutch masses of *Maiasaura peeblesorum* and *Massospondylus* did fit neither to the reptile nor to the bird model, but the reptile model was somewhat better than the bird model (Figure 3.3). For all dinosaurs relative fits ranged from 0.52 (lambeosaurine dinosaur) to -1.39 (*Massospondylus*) for the reptile model and from 0.95 (*Troodon formosus*) to -1.97 (*Massospondylus*) for the bird model (Table 4 in appendix A).

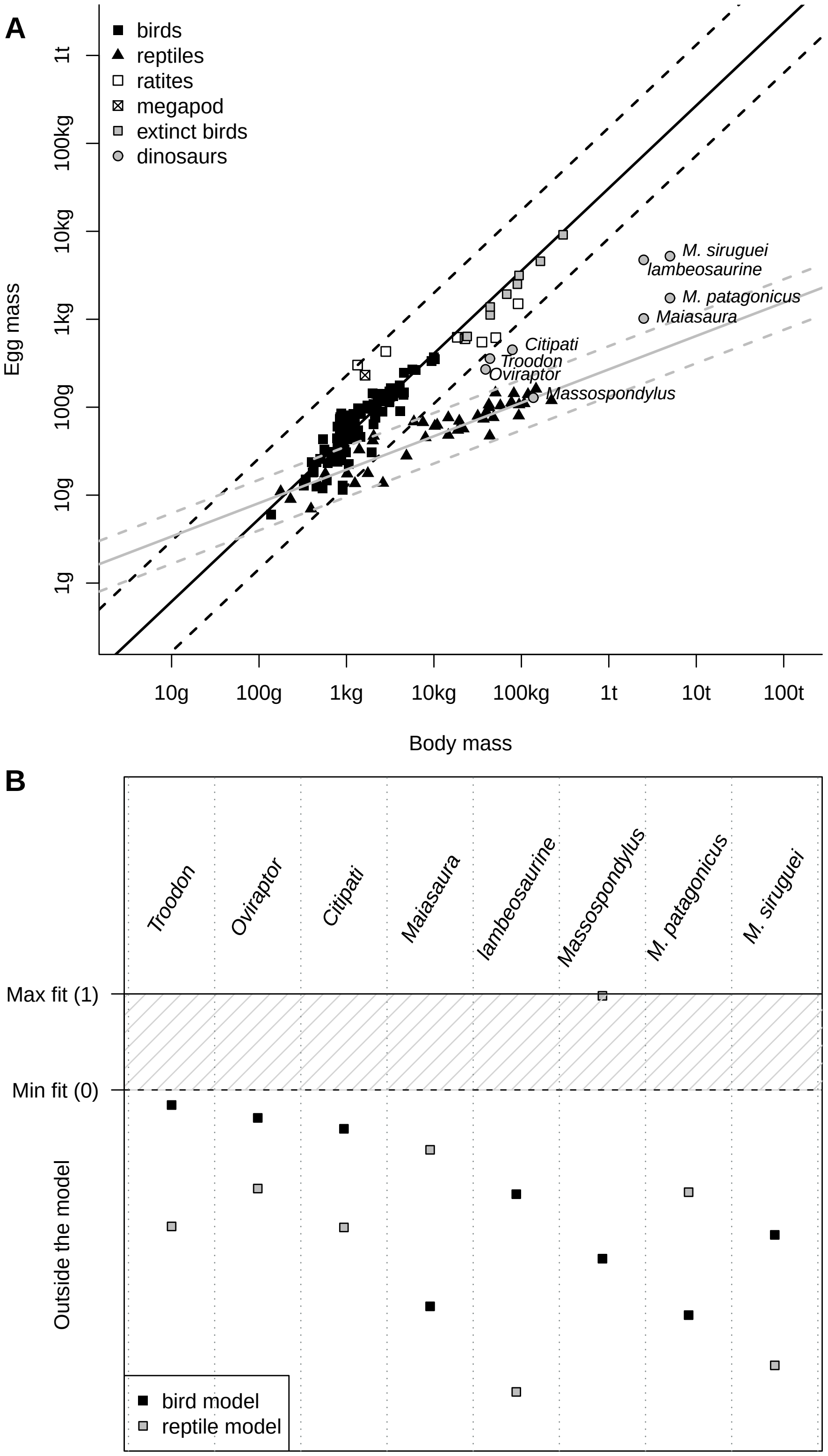


Figure 3.1. (**A**) Allometry of egg mass (EM) and body mass (BM) for birds (black line, common regression) and reptiles (grey line, common regression). Data points of different extant and extinct taxa are plotted. Scattered parallel lines are lower and upper “borderlines” of the specific regression model, which have the same slopes as the model itself. The normalization constants of these borderlines were i±rs, where i is the normalization constant of the common regression line and rs is the maximal observed residual value of extant species. To calculate rs we used all available data points from an extant taxon including also those that were omitted in the regression analyses (see text). (**B**) Relative fits of dinosaur EM to BM relations to the bird (black squares) and reptile (grey squares) model. Only points located within the grey shaded area or adjacent to the horizontal lines coincide with the respective model, otherwise the EM to BM relation of the dinosaur is outside the respective model.

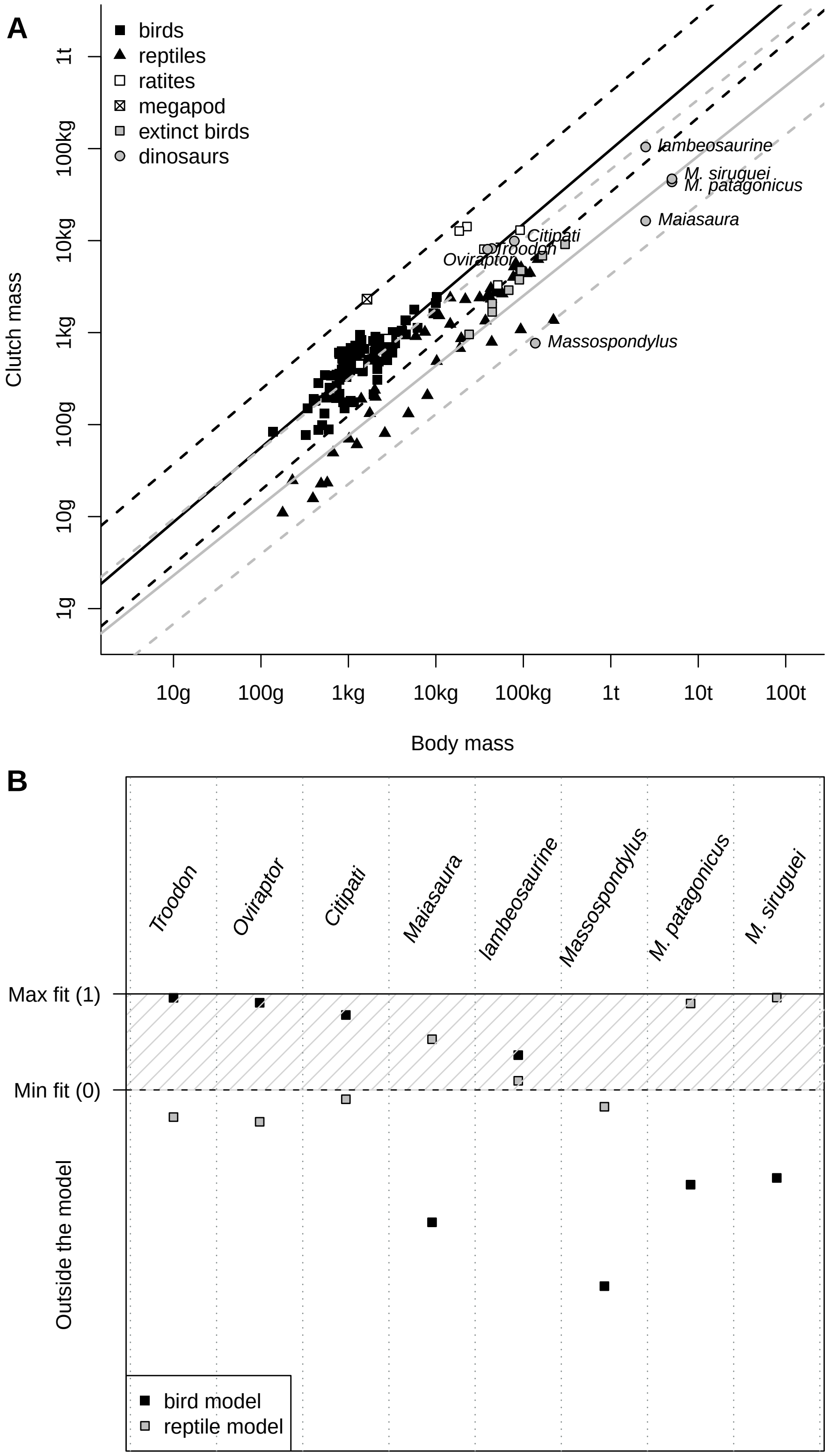


Figure 3.2. (**A**) Allometry of clutch mass (CM) and body mass (BM) for birds (black line, common regression) and reptiles (grey line, common regression). Data points of different extant and extinct taxa are plotted. Scattered parallel lines are lower and upper “borderlines” of the specific regression model, which have the same slopes as the model itself. The normalization constants of these borderlines were i±rs, where i is the normalization constant of the common regression line and rs is the maximal observed residual value of extant species. To calculate rs we used all available data points from an extant taxon including also those that were omitted in the regression analyses (see text). (**B**) Relative fits of dinosaur CM to BM relations to the bird (black squares) and reptile (grey squares) model. Only points located within the grey shaded area or adjacent to the horizontal lines coincide with the respective model, otherwise the CM to BM relation of the dinosaur is outside the respective model.

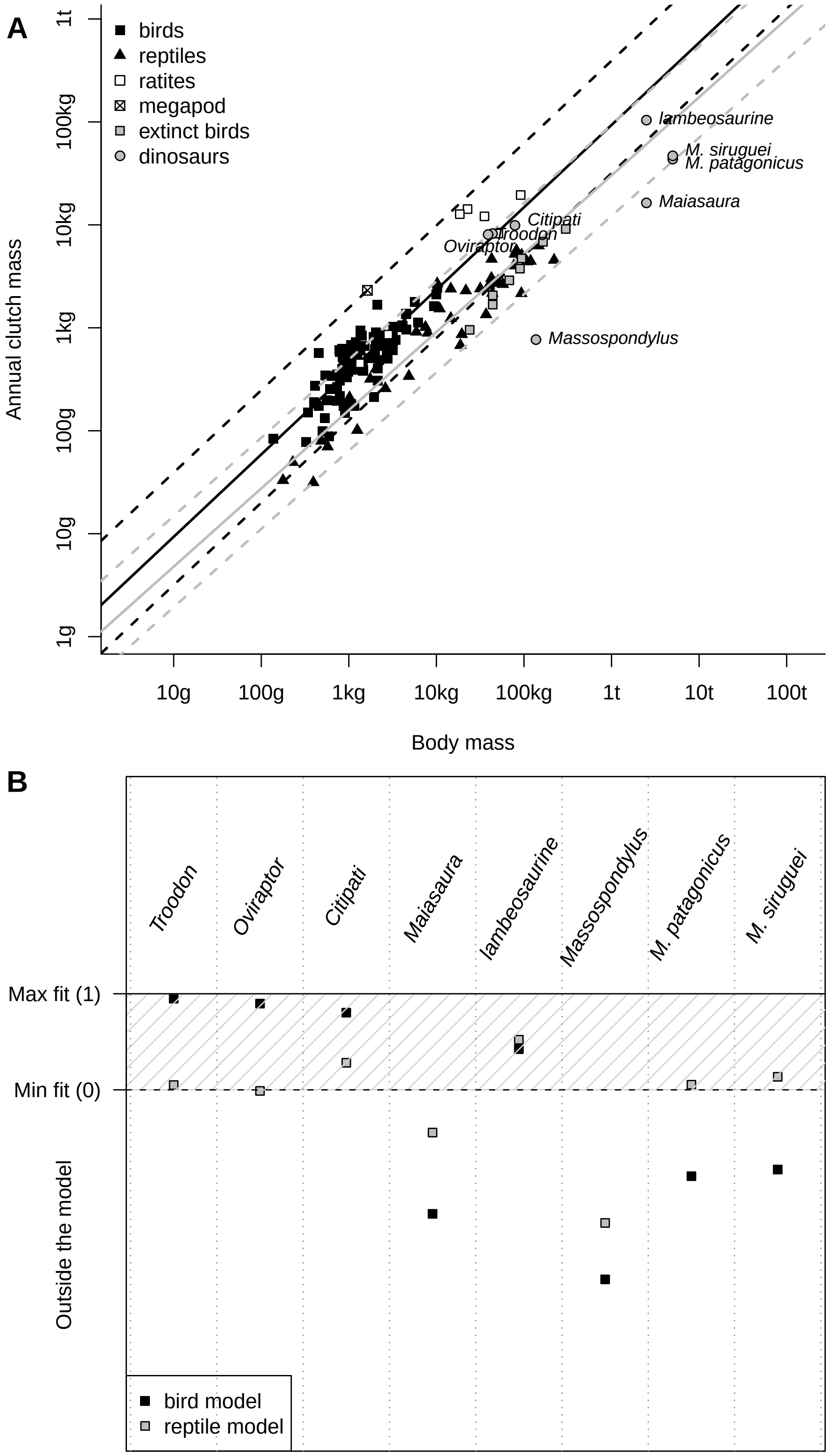


Figure 3.3. (**A**) Allometry of annual clutch mass (ACM) and body mass (BM) for birds (black line, common regression) and reptiles (grey line, common regression). Data points of different extant and extinct taxa are plotted. Scattered parallel lines are lower and upper "borderlines" of the specific regression model, which have the same slopes as the model itself. The normalization constants of these borderlines were i±rs, where i is the normalization constant of the common regression line and rs is the maximal observed residual value of extant species. To calculate rs we used all available data points from an extant taxon including also those that were omitted in the regression analyses (see text). (**B**) Relative fits of dinosaur ACM to BM relations to the bird (black squares) and reptile (grey squares) model. Only points located within the grey shaded area or adjacent to the horizontal lines coincide with the respective model, otherwise the ACM to BM relation of the dinosaur is outside the respective model.

3.4.3 Estimates of clutch sizes, annual egg numbers and clutches per year

Extinct birds. The estimated clutch sizes, annual egg numbers and the corresponding numbers of clutches per year of extinct birds estimated from the bird model are given in Table 3.3. Denoted are also the estimates of the lower and upper boundaries of the respective common regression lines and the clutch sizes preserved in the fossil record.

Table 3.3. Estimated and observed (fossil record) clutch sizes (CS), estimated annual egg numbers (EY) and estimated numbers of clutches per year (CY) for moa and elephant bird. CY is EY divided by CS. The common regression and lower and upper "borderline" equations used for calculations are given in Table 2 in appendix A (bird model). The normalization constants of the borderlines were i±rs, where i is the normalization constant of the common regression model and rs is the maximal observed residual value of extant species. To calculate rs we used all available data points from an extant taxon including also those that were omitted in the regression analyses (see text). n.a. = not available.

	CS	EY	CY
Coastal moa (*Euryapteryx curtus*)			
borderline (i-rs)	2.57	2.51	0.98
common regression	7.48	7.42	0.99
borderline (i+rs)	32.03	31.19	0.97
fossil record	1.50	n.a.	n.a.
Upland moa (*Megalapteryx didinus*)			
borderline (i-rs)	2.39	2.32	0.97
common regression	6.95	6.86	0.99
borderline (i+rs)	29.77	28.81	0.97
fossil record	1.50	n.a.	n.a.
Little bush moa (*Anomalopteryx didiformis*)			
borderline (i-rs)	1.94	1.89	0.97
common regression	5.65	5.57	0.99
borderline (i+rs)	24.19	23.41	0.97
fossil record	1.50	n.a.	n.a.
Eastern moa (*Emeus crassus*)			
borderline (i-rs)	1.98	1.91	0.97
common regression	5.74	5.64	0.98
borderline (i+rs)	24.60	23.71	0.96
fossil record	1.50	n.a.	n.a.
Stout-legged moa (*Euryapteryx geranoides*)			
borderline (i-rs)	1.91	1.84	0.96
common regression	5.55	5.44	0.98
borderline (i+rs)	23.78	22.85	0.96
fossil record	1.50	n.a.	n.a.

Table 3.3 continued

	CS	EY	CY
Heavy-footed moa (*Pachyornis elephantopus*)			
borderline (i-rs)	1.58	1.52	0.96
common regression	4.57	4.48	0.98
borderline (i+rs)	19.60	18.82	0.96
fossil record	1.50	n.a.	n.a.
South Island giant moa (*Dinornis robustus*)			
borderline (i-rs)	1.71	1.64	0.96
common regression	4.98	4.85	0.97
borderline (i+rs)	21.32	20.36	0.96
fossil record	1.50	n.a.	n.a.
Elephant bird (*Aepyornis* sp.)			
borderline (i-rs)	1.39	1.32	0.95
common regression	4.04	3.91	0.97
borderline (i+rs)	17.30	16.43	0.95
fossil record	1	n.a.	n.a.

Dinosaurs. The analyses above revealed that reproductive traits of theropods were best explained by the bird model, that for the sauropods, the prosauropod and *Maiasaura peeblesorum* the reptile model was best and that for the lambeosaurine dinosaur both models were appropriate (Figure 3.1, 3.2 and 3.3). Table 3.4 lists the estimated clutch sizes, annual egg numbers and the corresponding numbers of clutches per year that were derived for each of the dinosaurs from the respective common regression lines of the best model (bird or reptile). For each species the estimates of the lower and upper boundaries of estimates of reproductive characteristics and the clutch size observed from the fossil record are also denoted in Table 3.4. For the lambeosaurine dinosaur, estimates for both models are shown, because both models performed equal.

Table 3.4. Estimated and observed (fossil record) clutch sizes (CS), estimated annual egg numbers (EY) and estimated numbers of clutches per year (CY) for different dinosaurs. CY is EY divided by CS. The common regression and lower and upper "borderline" equations used for the calculations are given in Table 2 in appendix A. The normalization constants of the borderlines were i±rs, where i is the normalization constant of the common regression model and rs is the maximal observed residual value of extant species. To calculate rs we used all available data points from an extant taxon including also those that were omitted in the regression analyses (see text). The model with the best fit, which we used for the calculations, is given after the taxon name. For the lambeosaurine dinosaur both models performed equal. n.a. = not available.

	CS	EY	CY
Troodon formosus (bird model)			
borderline (i-rs)	7.47	7.25	0.97
common regression	21.68	21.39	0.99
borderline (i+rs)	92.87	89.88	0.97
fossil record	23.00	n.a.	n.a.
Oviraptor philoceratops (bird model)			
borderline (i-rs)	9.03	8.78	0.97
common regression	26.24	25.92	0.99
borderline (i+rs)	112.39	108.91	0.97
fossil record	30.00	n.a.	n.a.
Citipati osmolskae (bird model)			
borderline (i-rs)	9.57	9.23	0.96
common regression	27.78	27.25	0.98
borderline (i+rs)	119.01	114.51	0.96
fossil record	22.00	n.a.	n.a.
lambeosaurine (bird model)			
borderline (i-rs)	14.92	13.91	0.93
common regression	43.32	41.06	0.95
borderline (i+rs)	185.59	172.51	0.93
fossil record	22.00	n.a.	n.a.
lambeosaurine (reptile model)			
borderline (i-rs)	1.86	5.17	2.78
common regression	6.13	12.83	2.09
borderline (i+rs)	25.18	39.71	1.58
fossil record	22.00	n.a.	n.a.
Maiasaura peeblesorum (reptile model)			
borderline (i-rs)	8.60	23.92	2.78
common regression	28.40	59.42	2.09
borderline (i+rs)	116.60	183.88	1.58
fossil record	16.00	n.a.	n.a.
Massospondylus (reptile model)			
borderline (i-rs)	7.56	21.03	2.78
common regression	24.98	52.25	2.09
borderline (i+rs)	102.53	161.68	1.58
fossil record	6.00	n.a.	n.a.

Table 3.4 continued

	CS	EY	CY
Megaloolithus patagonicus (reptile model)			
borderline (i-rs)	8.55	23.80	2.78
common regression	28.26	59.13	2.09
borderline (i+rs)	116.03	182.97	1.58
fossil record	25.00	n.a.	n.a.
Megaloolithus siruguei (reptile model)			
borderline (i-rs)	2.86	7.95	2.78
common regression	9.44	19.76	2.09
borderline (i+rs)	38.77	61.13	1.58
fossil record	9.00	n.a.	n.a.

3.5 Discussion

3.5.1 The allometries of body mass and reproductive investment in extant amniotes

Our results corroborate that body mass and reproductive investment (measured in egg mass, clutch mass or annual clutch mass) are highly correlated in reptiles and birds (Rahn et al.1975; Blueweiss et al. 1978; Rohwer 1988; Iverson 1992; Thorbjarnarson 1996; Dol'nik 2000; Ernest et al. 2003; Figuerola and Green 2006). In amniotes, the relative reproductive investment generally declines with body mass whereas the absolute reproductive investment increases (Reiss 1985; Ernest et al. 2003; Figure 3.1A, 3.2A and 3.3A; Table 3.1). The allometries of egg mass vs. body mass of birds suggest that Anseriformes have higher egg masses than similar sized Galliformes (Table 3.1 and 3.2). Within reptiles, however, crocodiles and tortoises did not significantly differ in their egg mass to body mass allometry, but studied crocodiles were larger than tortoises (median crocodiles: 42.6 kg; median tortoises: 1.878 kg; Wilcoxon test: W = 377, p-value <0.0001) and hence had higher absolute egg masses (median crocodiles: 0.094 kg; median tortoises: 0.028 kg; Wilcoxon test: W = 408, p-value < 0.0001). Our analysis showed in accordance with the literature (Dol'nik 2000) that large birds invest in higher egg masses than similar sized reptiles (Figure 3.1A). In contrast, large reptiles have higher numbers of eggs per clutch and/or per year than similar sized birds (Blueweiss et al. 1978; our results, compare Figure 3.1A with 3.2A and 3.3A) and this results in similar clutch and annual clutch masses of similar sized birds and reptiles (Figure 3.2A and 3.3A). While on average the studied Anseriformes also had higher clutch masses and annual clutch masses than similar sized reptiles, the Galliformes had not (Table 3.2). There was only one exception, clutch masses of Galliformes and tortoises differed (Table 3.2). Because many tortoises lay several clutches per year and the studied galliformes birds have only one clutch per year, the difference between Galliformes and tortoises disappeared at the level of annual clutch mass (Table 3.2, Table 1 in appendix A). The higher clutch or annual clutch mass of Anseriformes in comparison to Galliformes could result from their different life styles. Many Anseriformes are migratory, whereas Galliformes are not. Most Anseriformes search for food in or on the water and some others, such as geese and swans, additionally forage on land, whereas Galliformes mostly forage in terrestrial habitats. These different life styles could also result in higher metabolic rates in Anseriformes than in other non-passerine birds (Miller et al. 2006) and hence might explain the differences in clutch and annual clutch mass in Anseriformes and Galliformes. However, our sample size of Galliformes is small (N=11) and this could have eventually influenced our results. Additional studies are needed to definitely clarify whether Anseriformes have higher clutch or annual clutch masses than Galliformes. The observed differences in allometries on egg mass of birds and reptiles are most probably caused by their different reproduction strategies and different thermoregulation mechanisms. Birds are endothermic and incubate their eggs with their body heat (except megapodes), whereas reptile eggs are incubated by environmental heat. Birds intensively care for their offspring in contrast to reptiles. Fewer offspring should obtain a better parental care and could ensure a higher parental fitness (Monaghan and Nager 1997). This fitness advantage could result in fewer eggs in birds than in reptiles. Because only few eggs are produced, there might be more resources available for each egg and they could become larger. In addition, larger eggs as produced by birds store heat over a longer time than do smaller eggs (Turner 1985). This allows the parents to leave the nest for a longer time (e.g. for foraging), because the duration of absence from the nest is determined by the time required for an egg to cool down to a minimum temperature (Turner 1991). Hatchlings from large eggs are larger and better developed than hatchlings from smaller eggs and this should increase their ability of thermoregulation (Visser and Ricklefs 1995). These advantages of few, large eggs might explain that large, endothermic, precocial birds lay fewer larger eggs than large ectothermic, precocial reptiles that have high numbers of small eggs.

The slopes of allometries (the slopes of the regression lines) for body mass and clutch mass/annual clutch mass did not significantly differ between taxa (Table 3.2). This observation suggests that despite their different reproduction strategies and thermoregulation mechanisms all studied amniotes allocate a specific fraction of energy to their clutch or annual clutch masses (exponent), but the amount of the investment itself differs (intercepts can differ).

3.5.2 Allometries and predictions of the metabolic theory of ecology

Although we used SMA-regressions, the 95% confidence intervals of the estimated slopes included most values from literature that had been derived from ordinary least square regressions for reproductive investment (clutch mass or annual clutch mass) or for metabolic rate of amniotes (Blueweiss et al. 1978; Iverson 1992; Ernest et al. 2003; Savage et al. 2004; Packard and Birchard 2008). Our results thus corroborate that energy-dependent biological processes should be related to the metabolic rate (level) of the organisms examined (Brown et al. 2004; Glazier 2009). The slopes calculated for taxa did not statistically differ from 0.75 (Table 3.1). On the one hand, this result supported the metabolic theory of ecology (MTE) but on the other hand, our results also did not question the alternatives that no single slope exists or that the metabolic-level boundaries hypothesis is valid (MLB, Glazier 2009). The 95% confidence intervals of the slopes estimated for birds and reptiles were rather broad (Table 3.1). Slopes were also in the range (0.67 to 1) predicted by the MLB (Glazier 2009). Consequently, our results could neither rule out the hypothesis on the relationship between body mass and annual clutch mass of the MTE nor the MLB.

However, with respect to the MTE (Ernest et al. 2003; Brown et al. 2004) it is surprising that even the intercepts of the regression lines for body mass against annual clutch mass of reptiles and of galliformes birds do not statistically differ. First, reptiles are indeterminate growers (Shine and Iverson 1995) and might not allocate their total annual biomass production to reproduction, as do the fully-grown adult birds. Second, reptiles have a lower basal metabolic rate than birds and mammals (Hemmingsen 1960; Clarke and Pörtner 2010), which is caused by differences in internal thermal conditions (Brown et al. 2004; Clarke and Pörtner 2010). According to the MTE, these differences should be reflected by different intercepts of endothermic and ectothermic amniotes (Hemmingsen 1960; Brown et al. 2004; Clarke and Pörtner 2010). However, birds and mammals show more intensive parental care than do reptiles and this higher reproductive investment is omitted by our and other studies (e.g. Ernest et al. 2003). Second, even if ectotherms are unable to actively maintain their body temperature at higher levels, they are nevertheless able to partially control their body temperature by behavior (Shine 2005), and hence, their metabolic rate. In addition, most organisms, both ectotherms and endotherms, increase their metabolism during reproduction (Farmer 2000). The average factorial aerobic scope (the ratio of sustained to basal metabolic rate) is remarkably similar in mammals, birds and reptiles (Clarke and Pörtner 2010). Thus, assuming that birds and mammals process energy at higher rates than do reptiles but spend proportionally more energy on thermoregulation, maintenance (Schmidt-Nielson 1997) and parental care, implies that ectotherms and endotherms could use a similar fraction of energy for reproductive output (Ernest et al. 2003). A fast metabolic rate coupled with endothermy and incubation by body heat did not necessary imply that more energy is invested in reproduction mass, the reproductive processes should be faster and mostly independent of environmental temperature and this perhaps could be the greatest advantages of a high metabolic rate for reproduction in birds (and mammals). Finally, different environments, life styles and evolutionary histories could cause variation and overlapping in reproductive investment of similar sized ectotherms and endotherms. However, the clarification of mechanisms causing similar annual clutch masses in birds and reptiles is beyond the scope of this study.

We conclude that, independent whether a general rule on annual reproductive investment that is postulated by the MTE exists or not, our results and the results of other studies i) justify the use of common regression equations as a general model for the analyzed birds or reptiles and ii) it is appropriate to transfer the established allometries to extinct amniotes such as moa, elephant birds or dinosaurs.

3.5.3 Reproductive investment in extinct egg laying amniotes

In general, our results corroborated our hypotheses that reproductive traits of extinct birds coincided with those of extant birds and that traits of dinosaurs that are phylogenetically close to birds coincided with birds whereas traits of more basal dinosaurs coincided with reptiles. Nevertheless, in some cases there was a discrepancy between the estimates from the fossil record and the established allometries, but the source of this discrepancy was unclear (for further details see discussions below).

3.5.3.1 Extinct birds

Extinct birds - egg mass. For extinct birds, the estimated egg masses of all moa species and the elephant bird conformed well to the bird model (Figure 3.1, Birchard and Deeming 2009). This result suggests that egg masses of moa species and the elephant bird did not differ from extant large birds and the estimates of egg mass and body mass of the extinct bird species seem to be reliable. In particular, these birds did not have unusually large eggs in comparison to their body size, as often has been proposed (Anderson 1989; Worthy and Holdaway 2002).

Extinct birds - clutch mass/size. The bird model predicted larger clutch sizes for extinct birds than sizes derived from the fossil record. Even the estimates of clutch size that were obtained from the regression line of the lower boundary were slightly larger than the fossil clutch sizes (1 to 1.5 eggs, Table 3.3). These unexpected results could have been caused by a systematic overestimation of the true clutch size by the bird model. Moa had a distinct sexual size dimorphism with males being much smaller than females (Bunce et al. 2003; Huynen et al. 2003). Because a significant reversed sexual size dimorphism with male-only incubation is common in extant ratites (Davies 2002; Worthy and Holdaway 2002), it has been hypothesized that moa had also a male-only incubation (Birchard and Deeming 2009). Thus, smaller male body mass might be a better predictor of clutch mass and hence for clutch size than female body mass used in our analyses. However, contrary to this hypothesis Owens (2002) found that bird families showing male-only care do not necessarily differ in fecundity or relative egg size from families with female-only care. Moreover, our results revealed that ratites do not have lower clutch masses or annual clutch masses than other ground breeding precocial birds, whereas rather the opposite is true. Except for the cassowary, extant ratites have clutch masses close to or above the masses predicted by the regression line (Figure 3.2 and 3.3). Even the kiwi and the ostrich that had not been included to calculate the bird model and that strongly differ in their size, reproduction strategy (reversed sexual size dimorphism, cavity breeding, few large eggs vs. sexual size dimorphism, open breeding, many eggs), habitat use (forest, savanna), activity (nocturnal, diurnal) and range distribution (New Zealand, Africa) have clutch masses close to those expected from the bird model (Brown kiwi: calculated 0.84 kg, observed 0.86 kg, Little Spotted Kiwi: calculated 0.46 kg, observed 0.45 kg, ostrich: calculated 14.11 kg, observed 13 kg, Figure 3.2). Based on these arguments we think that a systematic overestimation of clutch size caused by a bias introduced by a significant reversed sexual size dimorphism is very unlikely to explain the larger clutch sizes predicted for extinct birds.

Support for the alternative hypothesis that the clutch sizes of the extinct birds had been larger than derived from the fossil record exists at least for moa. Unusual high shell thickness in comparison to incubator body mass often indicates a clutch size of one (Birchard and Deeming 2009). In many cases, the eggs of these birds are proportionately larger and the incubation period may be longer, thus extending the period over which egg breakage could occur (Birchard and Deeming 2009). However, moa did not have unusually thick eggshells neither in comparison to incubator mass nor in comparison to egg mass (Birchard and Deeming 2009). Moreover, references exist for higher clutch sizes in moa. Gill (2000) reported that a discrete group of eggshell fragments of *E. curtus* were scattered over less than 2 m² with a total weight of 361 g, which is enough shell for 5-6 eggs. This clutch size is much closer to our estimate of 7.48 eggs derived for this species (Table 3.3). Anderson (1989) cited literature sources reporting that “four or five young birds (Gibson 1865:22)” and “four distinct young birds of the same species (Allis 1865a:50)” had been found underneath an adult skeleton which was assigned to *Dinornis robustus*. This chicken number is again closer to our estimate of 4.98 eggs per clutch for *D. robustus* (Table 3.3) derived from the bird model. In total, based on our results, we question that all moa had clutch sizes between one and two eggs.

Extinct birds – annual clutch mass/egg number/clutches per year. Evidence that moa and elephant bird had one clutch per year comes from the studied bird species. This annual breeding frequency would result in annual clutch masses comparable to those of extinct birds if we assume the clutch sizes predicted by our bird model. However, if moa and elephant bird had only one or two eggs per clutch (Anderson 1989; Worthy and Holdaway 2002) and one clutch per year, they would have had a very low annual clutch mass in comparison to most other studied birds, especially in comparison to the annual clutch mass observed in extant ratites (Figure 3.3). Considering an annual clutch mass as observed in extant ratites two or perhaps three clutches per year would be more reliable for these species. Assuming this higher annual breeding frequency, the resulting annual egg numbers are close to our estimates derived from the bird model (Table 3.3) ranging between 3.91 (*D. robustus*) and 7.42 (*E. curtus*). In this case, assuming a male incubator (Birchard and

Deeming 2009) the reproduction strategy of moa would be comparable to the strategy of the cassowary or emu.

Extinct birds - conclusion. The established allometries for egg mass and body mass suggest that moa and the elephant bird had egg masses as observed in similar sized extant birds, but did not have high clutch sizes. Whether they had extremely low (only one to two eggs) or rather moderate clutch sizes (four to seven) is unclear. While most fossil data point to one or two eggs per clutch, our established allometries predict that, at least some moa and the elephant bird could have had clutch sizes twice or three times higher. If the clutch size derived from the few fossil data is correct then two or three clutches per year and female are realistic. If, alternatively, the true clutch size was consistent with the predictions from the allometries of extant taxa then one clutch per year is more reasonable. The discovery of further fossil clutches will clarify which of the two alternatives is true.

3.5.3.2 Dinosaurs

Dinosaurs - egg mass (overview). Our results suggest that most egg masses of dinosaurs fitted neither to egg masses of similar sized birds nor to those of similar sized reptiles but were in between (Figure 3.1). However, in total, as observed in extant reptiles and birds, dinosaur egg mass (EM) increases with body mass (BM; $EM = 0.032*BM^{0.53}$; $p = 0.008$; $R^2_{adj.} = 0.67$; $N = 8$, all dinosaur species studied). Although the difference in size between a dinosaur egg and the egg laying female is very impressive, the ratio of egg and body mass was similar to (in *Massospondylus*) or higher (in all other dinosaurs) than the ratio observed in extant reptiles, but was lower for all dinosaurs than in birds. This probably reflects that the reproductive strategy of most dinosaurs differed from the reproductive strategy of birds and of reptiles. It might be that some dinosaurs had a reproductive strategy intermediate to reptiles and birds (q. v. Grellet-Tinner et al. 2006). Moreover, the great differences in egg mass to body mass ratios within dinosaurs suggest that different reproductive strategies existed in dinosaurs (Figure 3.1). The existence of different reproduction strategies within dinosaurs is also supported by the observation of different egg shapes and different eggshell structures within the dinosaur eggs found (Carpenter et al. 1994, 1999; Horner 2000; Jackson et al. 2008). Under the assumption that the reptile reproductive model is plesiomorphic and the bird model is phylogenetically derived, we expected that basal dinosaurs have egg masses close to the reptile model. Conversely, if egg masses of non-basal dinosaurs are consistent with the reptile model, these dinosaurs should not belong to the dinosaurian lineage, from which birds evolved. As expected none of the studied dinosaurs with egg masses close to the reptile model belongs to the theropods (Figure 3.1).

Hadrosaurids - egg mass. Hadrosaurids included one species with an egg mass/body mass ratio closer to the reptile model (*Maiasaura*) and a second with a ratio closer to the bird model (lambeosaurine dinosaur) although the assumed body masses of both hadrosaurids were equal. This raises the question if different reproduction strategies existed within hadrosaurids (Horner 1999), or if the assignments of eggs to species or the estimation of the body and/or egg mass was wrong. In both cases, embryonic remains were used to identify the producer of the eggs (Horner 1999). Nevertheless, lambeosaurine dinosaur remains are extremely rare in the Judith River Formation of Montana (Fiorillo 1987) where the clutches were found, and not a single taxon of this formation has been identified (Horner 1989). However, hadrosaurids in general seem not to reach much more than 3 t (Pecziks 1994; Sander pers. comm.). Thus, we suggest that different reproduction strategies existed within hadrosaurids and that the difference in the egg mass/body mass ratios had not been caused by erroneous egg or body mass estimates.

Theropods – egg mass. As expected, the non-avian theropods, which share many of their characteristics with birds (Norell et al. 1995; Dong and Currie 1996; Varricchio et al. 1997; Varricchio and Jackson 2004; Zelenitsky and Therrien 2008a, b; Chiappe 2009) and which belong to the lineage that had evolved birds (Padian et al. 2001; Varricchio and Jackson 2004; Turner et al. 2007), had egg mass-body mass relations close to extant birds (Figure 3.1). Because embryonic theropod remains (Norell et al. 1994; Varricchio 2002) and theropods “sitting” on eggs (Norell et al. 1995; Dong and Currie 1996; Varricchio et al. 1997, 1999) had been found, the estimated egg masses and body masses seem to be accurate.

Prosauropods and sauropods – egg mass: As expected, the most basal saurischian dinosaur in our study, the prosauropod *Massospondylus*, had egg masses like similar sized reptiles. However, the sauropods included one species with an egg mass/body mass ratio closer to the reptile model and a second with a ratio closer to the bird model although the assumed body masses of both sauropods were equal. Again this raises the question if different reproduction strategies existed within the same taxa (Jackson et al. 2008; Sander et al. 2008) or if the assignments of eggs to species or the estimation of the body and/or egg mass was wrong. In both cases, it is unclear whether the mass of the egg laying sauropod was only 5 t. Nevertheless, the assignment of the eggs to a larger sauropod does not contradict a non-reptilian egg mass-body mass ratio for *M. siruguei*. Nevertheless, if we assume larger body masses, then after passing a threshold mass (> 14 t), the egg mass of *M. siruguei* will be closer to the reptile model than to the bird model. However, the egg mass will only be concordant with the reptile model when assuming unrealistic high body masses (≥ 485 t). However, the *M. patagonicus* egg mass is concordant with the reptile model if we assume a body mass greater than 27 t, but is only concordant with an "average" reptile (common regression) when we assume an unrealistic high body mass of 127 t. Thus, we conclude that some, but not all sauropod egg mass/body mass ratios fit to the reptile model whereas others were higher. Because of the different eggshell structures that existed in sauropods (Jackson et al. 2008, Sander et al. 2008), it is very likely that sauropods had different reproductive strategies, which were also expressed in different body mass to egg mass ratios.

Dinosaurs - clutch mass (overview). In contrast to the egg masses, all dinosaur clutch masses, except for *Massospondylus*, fit well to masses of similar sized birds or reptiles. This suggests that no discrepancy exists between female mass and clutch mass assumed for the studied dinosaurs. Nevertheless, the, clutch mass/body mass ratios estimated from the fossil record could be wrong. For example, for sauropods we do not know whether the body mass and their clutch size (see Jackson et al. 2008, Sander et al. 2008, but Vila et al. 2010) is correct. Larger sauropod body masses will lead to a discrepancy between assumed female mass and clutch mass. Additional, errors in clutch size will lead to errors in clutch mass and thus to errors in body mass/clutch mass ratios, too.

Hadrosaurids – clutch mass/size. The reptile model predicted clutch sizes for hadrosaurids that were larger (*Maiasaura*) or smaller (lambeosaurine dinosaur) than observed in the fossil record (Table 3.4). However, both estimated clutch sizes were within the range of possible clutch sizes derived from extant taxa (Table 3.4) and hence could be the result of natural variation. Nevertheless, the lambeosaurine dinosaur clutch size, fitted somewhat better to the bird model (Figure 3.2). This observation suggests a more bird-like reproduction strategy of the lambeosaurine dinosaur, in particular because the egg mass of this species also fitted better to the bird model. However, independent of whether the reptile or the bird model was used, the observed fossil clutch size of this dinosaur species fits to the range observed in extant taxa and thus the observed fossil clutch size of 22 eggs seems to be realistic for a 2.5-ton lambeosaurine dinosaur.

Theropods – clutch mass/size. As expected under our initial hypothesis the bird model predicted clutch masses/sizes for theropods similar to the fossil sizes. Fossils indicate that at least some avian reproductive characteristics such as that adults sit on eggs (Norell et al. 1995; Dong and Currie 1996; Varricchio et al. 1997, 1999), asymmetrical eggs (Norell et al. 1995; Horner and Weishampel 1996; Varricchio et al. 1997), unornamented eggshell surface and complex eggshell ultrastructure existed in non-avian theropods (Zelenitsky and Therrien 2008a). Thus, our results corroborate the hypothesized bird-like reproduction mode of theropods. Furthermore, vice versa our results on theropods suggest accurate body mass and egg mass estimates and the completeness of clutches found. Varricchio et al. (2008) assumed paternal care for some theropods because clutch-associated adults lack the maternal and reproductively associated histological features common to extant archosaurs and because of their relatively large clutch volumes. In the case of paternal care the estimated body mass will be mass of males rather than of females. However, the females had to be much larger to contradict our conclusions. In addition, our analyses revealed no large clutch masses relative to body masses for theropods in comparison to the studied birds, which practice mostly bipaternal or maternal care. Thus, it is questionable if the theropods “sitting” on eggs were really males.

Prosauropods and sauropods – clutch mass/size. For the prosauropod *Massospondylus* the clutch size predicted under the reptile model was 24.98 and thus higher than the fossil clutch size (6 eggs). In addition, the minimum clutch size predicted for this species was slightly higher (8.55 egg) than the fossil size (Table 3.4). Because within the extant species we did not observe such a low ratio in clutch and body mass, we think that the clutch size of this species was probable higher and that the clutch found was incomplete. A complete clutch of *Massospondylus* could have consisted of more than 8 eggs and less than 25 eggs (Table 3.4). Assuming a body mass of 5 t for the sauropods, the clutch sizes predicted from the reptile model were consistent with fossil sizes. We derived our estimate of the egg mass of *M. siruguei* from eggs found in clutches with an average size of 9 eggs (Chiappe et al. 1999; Jackson 2007; Jackson et al. 2008). However, groups of 3 to 8, exceptionally 18 eggs were also reported, which were assigned to the oospecies *M. mammilare* that contains all eggs of the *Megaloolithus* type from Spain and probably from southern France and thus of *M. siruguei*, too (Sander et al. 2008). Moreover, a new study suggests that a clutch of *M. siruguei* probably had 25 eggs (Vila et al. 2010). Nevertheless, each of the reported clutch sizes are consistent with our reptile model, which predicted a clutch size of 9.44 eggs with a range between 2.86 and 38.77 eggs based on extant variability.

It has been hypothesized that *M. siruguei* distributed their eggs over several small clutches due to the physiological constraints imposed on a large clutch (Seymour 1979; Seymour and Ackerman 1980; Sander et al. 2008). However, this seems not a very likely explanation of clutch size if we consider a female sauropod mass of 5-20 t and it could even be questioned if we assume a female mass of 70 t. For a 20-ton sauropod the reptile model estimates a clutch size of 27.08 eggs and for a 70-ton sauropod the reptile model estimates a clutch size of 70.17 eggs. Both estimates are indeed much larger than the 9 eggs from the fossil record (Chiappe et al. 1999; Jackson 2007; Jackson et al. 2008, Sander et al. 2008) and for a 70-ton sauropod they are much higher than the assumed fossil clutch size of 25 eggs (Vila et al. 2010). Nevertheless, the lower “borderline” of the reptile model estimates a clutch size of 8.19 eggs for a 20-ton sauropod and of 21.23 eggs for a 70-ton sauropod producing *M. siruguei* eggs of 5.211 kg. Thus, the assumption that the clutch size of the *Megaloolithus siruguei* oospecies are physiologically limited only remains plausible if (i) the egg producing sauropod was very large and/or produced smaller eggs than assumed by us or (ii) the clutch size of 9 eggs is true and the 25 eggs per clutch postulated by Vila et al. (2010) are wrong or (iii) contradict to our conclusion the bird model is more proper than the reptile model.

Dinosaurs - annual clutch mass (overview). For almost all dinosaurs (except for *Massospondylus* and *Maiasaura*), predicted annual clutch masses fitted either to reptiles or to birds although we assumed only one clutch per year. In addition, only for the lambeosaurine dinosaur the best model changed (from bird to reptile) between clutch mass and annual clutch mass. Thus, most dinosaurs with body masses in the range assumed in this study might have laid only one clutch per year. However, the estimates of the number of clutches per year depend on the assumed body masses and clutch sizes, and hence the estimates on the number of clutches per year will be only accurate if both characteristics are sufficiently accurate. Especially for sauropods, these characteristics could be erroneous.

Hadrosaurids – annual clutch mass/egg number/clutches per year. The annual clutch masses of the hadrosaur *Maiasaura peeblesorum* fitted neither to birds nor to reptiles. Because the minimal annual egg number (23.92 eggs) estimated for *Maiasaura peeblesorum* was larger than the fossil clutch size (16 eggs), we conclude that this species had more than one clutch per year. The 60 eggs per year predicted by the reptile model suggest three up to four clutches per year for this species. Analogously, the annual egg numbers estimated from the reptile model and from the bird model, suggest that the lambeosaurine dinosaur had one or two clutches per year.

Theropods – annual clutch mass/egg number/clutches per year. The predictions from allometries revealed that as expected annual clutch masses of theropods fitted best to the bird model and that the annual egg number was similar to clutch size. Thus, theropods had probably one clutch per year. Because the estimation of body mass and the observed clutch sizes seems to be accurate, these estimates seem to be accurate, too.

Prosauropods and sauropods – annual clutch mass/egg number/clutches per year. The minimal annual egg number (21.03 eggs) estimated for *Massospondylu*s was more than three times larger than the fossil clutch size (6 eggs). We, therefore, conclude that this species had more clutches per year. Assuming a clutch size between 8 and 25 eggs for this prosauropod (see discussion for clutch size), the reptile model predicts that the species had at least two or three clutches per year. Sauropods had larger eggs than similar sized reptiles and similar clutch masses but a lower annual clutch mass when assuming a body mass of 5 t and only one clutch per year. Nevertheless, for both sauropods the annual clutch mass is still within the observed range of extant reptiles. However, the reptile model predicted for an "average" reptile an annual egg number twice as high as the estimated clutch size and as the fossil size. Therefore, when assuming a mean clutch size of ~9 eggs for the *Megaloolithus siruguei* and of ~25-30 eggs for *Megaloolithus patagonicus* in accordance with the fossil record and as predicted by the reptile model for a 5-ton sauropod, these species had probably two clutches per year resulting in annual egg numbers of 18 and 60 eggs per year. However assuming a much larger body mass of 20 t or 70 t the reptile model predicts, depending on egg mass assumed (5.211 kg or 1.741 kg), annual egg numbers of 56.66 or 169.58 (20 t) and annual egg numbers of 146.81 or 439.41 (70 t), respectively. Because the estimated annual egg number depends not only on body mass but also on egg mass and because egg mass increases with body mass we think that the 439.41 eggs per year estimated from the lower egg mass is probably not correct for a 70-ton sauropod. However, large sauropods probably had laid several clutches per year. In how many clutches the eggs were exactly distributed depends on clutch size. We think as much as 6 to 7 clutches per year could be common in large sauropods. Maybe up to 16 clutches per year could be realistic if the clutch size was small (~ 9 eggs) and the sauropod large (70 t)

Dinosaur - conclusion. Despite their imposing difference in egg and body size, dinosaurs had egg mass to body mass relations that were mostly larger than we observed in extant reptiles and were between those of reptiles and birds. Thus, the reproductive strategy of dinosaurs might be an intermediate state between the extant reptile and bird strategy. For some dinosaurs egg mass to body mass relations were closer to similar sized reptiles (e.g. prosauropod and sauropods) whereas others were closer to birds (e.g. theropods). This probably indicates an evolution from a more reptile-like (many, small eggs) reproductive strategy in basal dinosaurs to a more bird-like (few, large eggs) reproductive strategy in phylogenetic derived lineages (perhaps linked with endothermy?), especially in the lineage (theropods) that evolved birds. Dinosaur clutch masses mostly fitted to clutch masses predicted from allometries of extant taxa. However, the clutch mass/body mass ratios estimated from the fossil record could be wrong. For example, for sauropods we do not know if the assumed body mass is correct. In addition, the clutch size observed in the fossil record could be erroneous and hence the assumed clutch mass. However, our results questions whether clutch sizes of sauropods result from physiological limits. Only in very large sauropods a physiological limit of the clutch size is reasonable and might cause a partitioning of eggs into several clutches (during one reproduction event). Established allometries also allow comparing hypothetical annual clutch masses of dinosaurs with those of extant taxa. This enables the estimation of annual egg numbers for dinosaurs. Dinosaurs, such as theropods, that show a more bird-like reproductive strategy had probably one clutch per year, and hence, their clutch size equals their annual egg number. Dinosaurs, such as moderate sized sauropods and as hadrosaurids, had a more reptile like reproductive strategy or a strategy intermediate to birds and reptiles with probably 2 up to 4 clutches per year, and hence, 18 up to 100 eggs per year (depending on dinosaur species). Large sauropods had probably 6-7 clutches per year and an annual egg number of over 150 eggs. Perhaps some very large sauropods (70 t) could occasionally have produced up to 500 eggs per year (divided into several clutches), but a higher annual egg number is not very likely and even most large sauropods seem to have not reached such high annual egg numbers.

3.6 Main conclusions

Comparisons of the reproductive investment of extinct taxa, measured in egg mass, clutch mass or annual clutch mass, with those of extant taxa give new insights in the reproduction of the former. Our study demonstrates that it is precarious to compare reproductive investment to body mass relations without taking the allometric effect of body mass into account. New paleontological hypotheses derived from fossils of extinct taxa and from extant taxa could be developed and tested, and the generality of ecological hypotheses could be tested on species that lived in the past. A synthesis between paleontological and ecological expertise adds to fully reconstruct the life-cycles of extinct organisms. In addition, this would enable paleontologists and biologist to study the evolution of traits that are either inaccurate or even not preserved in the fossil record.

4 Reproductive biology and its impact on body size: comparative analysis of mammalian, avian and dinosaurian reproduction

4.1 Abstract

Using terrestrial non-passerine birds as model for dinosaurs Janis and Carrano (1992) suggested that large dinosaurs might have faced a lower risk of extinction under ecological changes due to their higher potential reproductive output compared to similar sized mammals. In the present study we tested this assumption of the hypothesis by comparing the potential reproductive output (reflected in clutch/litter size and annual offspring number) of terrestrial herbivorous mammals, birds and dinosaurs. Our study improves substantially upon previous work by using a larger dataset of species, by analysing single orders, by controlling for phylogenetic effects and by using new data points for dinosaurs. With the exception of rodents, the differences in the reproductive output of birds and mammals proposed by Janis and Carrano (1992) existed even at the level of single orders. Furthermore, dinosaur clutches were larger than litters of similar sized mammals but were similar to clutches of similar sized birds. Because extinction risk (in birds and mammals) often correlates with low reproductive output, this implies a lower risk of population extinction in dinosaurs. Thus, compared to mammals the largest dinosaurs like sauropods may have more easily sustained populations of very large-bodied species over evolutionary time.

4.2 Introduction

Body size is one of the most fundamental attributes of any organism (Hunt and Roy 2006; Bonner 2006). While body size maxima for some organisms can be directly studied in living species, the largest terrestrial animals that have ever existed on earth, the sauropod dinosaurs, must be studied from the fossil record. Sander and Clauss (2008) have argued that the gigantism of these animals must result from their unusual biology. Their thesis is corroborated by the observation that body size influences nearly every aspect of the biology of currently existing organisms and that many life-history variables correlate with body size (Blueweiss et al. 1978; Stearns 1983; Sibly and Brown 2007). Variables, such as size or number of offspring are important for understanding life-history strategies, because they are directly related to the fitness of an organism (Lack 1947, 1954; Lloyd 1987; Godfray et al. 1991). These variables reflect several important trade-offs, e.g., investment of energy in somatic versus gonadic growth, in continuous or intermittent breeding, and in the investment in either many small or a few large offspring (Hendriks and Mulder 2008).

Kurtén (1953) already pointed out that body size limits of a taxon reflect not only mechanical or physiological constrains, but also the scaling of its reproductive parameters (Blueweiss et al. 1978; Tuomi 1980; Millar and Zammuto 1983; Reiss 1985; Hendriks and Mulder 2008). Following this idea, Janis and Carrano (JC, 1992) stated that terrestrial non-passerine birds, taken as a model for dinosaurs, differ from terrestrial mammals in terms of their reproductive biology. They found that, for terrestrial mammals, body mass was negatively correlated with litter size (number of offspring per litter; clutch size = number of offspring per clutch), breeding frequency (number of clutches/litters per year) and annual offspring number (total number of offspring per year = clutch/litter size x number of broods per year), whereas such relationships were absent in non-passerine birds. However, JC based their study on only 32 extant terrestrial birds and 75 terrestrial mammals, and did not control for phylogenetic effects as had been recommend (Diniz-Filho and Tôrres 2002; Martins et al. 2002; Paradis and Claude 2002; Rohlf 2006) when studying traits such as body size that are not phylogenetically independent (Gittleman et al. 1996; Abouheif and Fairbairn 1997; Abouheif 1999). JC also ignored life-history differences between trophic levels (i. e., carnivorous versus herbivorous; Wilbur et al. 1974; Sibly and Brown 2007) and differences in clutch size associated with different nesting modes (e.g. ground breeding, tree breeding and cave breeding; Martin and Li 1992; Jetz et al. 2008). In addition, none of the dinosaur data points JC used are valid with the today's state of knowledge.

Nevertheless, using terrestrial non-passerine birds as "dinosaur analogs", JC put forward the hypothesis (henceforth called the JC hypothesis) that different reproductive strategies in dinosaurs and mammals (ovipary in birds and dinosaurs versus vivipary plus lactation in mammals) have resulted in a different ability of dinosaurs and mammals to evolve and sustain large-bodied species over evolutionary time. JC suggested that, given their higher potential reproductive output compared to similar sized mammals, large dinosaurs may have faced a lower risk of extinction under ecological changes.

In the present study, we tested the underling assumptions of the JC hypothesis by comparing the potential reproductive output (reflected in clutch/litter size and annual offspring number) of terrestrial herbivorous mammals, birds and dinosaurs. For dinosaurs, we focused on sauropods because they were the largest known terrestrial animals that have ever existed on earth and both clutch size and body mass data are available for this dinosaur suborder. We considered only herbivorous species because the sauropods were herbivores (Sereno 1999; Sander and Clauss 2008) and because most bird species assumed to be close relatives of ancient dinosaurs are herbivores, too. Our study improves substantially upon previous work by using a larger dataset (116 birds and 376 mammals) and by controlling for phylogenetic effects using Felsenstein's independent contrasts (PIC, Felsenstein 1985; a widely used and well tested method) and the phylogenetic generalised least square regression (PGLS, Pagel 1997, 1999; Freckleton et al. 2002; this method performs well even if the assumptions of Felsenstein's method are not fulfilled). Additional, we analysed single orders to test whether the dependencies between body mass and reproductive variables underlying the JC hypothesis do exist within every avian and mammalian order. This approach counteracts a misinterpretation of results caused by an inhomogeneous dataset produced by different orders and sample sizes.

4.3 Material and methods

4.3.1 Analysed classes and orders

Aves. We focused on avian orders presumed to be close phylogenetic relatives of ancient dinosaurs. According to traditional taxonomy, these are the orders Struthioniformes and Tinamiformes, which are united as the subclass Paleognathae (Cooper et al. 2001; Haddrath and Baker 2001). Because phylogenetic analyses have revealed a close relationship of the orders Galliformes and Anseriformes with the Paleognathae (Sibley and Ahlquist 1990; Clarke et al. 2005; Pereira and Baker 2006b; Livezey and Zusi 2007) we also included these two orders in our analysis. We restricted our analyses to ground breeding and terrestrial species with an average body mass greater than about 600 g, because this is the approximate weight of small ancestral paravian dinosaurs (Turner et al. 2007). Given that sauropods, like most dinosaurs, were most probably ground breeders (Paul 1994; Chiappe et al. 1998; Horner 2000; Chiappe et al. 2004; Sander et al. 2008), we excluded cavity and tree breeding bird species, which are likely to differ profoundly in breeding ecology and life-history (Martin and Li 1992; Jetz et al. 2008). Furthermore, the majority of analysed avian species usually do not fly during their routine activities (e.g. foraging and feeding) and were herbivorous.

Mammals. In our analysis, we included mammalian species, which belonged to the orders Rodentia, Lagomorpha, Artiodactyla, Perissodactyla, Hyracoidea, Proboscidea, Diprotodontia and Primates. All species were herbivorous, terrestrial and had a minimum average body mass of around 600 g.

Dinosaurs. Detailed analyses were performed only for the dinosaurian suborder Sauropoda (sauropods). However, to enlarge our dataset, we also compared dinosaur clutch sizes with mammalian litter sizes and avian clutch sizes, considering all dinosaurs for which clutch size and body mass data are currently available (Table 1 in appendix B). In particular, assignments of eggs to producers only exist for three theropods (*Troodon formosus*, *Oviraptor philoceratops*, *and Citipati osmolskae*), two hadrosaurs (*Maiasaura peeblesorum*, lambeosaurine dinosaur), two sauropods (*Megaloolithus patagonicus*, *Megaloolithus siruguei*) and one prosauropod (*Massospondylus*). All analysed dinosaurs were terrestrial and larger than 600 g.

4.3.2 Life-history traits and data sources

Avian data on body mass and reproductive biology were collected from the literature (Crome 1976; Sick 1985; Naranjo 1986; Rohwer 1988; Dunning 1992; Hoyo et al. 1992; Dani 1993; Hoyo et al. 1994; Sarasqueta 1995; Fernandez and Reboreda 1998; Persson and Göransson 1999; Bellis et al. 2000; Sarasqueta 2000; Navarro and Martella 2002; Kimwele and Graves 2003; Barri et al. 2009). The literature was identified through keyword searches in databases of original publications (Web of Science), internet search engines (Google, Google scholar), as well as individual scanning of references in books and in original publications. Data sets for mammals were exclusively compiled from the database AnAge (Build 10, release date: April 18, 2008) provided by the Human Ageing Genomic Resources project (de Magalhaes 2005). This database has a good representation of mammalian orders that meet the relevant criteria of our study (body mass >0.600 kg, herbivorous, terrestrial). Information on mammalian diet was taken from Macdonald (2007). For dinosaurs, we collected all data sets that we could find in the literature (Table 1 in appendix B).

We gathered data on body mass, clutch/litter size, breeding frequency, and annual offspring number, for birds and mammals. Annual offspring number was calculated as clutch/litter size multiplied by the number of clutches/litters per year. For body mass we preferred estimates of the mass of females, because mass is more strongly linked to reproductive traits in females than in males. In many cases, however, it was not possible to distinguish between male and female body masses because only averages of both sexes were available. To maximize our sample size while minimizing any bias introduced by male body masses, we used female body masses wherever possible and averaged body masses otherwise. Relative to the range of body sizes included in our analysis (up to 100 kg in birds and up to 4.8 t (t = metric tons) in mammals), errors in the estimation of body mass for single species are likely to be negligible.

For dinosaurs, the fossil record provides data on non-sex-specific body mass and clutch size, but not on breeding frequency and annual fecundity.

4.3.3 Statistical analyses

To test the assumptions of the JC hypothesis we checked for relationships between body mass and reproductive variables (clutch size and annual offspring number) for birds and mammals using the following statistical methods.

Correlation and regression analysis. As a first step, following Janis and Carrano (1992), we calculated standard Pearson correlation coefficients (PEARSON) and carried out linear least square regressions (LS) on double log-transformed data, thus implicitly assuming statistical independence of species data.

As a next step, contrary to Janis and Carrano (1992), we controlled for phylogenetic dependency of data points (Diniz-Filho and Tôrres 2002; Martins et al. 2002; Rohlf 2006). This is important because body mass is not phylogenetically independent within birds and mammals (Gittleman et al. 1996; Abouheif and Fairbairn 1997; Abouheif 1999; Geffen and Yom-Tov 2001; Carvalho et al. 2006; Figuerola and Green 2006). We applied two phylogenetic comparative methods (PCMs) to control for phylogenetic effects in body mass and reproductive traits. PCMs are generally used to infer to what extent shared traits between species are attributable to common ancestry (Martins et al. 2002). However, they are based on the assumption that the traits of interest have evolved in a particular way along a specified phylogenetic tree. Because the underlying evolutionary model could be violated and/or the phylogenetic tree utilized by PCMs could be inaccurate (phylogeny, branch lengths), we performed additional standard analyses based on subsets of species with different body size classes by comparing their means.

Phylogenetic comparative methods. As phylogenetic comparative method, we first chose Felsenstein’s independent contrasts (PIC, Felsenstein 1985) a method that is widely used and well tested (Ricklefs and Starck 1996; Carvalho et al. 2006). It performs best when the underlying evolutionary model is valid (Felsenstein 1985, 1988; Diniz-Filho and Tôrres 2002; Martins et al. 2002). Second, we used the phylogenetic generalised least square regression (PGLS, Pagel 1997,1999; Freckleton et al. 2002), because this method performs well even if the assumptions of Felsenstein’s method are not fulfilled (Martins et al. 2002; Rohlf 2006). In general, PCMs perform best when the phylogeny itself and branch lengths are correct (Felsenstein 1985, 1988; Martins et al. 2002).

We constructed phylogenetic relationships based on published consensus trees derived from morphological and genetic markers when available. To solve the problem that no complete phylogeny was available for all bird species, we constructed a new tree based only on the hierarchies of different published phylogenetic trees of different taxonomic levels (Figure 1 in appendix B). For example, if one phylogeny resolved to genus level and another phylogeny resolved from genus to species level, we fused the two trees. All branch lengths were set to one (with the exception of polytomies, in this case branch lengths were set to 0.0000001), because markers and clustering methods used to construct trees might have been different and thus might have affected branch lengths. If more than one phylogenetic tree was available for one taxonomic level, we chose the best supported one (e.g. different papers and/or methods that result in a similar phylogeny).

For mammals, we used the complete phylogeny given in Bininda-Emonds et al. (2007, Supplementary Figure 1, tree mammalST_bestDates), excluded all taxa that were not in our mammalian dataset and set all branch lengths of this tree to one (with the exception of polytomies, in this case branch lengths were set to 0.0000001) to allow a comparison of results to those obtained for birds (the inclusion of original branch lengths, however, did not change our conclusions on the JC hypothesis).

All correlations (PEARSON, PCMs) and regressions (LS, PCMs) were computed with COMPARE, version 4.6b (Martins 2004). We performed significance tests (t-tests) for correlations and differences between slopes of the regression lines obtained for mammals and birds, and for those obtained for different avian and mammalian orders. The tests were calculated using the statistical software R (version 2.7.1).

Additional analyses on subsets of birds and mammals. We compared the medians of clutch/litter sizes of the orders in each phylogenetic class (birds, mammals) using Kruskal-Wallis tests. Additionally, we grouped birds and mammals into five weight classes. Each class had an equal width of 0.444 on a logarithmic scale. The first class starts at ~0.56 kg (smallest bird) and the last ends at ~93 kg (largest bird). To check for patterns in the average values of reproductive traits, we computed pairwise Wilcoxon tests for birds and mammals of equal weight classes. These tests were also calculated using R.

Comparisons between dinosaurs and birds and between dinosaurs and mammals. To compare dinosaur clutch sizes with bird and mammal clutch/litter sizes, we plotted dinosaur data alongside bird and mammal data. In addition, we calculated

95% confidence intervals (prediction intervals) of the regression lines of birds and mammals, respectively.

4.4 Results

4.4.1 Correlation and regression analysis for birds and mammals

Clutch/litter size and body mass. Whether controlling for phylogenetic effects or not, we found no correlation between clutch size and body mass in birds presumed to be close relatives of ancient dinosaurs (Table 4.1); neither did we find such a correlation within single bird orders (Table 4.2). The only exception was the significant negative PEARSON correlation in the Anseriformes, which disappeared when we controlled for phylogenetic effects (Table 4.2).

Table 4.1. Correlations between body mass and reproductive characteristics for birds and mammals. Correlations are given for double log-transformed data using Pearson's correlation coefficient (PEARSON) and two phylogenetic methods (PIC = Felsenstein's independent contrasts; PGLS = phylogenetic generalised least square regression). → no correlation, ↗ significant positive correlation, ↘ significant negative correlation. Significance levels: * < 0.05, ** < 0.01, *** < 0.001.

Correlations	Class	PEARSON	PIC	PGLS	N
Body mass vs. clutch/litter size	Birds	→	→	→	116
	Mammals	↘***	↘***	↘***	353
Body mass vs. annual offspring number	Birds	→	↗*	↗*	116
	Mammals	↘***	↘***	↘***	203

Independent of the statistical method used, we found a significant negative correlation between litter size and body mass in mammals (Table 4.1). This pattern, however, was not found at the level of single orders. For PEARSON and PCMs, we found a significant negative correlation between body mass and litter size in artiodactyls, but none in any of the other mammalian orders (Table 4.2). The dataset of Hyracoidea and Proboscidea was too small (< 6) to carry out the respective correlation analyses.

The slopes of regression lines predicting clutch size for birds and litter size for mammals differed significantly (Table 4.3) with the exception of PGLS, where the difference in slopes was marginally significant ($t = 1.74$, $df = 465$, $p < 0.1$).

Table 4.2. Correlations between body mass and reproductive characteristics for different avian and mammalian orders. Correlations are given for double log-transformed data using Pearson's correlation coefficient (PEARSON) and two phylogenetic methods (PIC = Felsenstein's independent contrasts; PGLS = phylogenetic generalised least square regression). → no correlation, ↗ significant positive correlation, ↘ significant negative correlation. Significance levels: * < 0.05, ** < 0.01, *** < 0.001.

	body mass vs. clutch/litter size				body mass vs. annual offspring number			
Order	PEARSON	PIC	PGLS	N	PEARSON	PIC	PGLS	N
Struthioniformes	→	→	→	6	→	→	→	6
Tinamiformes	→	→	→	6	→	→	→	6
Galliformes	→	→	→	46	→	→	→	46
Anseriformes	↘***	→	→	58	↘***	→	→	58
Rodentia	→	→	→	60	→	→	→	32
Lagomorpha	→	→	→	14	↘***	→	↘**	12
Artiodactyla	↘*	↘*	↘*	144	↘***	↘***	↘***	87
Perissodactyla	→	→	→	15	↘***	↘*	↘***	11
Primates	→	→	→	80	↘***	↘***	↘***	59
Diprotodontia	→	→	→	35				

Table 4.3. Comparison of slopes of regression lines of body mass vs. reproductive characteristics for birds and mammals. Regressions were calculated for double log-transformed data using LS (linear least square regression) and two phylogenetic methods (PIC = Felsenstein's independent contrasts; PGLS = phylogenetic generalised least square regression). SE: standard error. Significance levels: * < 0.05, ** < 0.01, *** < 0.001.

	Method		
	LS	PIC	PGLS
Body mass vs. clutch/litter size			
Birds (N = 116):			
Intercept (SE)	0.85 (0.02)	0.76 (0.03)	0.82 (0.08)
Slope (SE)	0.01 (0.04)	0.09 (0.06)	0.06 (0.06)
Mammals (N = 353):			
Intercept (SE)	0.19 (0.02)	-0.21 (0.00)	0.16 (1.18)
Slope (SE)	-0.08 (0.01)	-0.05 (0.02)	-0.05 (0.02)
Different slopes in birds and mammals	Yes*	Yes*	No
Body mass vs. annual offspring number			
Birds (N = 116):			
Intercept (SE)	0.84 (0.02)	0.78 (0.03)	0.82 (0.07)
Slope (SE)	0.07 (0.05)	0.15 (0.06)	0.12 (0.06)
Mammals (N = 203):			
Intercept (SE)	0.43 (0.04)	3.11 (0.00)	2.09 (0.60)
Slope (SE)	-0.24 (0.03)	-0.95 (0.00)	-0.95 (0.00)
Different slopes in birds and mammals	Yes***	Yes***	Yes***

Annual offspring number and body mass. Birds showed either no significant correlation between annual offspring number and body mass (PEARSON) or a positive correlation (PIC and PGLS; Table 4.1). At the level of single bird orders, we obtained for the relationship between body mass and annual offspring number similar results as for body mass versus clutch size (Table 4.2), because most species have only one brood per year (except for ratites with one to two clutches per year). At this phylogenetic level, none of the three statistical methods revealed a correlation between body mass and annual offspring number, except for the Anseriformes, which showed a significant decrease according to PEARSON.

Mammals, however, showed a significant negative correlation between annual offspring number and body mass under all methods used (Table 4.1). With two exceptions (Rodentia, Lagomorpha), this general pattern was also found within single mammalian orders (Table 4.2). Independent of the method used, rodents showed no correlations between these traits. Annual offspring number and body mass were negatively correlated in lagomorphs according to PEARSON and PGLS, but not to PIC. All other mammalian orders showed overall significant negative correlations between body mass and litter size (Table 4.2). The dataset of Hyracoidea, Diprotodontia and Proboscidea was too small (< 6) to carry out the respective correlation analyses.

Independent of the statistical method used the slopes of regression lines predicting annual offspring number from body mass for birds and mammals differed significantly (Table 4.3).

4.4.2 Additional analyses on subsets of birds and mammals

None of the studied bird orders differed in their median clutch size (Kruskal Wallis test: $\chi^2 = 5.49$, $df = 3$, $p = 0.139$; Figure 4.1A), whereas the medians of litter size of studied mammalian orders were inhomogeneous (Kruskal Wallis test: $\chi^2 = 149.45$, $df = 7$, $p < 10^{-6}$; Figure 4.1A). In birds, the medians of the annual offspring number of all orders were homogeneous (Kruskal Wallis $\chi^2 = 4.04$, $df = 2$, $p = 0.132$), except for the ratites whose median differed from that of the other bird orders (Kruskal Wallis test: $\chi^2 = 10.58$, $df = 3$, $p = 0.014$; Figure 4.1B). However, the medians of annual offspring number of all mammalian orders were inhomogeneous (Kruskal Wallis test: $\chi^2 = 133.36$, $df = 5$, $p < 10^{-6}$; Figure 4.1B).

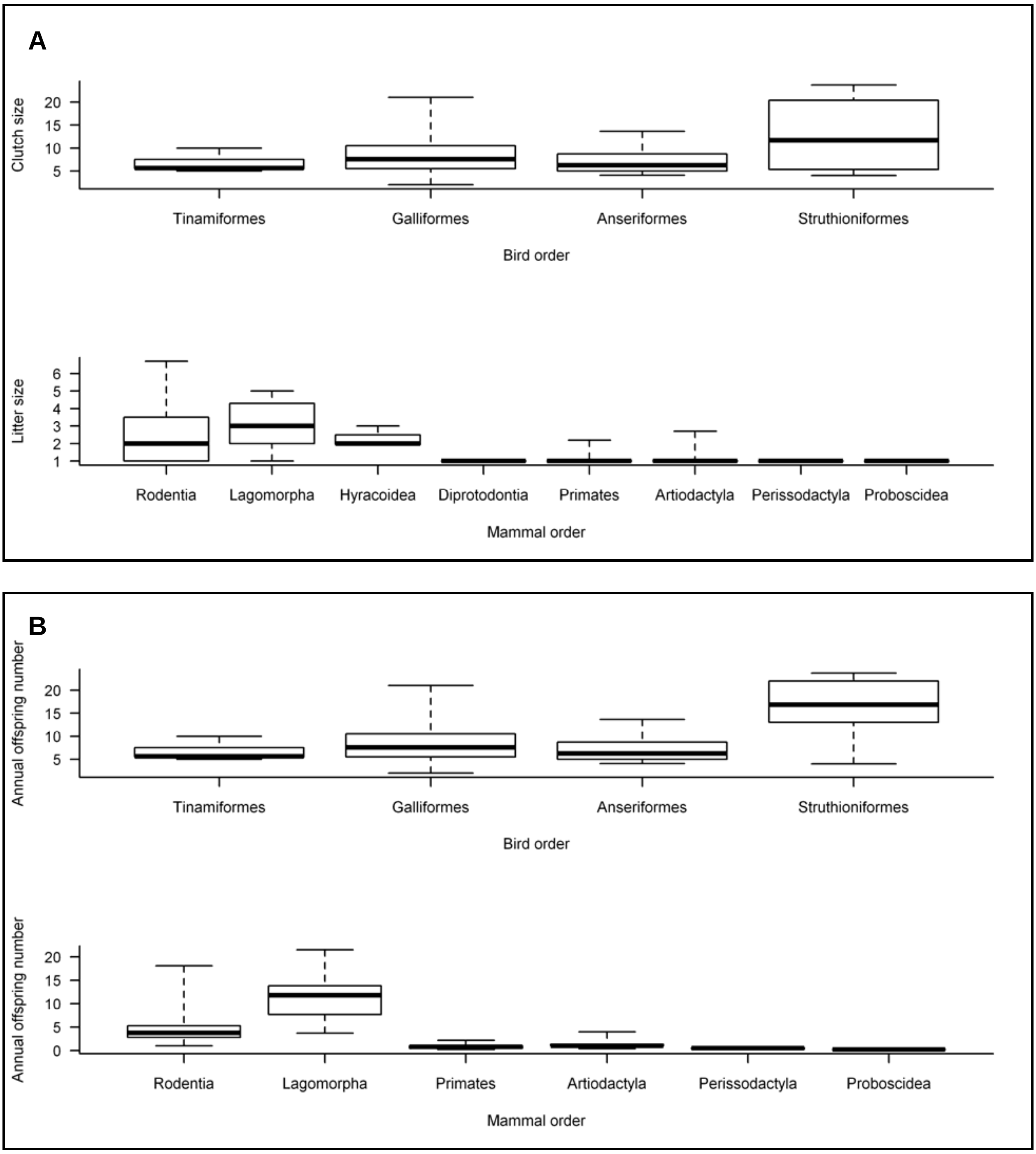


Figure 4.1. Comparison of the median clutch/litter size and annual offspring number of different bird orders (**A**) and mammal orders (**B**). Species orders are ordered by body mass, starting with the lowest median body mass on the left side. All studied bird orders do not differ in their median clutch size whereas the medians of litter size of studied mammalian orders are inhomogeneous. In birds, the medians of the annual offspring number of all orders are homogeneous, except for the ratites. The medians of annual offspring number of all mammalian orders are inhomogeneous. For the detailed results of the statistical analyses, refer to the text. Box plots show medians, quartiles, minima and maxima of clutch sizes/annual offspring number.

Similar sized birds of all weight classes had a higher median clutch/litter size than mammals (Figure 4.2A; exact Wilcoxon tests, N1 = sample size birds, N2 = mammals : Class [0.56, 1.56[, Z = 7.79, N1 = 57, N2 = 39, $p < 10^{-6}$; Class [1.56, 4.33[, Z = 8.49, N1 = 43, N2 = 57, $p < 10^{-6}$; Class [4.33, 12.02[, Z = 6.69, N1 = 10, N2 = 87, $p < 10^{-6}$; Class [12.02, 33.42[, Z = 3.26, N1 = 3, N2 = 43, $p < 10^{-4}$; Class [33.42, 92.90[, Z = 3.26, N1 = 3, N2 = 58, $p < 10^{-4}$) and these differences between birds and mammals tended to be larger in the higher weight classes than in the lower classes (Figure 4.2A). Similar sized birds had also on average (median) a higher annual offspring number than mammals in all weight classes (Figure 4.2B; exact Wilcoxon tests, N1 = sample size birds, N2 = mammals: Class [0.56, 1.56[, Z = 2.28, N1 = 57, N2 = 23, $p = 0.02$; Class [1.56, 4.33[, Z = 4.07, N1 = 43, N2 = 23, $p < 10^{-4}$; Class [4.33, 12.02[, Z = 4.57, N1 = 10, N2 = 48, $p < 10^{-6}$; Class [12.02, 33.42[, Z = 2.58, N1 = 3, N2 = 23, $p = 0.003$; Class [33.42, 92.90[, Z = 2.91, N1 = 3, N2 = 33, $p = 0.0003$) and the differences between birds and mammals tended to be larger in the higher weight classes than in the lower ones (Figure 4.2B).

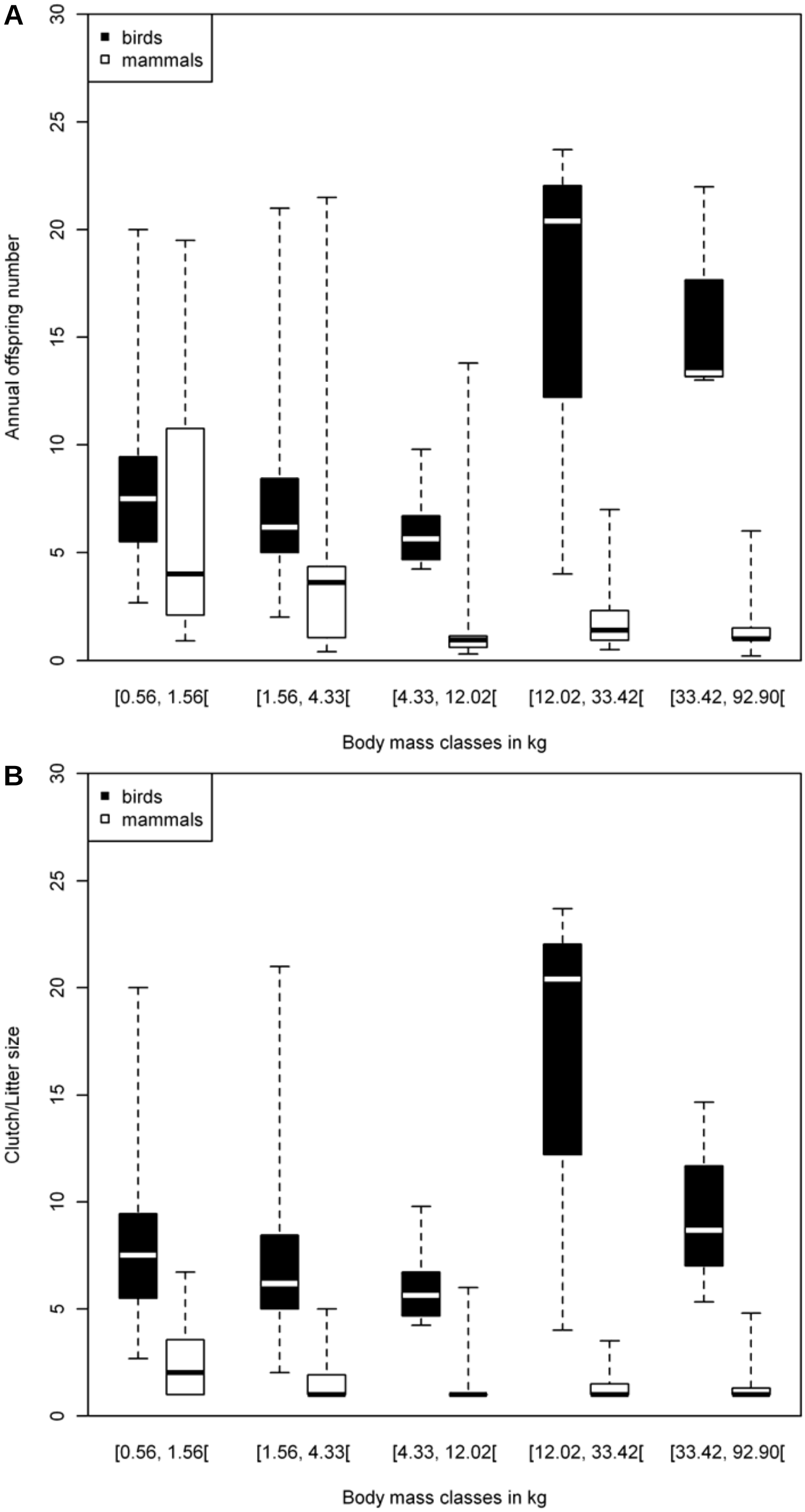


Figure 4.2. Comparison of medians of clutch/litter sizes (**A**) and annual offspring number (**B**) of birds and mammals for species groups of different weight classes. Each interval has a width of 0.444 (unit is kg) on a logarithmic scale. Similar sized birds of all weight classes had a higher median clutch/litter size than mammals. Similar sized birds had on average (median) more offspring per year than mammals in all weight classes. For the detailed results of the statistical analyses, refer to the text. Box plots show medians, quartiles, minima and maxima of clutch sizes and litter sizes.

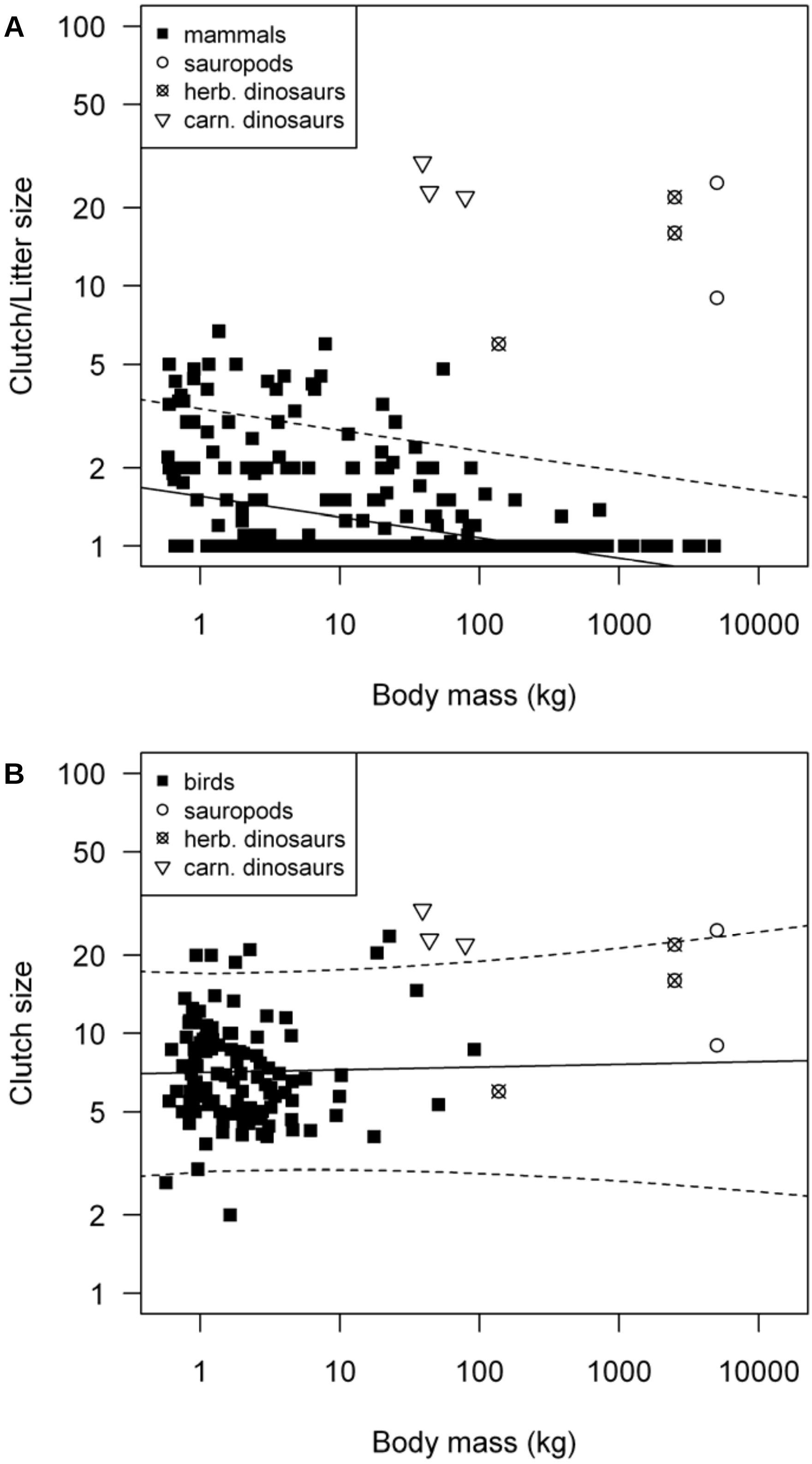


Figure 4.3. Relationship between clutch/litter size and body mass in birds (**A**, black squares) and in mammals (**B**, black squares) using least square regression analysis (solid line) and the corresponding 95% confidence intervals (dashed lines, in **B** only the upper limit of the confidence interval is drawn). Sauropod clutch sizes (open circles) do fit well to those of birds or lay somewhat above the upper limit of the confidence interval (**A**) but do not fit to litter sizes of mammals (**B**). Carnivorous (open triangles) and other herbivorous dinosaurs (circles with crosses) do also fit better to clutch sizes of birds (**A**) than to litter sizes of mammals (**B**). Clutch sizes and body masses of dinosaurs are summarized in Table 1 in appendix B.

4.4.3 Comparisons between dinosaurs and birds and between dinosaurs and mammals

In general, dinosaur clutch sizes differed from litter sizes of similar sized mammals but were similar to those of similar sized birds (Figure 4.3). Especially sauropod and other herbivorous dinosaur clutch sizes were bird-like (Figure 4.3A) rather than mammal-like (Figure 4.3B).

4.5 Discussion

4.5.1 Comparison of birds and mammals at class level

Our results corroborate the hypothesis of Janis and Carrano (1992) for terrestrial, herbivorous birds and mammals. This hypothesis states that different reproductive strategies have resulted in a different ability of dinosaurs and mammals to evolve and sustain large-bodied species over evolutionary time. Because of their higher potential reproductive output (reflected in clutch/litter size and annual offspring number) compared to similar sized mammals, large dinosaurs may have faced a lower risk of extinction under ecological changes. Our analyses revealed that the differences in the life-history of birds and mammals proposed by Janis and Carrano (1992) exist, such that herbivorous, terrestrial mammals, but not birds, show a significant decrease in clutch/litter size and annual offspring number with increasing body mass.

Our results are supported by Paul’s (1994, 1997) statistical analysis of annual offspring number and body size in reptiles, birds, monotremes, marsupials and placentals. He stated that in extant taxa with an adult mass of 1 g to 10 kg, annual offspring number is broadly similar in egg layers and livebearers. Above 10 kg the number of young of the two types diverges significantly, with many oviparous taxa being much more prolific than mammals. Furthermore, we have shown that similar sized birds of all weight classes had a higher median clutch size and annual offspring number than mammals. Moreover, these differences between birds and mammals tended to be larger in the higher weight classes than in the lower classes. One reason for this effect could be that, the offspring of large mammals tend to be much bigger than the eggs of large birds. Large mammals have one to two young per year, whereas small mammals, such as rodents, are frequently quite fecund (Roff 2002; Figure 4.1). This bimodal distribution of litter size leads to an overall decrease in litter size and annual offspring number with increasing body size for mammalian vertebrates. In birds, we did not find such a bimodal distribution (Figure 4.1).

4.5.2 Comparison of birds and mammals at the level of single orders

The JC hypothesis was also supported by our results when birds and mammals were compared at the level of single orders, except for rodents. In birds, at the level of single orders, the Anseriformes showed significant negative PEARSON correlation coefficients for body mass versus clutch size or versus annual offspring number (see also Geffen and Yom-Tov 2001) whereas, in accordance with the literature (Geffen and Yom-Tov 2001; Figuerola and Green 2006), we found no correlations using methods that control for phylogenetic effects. The negative PEARSON correlation between body mass and clutch size/annual offspring number in Anseriformes may be uninformative because of statistical dependency of the data, which is corrected for by the phylogenetic methods. However, no other avian orders have significant correlation coefficients (Table 4.2). In addition, all studied bird orders have similar median clutch sizes and similar annual offspring numbers (with the exception of the ratites). Thus, the potential reproductive output in the different avian orders is very similar (Figure 4.1).

Conversely, the studied mammalian orders are inhomogeneous in their potential reproductive output and adult body size. Most species from the orders Rodentia and Lagomorpha produce larger litters, have higher annual offspring numbers, and are smaller than species from the orders Artiodactyla, Perissodactyla, Primates, and Diprotodontia (Figure 4.1). This inhomogeneous distribution in reproductive variables is most probable caused by different development modes. Altricial mammalian species have more and smaller offspring than precocial species (Derrickson 1992). Species from the orders Rodentia and Lagomorpha are mostly altricial, whereas species from the other orders are mainly precocial (Martin and MacLarnon 1985; Derrickson 1992; Primates intermediate). Therefore, on average the orders Rodentia and Lagomorpha have more offspring (per litter and per year) than other mammalian orders comprising only precocial species (Artiodactyla, Perissodactyla, Primates, Diprotodontia). However, the development mode is only one reason for the inhomogeneous distribution of litter sizes and annual offspring numbers in mammals. Small precocial species from the order Hyracoidea also have higher litter sizes than large precocial species from other orders (Figure 4.1A). Within the order Artiodactyla, small species have higher litter sizes than large ones (Table 4.2), and, within the orders Artiodactyla, Perissodactyla and Primates, small species have higher annual offspring numbers than large ones (Table 4.2).

The absence of a correlation between litter size and body mass in the orders Perissodactyla, Primates and Diprotodontia, and the weak significant negative correlation in artiodactyls, is more or less trivial, because these species have reached the lower limit for litter size producing only one single offspring at a time. In contrast, the absent correlation between body mass and litter size in rodents and lagomorphs is not explainable by reaching the lower limit (Figure 4.1A). Lagomorphs showed a significant decrease in annual offspring number with increasing body mass, whereas rodents showed no correlation. The non-correlation between reproductive output and body mass in rodents could be caused by the two different development modes found in rodents (i.e. altricial and precocial) and/or because we did not include many rodents in our study due to of lack of data or because individuals of species are smaller than 600 g.

In addition, it is important to note that all studied large mammalian and all studied large avian species are precocial. Precocial mammalian species generally have fewer offspring than altricial species (Martin and MacLarnon 1985; Derrickson 1992), whereas the opposite is true in birds. Precocial avian species have on average more offspring than altricial birds (Jetz et al. 2008).

4.5.3 Reproduction and gigantism

The comparison of sauropod clutch sizes to the clutch/litter sizes of hypothetical similar sized avian or mammalian species demonstrated that dinosaur reproductive output is bird-like (rather than mammal-like). However, this is not to say that reproduction of sauropods resembled reproduction of ancient terrestrial herbivorous birds. Additionally, the extrapolation of the bird model to body sizes that are magnitudes larger than those of extant animals could be very erroneous. Furthermore, the data points for clutch size and body mass of sauropods are much less accurate than for birds and mammals. Nevertheless, our results show that the reproductive output of large herbivorous terrestrial mammals is very different from sauropods and, in view of many species characteristics shared between birds and dinosaurs (Varricchio et al. 1997; Sereno et al. 2008; Varricchio et al. 2008), it is probable that some dinosaurs were bird-like in aspects of their reproductive biology. However, we do not know how many clutches sauropods (and dinosaurs in general) laid per reproductive event or per breeding season. Some palaeontologists argue that they might lay more than one clutch per reproductive event (Sander et al. 2008). Evidence for this comes from the large size of adult sauropods in comparison to their small eggs, and the fact that the clutch size of some sauropods might have been limited by physiological constrains of the clutch (Seymour 1979; Jackson et al. 2008). If they laid more than one clutch per reproductive event, the “bird model” derived here is wrong, because sauropods would have had a higher reproductive output than recent birds. Results from Grellet-Tinner et al. (2006) call the bird model into question. These authors noted that the spatial arrangement of eggs in titanosaur (sauropod) nests (Chiappe et al. 2004) and the random spatial distribution of clutches resembles the reproductive mode of modern crocodilians and chelonians and they concluded that the titanosaur reproductive mode was probably closer to basal reptilians than modern birds. In this case, either the true clutch size of sauropods would resemble extant reptiles, which show an increase in clutch size with increasing body mass (Blueweiss et al. 1978; Frazer and Richardson 1986; Hailey and Loumbourdis 1988; Iverson 1992; Thorbjarnarson 1996; King 2000) or it could represent an intermediate state between reptiles and birds. However, whether the reproductive biology of large sauropods was bird-like, reptile-like or intermediate, they would always have had a higher potential reproductive output than similar sized mammals.

Janis and Carrano (1992) argue that this difference in the reproductive biology of dinosaurs and mammals made them less vulnerable to extinction. Several studies have shown that the extinction risk of species often correlates with a low reproductive output (Bennett and Owens 1997; Johnson 2002; Cardillo et al. 2005). In mammals, large species with a lower reproductive output are at higher risk of extinction than smaller ones (Cardillo et al. 2005; Schipper et al. 2008). Johnson (2002) found the same relationship for the Pleistocene mammalian extinctions and Cardillo (2003) for extant terrestrial Australian mammals. In addition, the evidence of the late Pleistocene extinctions illustrates the vulnerability of large mammals to environmental change (Kiltie 1984). Using a large fossil dataset of mammals Liow et al. (2008) found the recurring pattern that large mammal genera and species have higher speciation and extinction rates, and existed therefore over shorter times than small ones. Furthermore, they found that the differences in extinction rates, between large and small mammals, are greater than in speciation rates. A simple explanation for this observation is that most small mammals have a higher reproductive output than large ones and therefore may have faced a lower risk of extinction under ecological changes (JC hypothesis).

If a high potential reproductive output enables gigantism, then, as noted by Farlow et al. (1995), this raises the question why there were no multi-ton ground birds in the Tertiary. Since the evolution of life-history traits is always subject to constraints, other factors may have prevented birds and other taxa with high reproductive output from becoming multi-ton animals. These may be any ecological, morphological or physiological factors in general, or, in the case of the Tertiary birds, competition from mammals, or their habit of flight or, we think the most reasonable, because they incubate their eggs by body heat. Flightless birds evolved from birds able to fly, which definitely influenced their bauplan. In contrast, large mammals evolved from terrestrial animals. Furthermore, as Deeming and Birchard (2009) noted body size has been limited in contact incubating birds because of the strength of the eggshell. They stated that reproductive characteristics limit mass in flightless birds and that if fossil evidence ever arises to support proper contact incubation in a non-avian theropod then it is predicted that it will only be from a small (<250 kg) species (Deeming and Birchard 2009). This constrain seems to be crucial and that is why we only find relative gigantism in flightless birds, for example in the moa from New Zealand, the elephant birds from Madagascar or in the flightless birds in the Early Tertiary of the northern hemisphere and throughout the Tertiary of South America (Matthew and Granger 1917; Troxell 1931; Fisher 1978; Buffetaut 1997).

In addition, reptiles have a high potential reproductive output (Blueweiss et al. 1978; King 2000; Figure 5.1 in chapter 5), too. This raises the question why there were no multi-ton reptiles. Again, only relative gigantism is known from extant tortoises inhabiting several islands (genus *Dipsochelys* from the Seychelles, *Chelonoidis nigra* from Galápagos). A reason why we do not have multi-ton reptiles today could be their slow growth pattern. For example, absolute gigantism is known from the fossils of the giant crocodyliform *Sarcosuchus imperator* from the Cretaceous of Africa (Sereno et al. 2001) which had probably the body mass (8 t) of very large theropods. In this crocodyliform a maximum adult size was achieved only after 50 to 60 years by extending the duration of rapid growth (Sereno et al. 2008). Additionally, this species could have fed on large animals like dinosaurs, which were abundant in the region where it had lived (Sereno et al. 2008). Perhaps the abundance of larger prey in comparison to today's fauna also enables the larger body size of *Sarcosuchus imperator*.

4.6 Conclusion

We suggest that the reproduction strategy is an important aspect in explaining why sauropods - and dinosaurs in general - could reach such extreme body sizes in comparison to the recent terrestrial mammalian fauna. Using birds that are suggested to be close phylogenetic relatives of dinosaurs, we found that herbivorous, terrestrial birds and mammals differ in their life-history in that reproductive output decreases with body mass in mammals but not in birds. Furthermore, dinosaur clutches were larger than litters of similar sized mammals but were similar to clutches of similar sized birds (Figure 4.3). Because extinction risk (in birds and mammals) often correlates with low reproductive output, this implies a lower risk of population extinction in dinosaurs. Thus compared to mammals the largest dinosaurs like sauropods may have more easily sustained populations of very large-bodied species over evolutionary time.

5 Allgemeine Diskussion und Schlussfolgerung

Die life-history ist ein wichtiger Bestandteil zur Beschreibung und Charakterisierung eines Lebewesens. Während diese an rezenten Organismen direkt beobachtbar ist, kann sie für ausgestorbene Organismen nur indirekt hergeleitet werden. Ein wichtiger Teil jeder life-history ist die Reproduktion. Fossilfunde von Dinosauriereiern und -gelegen, sowie Studien an rezenten nahen Verwandten der Dinosaurier, wie Vögel und Reptilien, ermöglichen es diesen Aspekt der life-history bei den größten Landtieren der Erdgeschichte, den Sauropoden, zu untersuchen und einen möglichen Zusammenhang zwischen Gigantismus und Reproduktion zu erforschen.

5.1 Die life-history der Sauropoden

Als erster Ansatz wurde beruhend auf einer Literaturrecherche die life-history eines Sauropoden anhand von Erkenntnissen aus Fossilfunden und Vergleichen mit rezenten Amnioten in Kapitel 2 skizziert. Dabei wurde insbesondere auch deren Reproduktion betrachtet. So begann das Leben eines Sauropoden in einem Ei, welches eine harte kalkhaltige Schale besaß. Nach dem Schlüpfen wuchs er sehr schnell und erreichte die Geschlechtsreife im zweiten Jahrzehnt seines Lebens. Elterliche Fürsorge war sehr unwahrscheinlich oder nur sehr gering. Daher war die Mortalität in der Juvenilphase seines Lebens vermutlich hoch, was durch die hohen Raten des Körperwachstums gestützt wird. Weibliche Sauropoden aus Europa oder Indien vergruben ihre Gelege, während argentinische Sauropoden offene Nester hatten, die weder mit Sediment noch mit Pflanzenmaterial bedeckt wurden. Koloniales Nistverhalten, wie es auch bei heutigen Vögeln zu beobachten ist, ist für Sauropoden aus Argentinien wahrscheinlich, während das Vorhandensein von mehreren fossilen Gelegen auf einer lokal begrenzten Fläche bei europäischen und indischen Sauropoden eher auf ein wiederholtes Aufsuchen der Nistgründe hinweist. Aufgrund meiner Literaturrecherche vermutete ich, das die Gelegegröße der Sauropoden gering (<8 Eier in Europa und Indien, <40 Eier in Argentinien) und die Eier klein im Vergleich zur Größe eines ausgewachsenes Tieres waren. Mehrere

Gelege pro Jahr und mehrere hundert gelegte Eier pro Jahr wurden von mir in Übereinstimmung mit anderen Autoren als wahrscheinlich angenommen.

5.2 Die Reproduktion in rezenten Amnioten und ihre Konsequenzen für die life-history der Sauropoden

In einem weiteren Ansatz (Kapitel 3) habe ich die Reproduktion von verschiedenen Dinosauriern genauer betrachtet. Dazu untersuchte ich rezente Amnioten und erstellte anhand der für rezente Taxa (nestflüchtende Vögel, Krokodile, Landschildkröten) gefundenen Allometrien Modelle zu verschiedenen Merkmalen der Reproduktion (Eigewicht, Gelegegewicht, jährliches Gelegegewicht (=Gelegegewicht x Anzahl Gelege pro Jahr)) in Abhängigkeit der Körpermasse für Dinosaurier. Diese Modelle habe ich zuerst anhand von ausgestorbenen Laufvögeln den Moa und dem Elefantenvogel validiert. Daraus ergab sich, dass zwar die von mir aus Allometrien geschätzten Eigewichte, nicht aber die ebenfalls von mir aus den Allometrien geschätzten Gelege- und die jährlichen Gelegegewichte zu den aus den Fossilfunden abgeleiteten jeweiligen Gewichten passten. Ich gehe davon aus, dass diese Diskrepanz, zwischen geschätzten und beobachteten Werten eher auf einer Unterschätzung aufgrund unsicherer fossiler Datenlage und unzureichender Fossilfunde beruht als auf einer systematischen Überschätzung durch die Allometrien. Wendet man die für Reptilien und Vögel gefundenen Allometrien auf Dinosauriertaxa an, ergibt sich, dass basale Dinosaurier, wie Prosauropoden, in ihrer Reproduktion eher reptilien-ähnlich gewesen sind, während vogel-ähnliche Theropoden eine Reproduktion hatten, die sich besser durch ein Vogelmodell beschreiben lässt. Andere Dinosaurier, wie Sauropoden und Hadrosaurier, lassen sich nicht eindeutig durch eines der beiden Modelle beschreiben und/oder die wahrscheinlichsten Modelle variierten in Abhängigkeit des betrachteten Reproduktionsmerkmals. Trotzdem war eine Abschätzung zur Gelegegröße oder der Anzahl der jährlich gelegten Eier, welche meist nur ungenau oder überhaupt nicht aus Fossilien ableitbar sind, auf Grundlage der erstellten Allometrien für alle untersuchten Dinosaurier möglich. Diese Schätzungen ergaben, dass die im zweiten Kapitel vermutete hohe Reproduktionskapazität von mehreren hundert Eiern pro Jahr nur für extrem große Sauropoden (70 t) haltbar ist und auch nur dann wenn sie relativ kleine Eier gelegt haben (~2 kg) oder deren Gelegegewicht durch die obere Grenzlinie des Reptilienmodels am Besten beschrieben ist. Die Überschätzung der Gelegemasse erfolgte durch Nichtberücksichtigung des allometrischen Effekts. Das absolute Reproduktionsinvestment gemessen in Ei-, Gelege- oder jährlichem Gelegegewicht nimmt zwar mit zunehmender Körpergröße zu, aber das relative Investment nimmt ab. Trotzdem hatten, wie meine Ergebnisse zeigen, alle untersuchten Dinosaurier eine hohe Reproduktionskapazität im Vergleich zu Säugetieren. Basierend auf meinen Ergebnissen gehe ich jetzt davon aus, dass die Gelegegröße eines etwa 5 t - 10 t schweren Sauropoden aus Europa oder Indien ungefähr 3 - 9 Eier betragen haben könnte, während ein Gelege eines gleich schweren argentinischen Sauropoden etwa 25 - 40 Eier umfasste. Die Eier der Sauropoden waren, im Vergleich zur Größe eines ausgewachsenen Tieres, kleiner als bei einem rezenten, nestflüchtenden Vogel, aber größer als bei einem rezenten Reptil. Sechs bis sieben Gelege pro Jahr erscheinen mir für große Sauropoden (70 t) und moderate Sauropoden (20 t) die kleine Eier (< 2 kg) gelegt haben wahrscheinlich. Bei der Schätzung der Anzahl der Gelege pro Jahr ist aber zu bedenken, dass diese stark von der angenommenen Gelegegröße bestimmt wird und diese im Fossilbeleg oft fehlerbehaftet ist.

5.3 Gigantismus und Reproduktion

In einem anderen Ansatz (Kapitel 4) habe ich überprüft, ob die hohe Reproduktionskapazität der Dinosaurier dazu beigetragen hat, dass sie so viel größer im Vergleich zu landlebenden Säugetieren wurden (Hypothese von Janis und Carrano, 1992). Meine Untersuchungen ergaben erstens, dass große, nestflüchtende Vögel, insbesondere Laufvögel, eine höhere Reproduktionskapazität hatten als gleichgroße Säugetiere und zweitens dies auch für alle großen Dinosaurier, denen bisher Gelege zugeordnete werden konnten, zutraf. Des Weiteren haben Reptilien (Blueweiss et al. 1978; King 2000) und wie weitere eigene Untersuchungen zeigen, insbesondere alle nahen Dinosaurierverwandte aus der Gruppe der Reptilien, wie Krokodile und Landschildkröten (Abb. 5.1), eine höhere Reproduktionskapazität als gleichgroße Säugetiere. Das heißt, alle großen Vertreter der Taxa, die als nahe Verwandte der Dinosaurier betrachtet werden, sowie alle studierten Dinosaurier selbst, hatten eine höhere Reproduktionskapazität als gleichgroße Säugetiere. Dies lässt darauf schließen, dass im Allgemeinen alle großen Dinosaurier eine höhere Reproduktionskapazität hatten als gleichgroße Säugetiere. Studien belegen, dass ein erhöhtes Extinktionsrisiko in Tieren mit einem niedrigen Reproduktionspotential auftritt. Auch die heutige beobachtete rechtsschiefe Verteilung der Körpergröße in Säugetieren (Blackburn und Gaston 1998) lässt sich unter Annahme eines höheren Aussterberisikos bei großen Säugetieren modellieren (Clauset und Erwin 2008). Alle diese Beobachtungen weisen darauf hin, dass die Reproduktion der Dinosaurier ein Faktor ist, der zu ihrem Gigantismus beigetragen hat. Auf jeden Fall hat die Reproduktion der Dinosaurier, im Gegensatz zu den Säugetieren, zumindest nicht als limitierender Faktor auf die Evolution der Körpergröße gewirkt. Andererseits zeigt dies auch, dass noch andere Faktoren bei der Entstehung des Gigantismus eine Rolle gespielt haben müssen, da die meisten Dinosaurier nicht so groß wurden. Denkbar wäre z.B., dass auch die Größe der Landfläche eine Rolle gespielt haben könnte. Zum Beispiel haben Burness et al. (2001) einen positiven Zusammenhang zwischen Landfläche und Körpergröße gefunden. Das dieser Zusammenhang aber eine Rolle bei dem Gigantismus der Dinosaurier bzw. Sauropoden gespielt hat, halte ich aus mehreren Gründen für sehr unwahrscheinlich. Erstens hat ihre Studie auch gezeigt, dass Dinosaurier im Vergleich zu den meisten anderen untersuchten Taxa zu groß in Bezug zur Landfläche, auf der ihr Vorkommen vermutet wird, waren. Dies spricht nicht dafür, dass die Größe der Landfläche etwas mit dem Gigantismus der Dinosaurier zu tun hat. Wie die Autoren selbst anmerkten, lässt sich durch ihre Studie der Gigantismus bei Dinosauriern nicht erklären: „…the never-since-surpassed size of the largest dinosaurs remains unexplained.“ (Burness et al. 2001). Zweitens zeigen eigene Studien, dass ein positiver Zusammenhang zwischen Landfläche und Körpergewicht nicht für alle Taxa existieren muss (Vögel, Landschildkröten, Abb. 5.2). Drittens zeigen Studien, die sich mit der Änderung der Körpergröße von Tieren auf Inseln im Vergleich zu nahen verwandten Festlandpopulationen oder -arten beschäftigten (Heaney 1978; Marquet und Taper 1998; Cassey und Blackburn 2004; Lomolino 2005; Raia und Meiri 2006; Meiri 2008), dass diese sowohl größer (meist kleine Tierarten) als auch kleiner (meist große Tierarten) als auf dem Festland werden können, es aber anscheinend keine allgemeingültige Regel (island rule) betreffend der Körpergröße gibt (Meiri et al. 2008). Viertens erfuhren die Säugetiere erst nach der K-T Grenze (Übergang vom Kambrium zum Tertiär) eine deutliche Zunahme in ihrer Körpergröße (Alroy 1998;

Falkowski et al. 2005), obwohl sie zuvor schon existierten als es noch größere verbundene Landflächen gab (Rougier und Novacek 1998; Luo 2007).

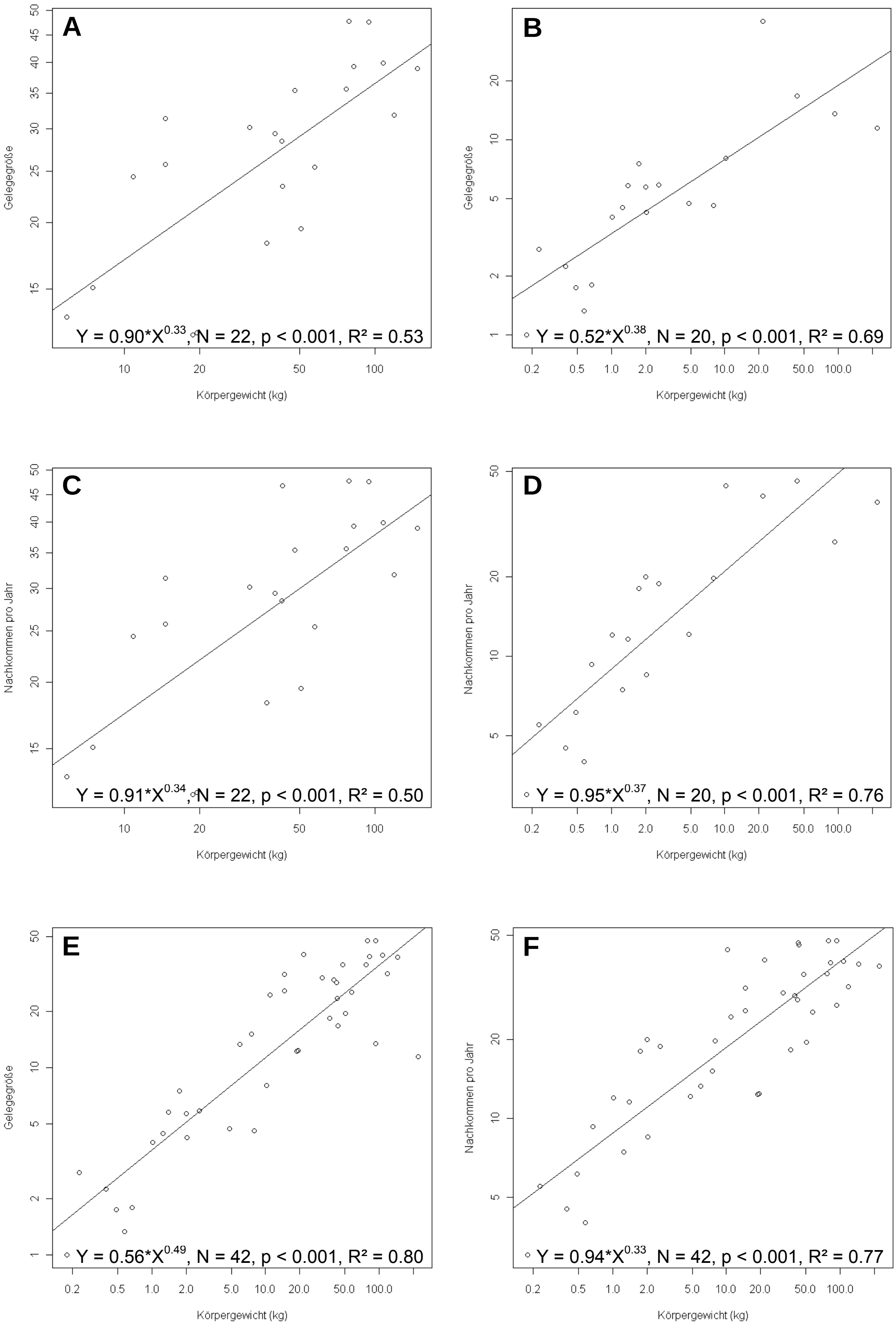
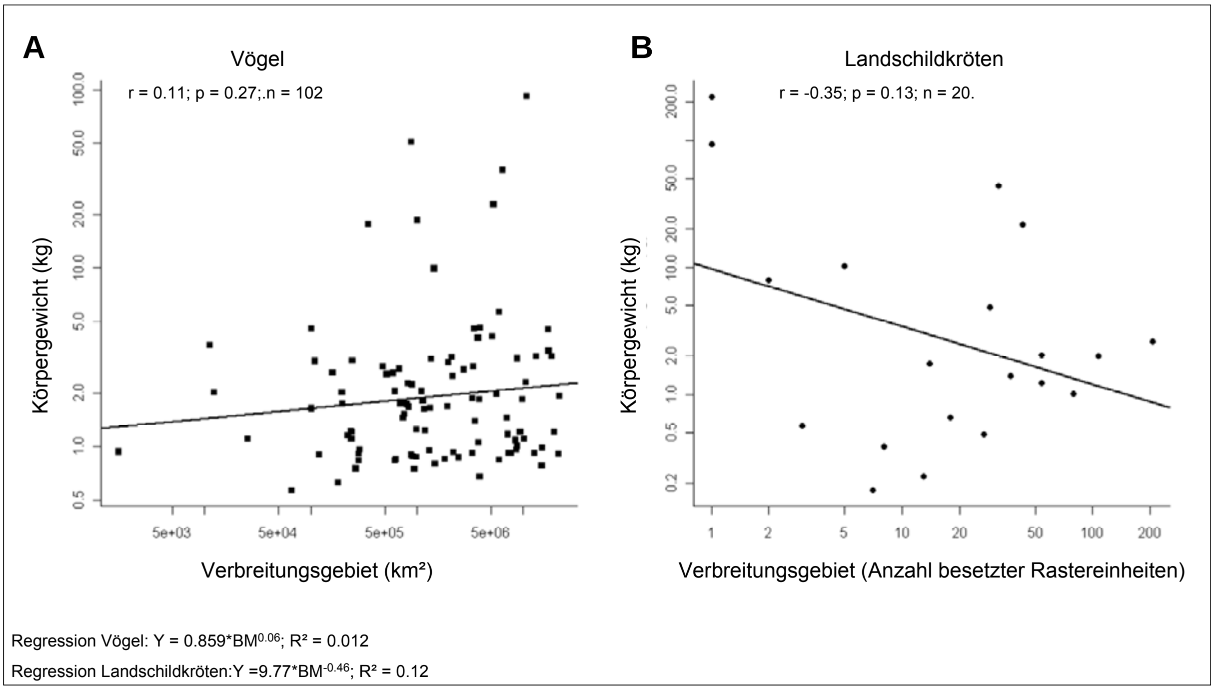


Abb. 5.1: Korrelation zwischen dem Körpergewicht und der Gelegegröße bzw. der Anzahl an Nachkommen pro Jahr bei Krokodilen (**A**, **C**) und Landschildkröten (**B**, **D**) sowie bei Krokodilen und Schildkröten zusammengefasst (**E**, **F**). Innerhalb der Abbildungen ist jeweils die zugehörige Regressionsgleichung, die Stichprobengröße (N), der p-Wert (p) und das R-Quadrat (R²) angegeben.



Regression Vögel: $Y = 0.859*BM^{0.06}$; $R^2 = 0.012$

Regression Landschildkröten: $Y = 9.77*BM^{-0.46}$; $R^2 = 0.12$

Abb. 5.2: Korrelation zwischen der Größe des Verbreitungsgebietes und dem Körpergewicht bei nestflüchtenden Vögeln (**A**) und Landschildkröten (**B**). Sowohl bei Vögeln als auch bei Landschildkröten besteht kein statistisch signifikanter Zusammenhang (Pearson-Korrelationskoeffizient, r). Die Größe des Verbreitungsgebietes in **B** ist als Anzahl der besetzten Rastereinheiten aus dem Verbreitungsatlas von Ernst et al. (2000) angegeben. Eine Rastereinheit entspricht einem Quadrat von 2° geographischer Länge mal 2° geographischer Breite.

Fünftens traten die meisten größeren Dinosaurier erst auf als der Superkontinent Pangaea nicht mehr existierte und auch Gondwana bereits auseinander brach (Sereno 1999; Mazzetta et al. 2004; Novas et al. 2005). Dies alles deutet darauf hin, dass große Landflächen nicht für den Gigantismus ausschlaggebend waren. Eher spielten, außer der Reproduktion und physiologische, bauplan- bzw. ernährungsspezifische Faktoren (siehe Sander et al. 2010), weitere Faktoren, wie interspezifische und intraspezifische Konkurrenz, Prädation oder die Verteilung von Ressourcen in Raum und Zeit eine Rolle. So sind z.B. Douglas-Hamilton und Kollegen (2007) der Meinung, dass Konkurrenz zwischen Perissodactyla und Elephantidae dazu geführt hat, das letztere so groß geworden sind. Lomolino (2005) schließt aus seinen Forschungen, dass Konkurrenz sowie Prädation wichtige Faktoren sind, die dazu führen, dass Tiere auf Inseln entweder größer oder kleiner werden als auf dem Festland. Insbesondere scheint auch die Verteilung von Ressourcen eine Rolle beim Gigantismus zu spielen, da häufig dort wo Ressourcen räumlich weit verstreut vorkommen auch große Tiere zu finden sind. So sind die

Lebenszyklen von Bartenwalen, zu denen auch das größte rezente Tier der Blauwal gehört, eng verknüpft mit deren saisonal bedingten Migrationen. Auf beiden Erdhalbkugeln paaren sich die Wale im warmen Wasser geringerer Breiten und wandern danach zu ihren jeweiligen Nahrungsgründen, wo sie 3-4 Monate verweilen und sich von dem dort vorkommenden reichhaltigen Plankton zu ernähren. Nach dieser intensiven Periode der Nahrungsaufnahme wandern sie wieder zurück in die nahrungsärmeren temperaten Zonen, wo auch ihre Kälber geboren werden (Gambell und Tyack 2007). Das größte heute existierende Landtier, der afrikanische Elefant, lebt in Gebieten in denen in Trockenzeiten sowohl Nahrung als auch Wasser nur sehr vereinzelt vorkommt und daher lange Wanderungen vollzogen werden müssen, um an diese Ressourcen zu gelangen (Douglas-Hamilton 1971; Leuthold und Sale 1973; Lindeque und Lindeque 1991; Thouless 1995, 1996; Whyte 1996; Blake et al. 2002; Douglas-Hamilton et al. 2005; Wittemyer et al. 2008). Auch in der Tiefsee, wo Nahrung knapp ist bzw. lokal begrenzt vorkommt, tritt Gigantismus auf (Timofeev 2001; Gad 2005; McClain et al. 2006).

5.4 Szenario zu der Entstehung und dem Untergang des Gigantismus in Dinosauriern insbesondere in Hinblick auf die Reproduktion

Im Folgenden wird die Entstehung und der Untergang des Gigantismus bei Dinosauriern, insbesondere in Hinblick auf die Reproduktion, diskutiert, wobei weitere Erkenntnisse aus der Forschergruppe und anderen Publikationen sowie eigene Spekulationen einfließen.

5.4.1 Entstehung des Gigantismus

Konkurrenz (Fiorillo 1998), Prädation (Buffetaut und Suteethorn 1989; Farlow und Holtz 2002; Hu et al. 2005; Cooper et al. 2008; Wilson et al. 2010) und eine weite räumliche und/oder zeitliche Verteilung von Ressourcen, wie Nahrung, Wasser (Engelmann et al. 2004; Rees et al. 2004) und Nistgründe führen dazu, dass ein starker Selektionsdruck in Richtung größere Körpergrößen bei bestimmten herbivoren Dinosauriern, wie z.B. den Prosauropoden/Sauropoden existiert haben könnte. Die Größenzunahme ihrer Beute und/oder starke Konkurrenz und die weite Verteilung von Ressourcen führen wiederum dazu, dass auch in einigen carnivoren/negrophagen Dinosauriern ein Selektionsdruck in Richtung große Körper entsteht. Der Bauplan unterliegt daher in beiden Gruppen einem Selektionsdruck hinsichtlich der Vergrößerung der Körpergröße. Schon vorhandene Eigenschaften, wie schnelles Wachstum, die senkrechte Beinstellung oder der lange Hals der Sauropoden ermöglichen bzw. begünstigen die Größenzunahme und auch eine extreme Leichtbauweise zusammen mit einer Vogellunge bedeuten möglicherweise einen Selektionsvorteil (für eine ausführliche Diskussion der Evolution des Gigantismus bei Sauropoden siehe Sander et al. 2010).

Im Gegensatz zu den Säugetieren ist die Reproduktion bei großen Dinosauriern kein limitierender Faktor, sondern begünstigt sogar den Gigantismus, denn physiologische Einschränkungen (z.B. harte Eischale) in der Reproduktion ermöglichen größeren Tieren im Vergleich zu kleineren Artgenossen nur absolut mehr Eier, aber nicht nennenswert größere zu legen, so dass große Dinosaurier eine höhere Reproduktionskapazität hatten als kleinere (siehe Kapitel 3, Sander et al. 2008).

Auch die Entstehung eines erhöhten Metabolismus (wenn er nicht schon vorhanden war) ist vorteilhaft, da dieser ein schnelles Körperwachstum ermöglicht bzw. schnelles Wachstum kann nur durch erhöhten Stoffwechsel erfolgen (Hendriks 2007; Montes et al. 2007; Sander et al. 2010). Das schnelle Wachstum hat mehrere Vorteile. Schnell wachsende und dadurch größere Individuen sind konkurrenzstärker als langsam wachsende kleinere Artgenossen. Erstere sind wahrscheinlich eine kürzere Zeitspanne einem hohem Prädationsdruck ausgesetzt als Letztere (Cooper et al. 2008), sie können vermutlich eher weitere Strecken zurücklegen und auch die benötigte Zeit bis zum Erreichen der Geschlechtsreife oder der Körpergröße ab welcher Gigantothermie wirken könnte (und somit eine konstante Körpertemperatur ohne viel Energieaufwand aufrechtgehalten werden könnte) ist verringert. Das schnelle Wachstum hat aber auch einen bedeutenden Nachteil, es wird in einem kürzeren Zeitraum mehr Energie für das Wachstum benötigt als im Vergleich zu langsam wachsenden Artgenossen. Solange aber genügend Ressourcen vorhanden sind, zum Beispiel dadurch, dass die Abundanz der größeren Tiere um einiges niedriger ist als die der kleineren, besteht dieser Nachteil nicht. Die niedrige Abundanz könnte sogar vorteilhaft sein, da bei gleicher Biomasse die Population von größeren Tieren aufgrund des allometrischen Zusammenhangs von Körpermasse und metabolischer Rate weniger Ressourcen benötigt als eine Population von kleinen Tieren. Ebenso würde zwar auch, aufgrund des allometrischen Zusammenhangs zwischen Körpermasse und Reproduktionskapazität, bei gleicher Biomasse eine Population von großen Tieren weniger in die Reproduktion investieren als eine Population von kleinen Tieren. Wenn aber die Mortalitäten innerhalb der Populationen ähnlich sind oder in der Population der großen Tiere diese hauptsächlich dichteabhängig sind und die Reproduktionskapazität eines einzelnen großen Tieres hoch ist (siehe dazu Kapitel 4), sollte dies nicht nachteilig sein, vor allem da ja auch die Anzahl der möglichen Individuen in der Population der großen Tiere niedriger ist (bei gleicher Umweltkapazität).

Dinosaurier, die schnell wachsen produzieren Wärme, da bei Energieumsetzung immer Energie in Form von Wärme frei wird (Peterson et al. 1999). Anfangs sind die Dinosaurier nicht isoliert, da es vermutlich nur um das schnelle Wachstum ging und nicht um die Absorption und Ausnutzung der Wärme. Eine Isolierung in Form von Haaren oder Federn muss nicht unbedingt notwendig gewesen sein, um hohe Stoffwechselraten und somit auch Wachstumsraten aufrecht zu erhalten (z.B. bei Sauropoden, Sander et al. 2010). Ein Grund dafür könnte sein, dass es im Allgemeinem während dem Mesozoikum warm war (Engelmann et al. 2004; Rees et al. 2004). Es ist auch anzunehmen, dass geeignete Nistgründe wahrscheinlich eher in warmen Regionen zu finden waren, so dass juvenile Dinosaurier auch erstmal dort aufwuchsen. Schnell wachsende juvenile Dinosaurier könnten also tachymetabolisch (schneller Stoffwechsel, erhöhter Grundumsatz) und damit zwischen ektotherm (da sie eine hohe Umgebungstemperatur brauchen, um ihren hohen Stoffwechsel aufrecht zu erhalten) und endotherm (schneller Stoffwechsel produziert Wärme, erhöht also die Körpertemperatur, aber der Stoffwechsel wird noch nicht wirklich zur Körpertemperaturregulation verwendet) also heterotherm gewesen sein. Diesen Zustand kann man vielleicht mit Vogelembryonen bzw. wenige Tage/Wochen alten nesthockenden Küken vergleichen. So sind z.B. Vogelembryonen und Nestlinge noch nicht in der Lage ihre Körpertemperatur effektiv zu regulieren (Deeming und Ferguson 1991a) und auch wenige Tage alte nestflüchtende Küken sind nicht in der Lage ihre Körpertemperatur in dem Maß zu regulieren, wie es adulte Vögel können (Visser und Ricklefs 1995; Brown und Downs 2002). Trotzdem besitzen sie im Vergleich zu rezenten Reptilien eine hohe

Stoffwechsel- bzw. Wachstumsrate (Deeming und Ferguson 1991b; Nagy 2000), da die Schwankung in der Umgebungstemperatur von den Eltern durch Bebrüten kontrolliert wird oder sie in einer geeigneten klimatischen Umgebung (z.B. Temperaturhühner) heranwachsen. Anzumerken ist auch noch, dass in Reptilien die Temperatur bei der das Ei bebrütet wurde ausschlaggebend für die potentielle adulte Wachstumsrate ist und nicht die Größe des Schlüpflings oder die endgültige Körpergröße (Deeming und Ferguson 1991a). Damit wäre die kleinere Eigröße bei Dinosauriern im Verhältnis zur Körpergröße im Vergleich zu heutigen Vögeln nicht unbedingt nachteilig, wenn es um schnelles Wachstum geht.

Bei großen Dinosauriern wäre eine Isolierung wahrscheinlich sogar hinderlich, da sie eher das Problem haben, die Hitze, die ihr Stoffwechsel produziert, wieder abzugeben, wie bei den heutigen Elefanten und Nashörnern beobachtet werden kann. Außerdem bietet vermutlich allein ihre Größe genügend Schutz gegen klimatische Schwankungen (Gigantothermie, Paladino et al. 1990; Sander et al. 2010). Aufgrund ihrer Größe ist aber eine Änderung der Reproduktionsstrategie bei Sauropoden und anderen größeren Dinosauriern nicht möglich. Auch wenn sie möglicherweise in der Lage gewesen sein sollten, ihre Körpertemperatur durch ihren Stoffwechsel mehr oder weniger effizient zu regulieren, ist ein Bebrüten der Eier auf Grund ihres hohen Gewichts unmöglich (ab >250 kg, Deeming und Birchard 2009) und auch elterliche Fürsorge ist bei vielen Nachkommen und dem riesigen Größenunterschied zwischen dem adulten Tier und seinen Nachkommen wahrscheinlich nicht wirklich effektiv (Sander et al. 2010). Dies alles führt dazu, dass sich die Reproduktionsstrategie bei den größeren Dinosauriern, wie den Sauropoden, über einen langen Zeitraum kaum ändert bzw. ändern kann.

Die Entstehung von Federn bzw. Daunen als Isolation bei einigen kleinen bis mittelgroßen fleischfressenden Dinosauriern, den Theropoden, (Prum und Brush 2002; Grellet-Tinner 2006) deutet daraufhin das diese in einem gewissen Rahmen die von ihrem Stoffwechsel produzierte Wärme absorbieren konnten und eventuell in der Lage waren ihre Körpertemperatur durch ihren Stoffwechsel zu erhöhen und auch zu regulieren (Endothermie). In klimatisch kälteren bzw. unbeständigen Gebieten oder in Gebieten mit kurzer Brutsaison könnten in diesen Theropoden auch erste Ansätze des Bebrütens ihrer Gelege (Norell et al. 1995; Varricchio et al. 1997, 1999) entstanden sein. (Anmerkung: es gibt viele verschiedene Hypothesen zur Entstehung des Bebrütens und hoher Körpertemperatur bzw. Endothermie, diese alle ausführlich zu diskutieren würde den Rahmen der Doktorarbeit sprengen, wichtig für die weitere Diskussion ist das es in der Kreidezeit sehr wahrscheinlich endotherme, brütende Dinosaurier bzw. Vögel gab).

5.4.2 Der Untergang des Gigantismus

Die Nahrungsverfügbarkeit und das Klima ändern sich global (Schulte et al. 2010). Es wird kälter (Pope et al. 1997; Pierazzo et al. 2003) und/oder das Klima ist nicht mehr über einen längeren Zeitraum z.B. über die Brutzeit beständig. Dadurch kommt es auch zu extremeren saisonalen Schwankungen in der Nahrungsverfügbarkeit. Brutgebiete für die meisten Dinosaurier gibt es daher nur noch wenige und die Nahrung ist ebenfalls knapp, bzw. Brutgebiete und Gebiete, die genügend Nahrung und/oder geeignetes Klima über längere Zeit bieten, sind möglicherweise nicht miteinander verbunden, d.h. auch bei eventuell erfolgreichem Schlüpfen verhungern oder erfrieren die juvenilen Dinosaurier. Auch wenn es großen adulten Dinosauriern gelingt zwischen den Gebieten hin und her zu wandern, die für die Eiablage geeignet sind und die mehr Nahrung bieten (können kälter und/oder stärkeren klimatischen Schwankungen ausgesetzt sein), ist es für ihre Jungen unmöglich diese weiten Strecken zu überbrücken oder in ihrer Brutregion erfolgreich aufzuwachsen. Die Populationen der meisten großen Dinosaurier sterben daher aus.

Kleine endotherme Dinosaurier aus der Gruppe der Theropoden, den Vorfahren der heutigen Vögel, die ihre Eier bebrüten und Säugetiere deren Nachkommen in der Gebärmutter heranreifen, können auch in Gebieten überleben, die eventuell sogar für große Dinosaurier genügend Nahrung, aber keine klimatisch geeigneten Brutgebiete für Dinosaurier und Reptilien bieten.

Auch Reptilien überleben, da sie, im Gegensatz zu den großen Dinosauriern, aufgrund ihres niedrigeren Grundstoffwechsels und ihrer Fähigkeit bei Kälte in Winterstarre (Bauwens 1981; Storey und Storey 1992) und bei wärmeren Temperaturen aber andauernder Nahrungsknappheit in eine sogenannte Sommerruhe (Grigg et al. 1986) zu fallen, unbeständige klimatische Bedingungen und Nahrungsknappheit (McCue 2007) überstehen und somit auch in Gebieten überleben, die zwar geeignete Eiablageplätze, aber nur wenig Nahrung und/oder zeitweise ungünstige Klimabedingungen bieten (Tsuji 1988). Da der Stoffwechsel in juvenilen Reptilien im Vergleich zu adulten Tieren nicht erhöht ist (Nagy 2000), können sie im Gegensatz zu juvenilen Dinosauriern, die einen hohen Metabolismus haben, auch mit wenig Nahrung auskommen und somit in den zwar klimatisch geeigneten aber wenig Nahrung bietenden Brutgebieten überleben, so dass ein Fortbestehen der Population gesichert ist.

5.5 Generelle Schlussfolgerung

Meine Arbeit zeigt, dass sich durch eine Zusammenarbeit von Biologen und Paläontologen, bisher nur sehr unsichere oder gar nicht erfassbare life-history Merkmale ausgestorbener Lebewesen, wie z.B. die Gelegegröße oder die jährliche Anzahl an gelegten Eiern, rekonstruieren lassen. Weiterhin belegt sie, dass der allometrische Effekt bei Vergleichen von life-history Merkmalen, gerade wenn Organismen unterschiedlichster Größe betrachtet werden, stets berücksichtigt werden muss, um Fehleinschätzungen zu vermeiden. Da Körpergröße häufig recht gut mit anderen Merkmalen korreliert, kann diese als „black box“ Prädiktor verwendet werden, um anhand von allometrischen Vergleichen Aussagen über aus Fossilien nicht ableitbare Merkmalen zu treffen, ohne dabei notwendigerweise die Kausalitäten hinter ihnen zu verstehen. Auch bestärken meine Untersuchungen der Reproduktion von Dinosauriern, insbesondere bei Sauropoden, die Hypothese, dass Dinosaurier im Vergleich zu Säugetieren aufgrund ihrer hohen Reproduktionskapazität so viel größer werden konnten. Vermutlich spielten aber auch weitere Faktoren wie der Bauplan (Leichtbauweise, Beinstellung, Hals etc.), schnelles Wachstum, Ernährung (Verdauung), Konkurrenz, Prädation und die Verteilung von Ressourcen bei der Entstehung des Gigantismus eine wichtige Rolle. Welche dieser Faktoren am meisten zur Evolution des Gigantismus bei Dinosauriern beigetragen haben bzw. den stärksten Selektionsdruck in Richtung Gigantismus verursacht haben, wird wahrscheinlich auf Grund der Tatsache, dass die Dinosaurier ausgestorben sind, nie ganz gelöst werden.

6 Zusammenfassung

Es wurde ein Teil der life-history, die Reproduktion, von Dinosauriern, speziell der Sauropoden, den größten bekannten jemals auf der Erde existierenden Landtieren, untersucht, um unter anderem den Zusammenhang zwischen Gigantismus und Reproduktion zu erforschen. Hierzu wurde eine mögliche life-history für Sauropoden, auf Grundlage des heutigen Forschungsstands in der Biologie und der Paläontologie, anhand einer Literaturrecherche erstellt. Des Weiteren wurde ein Modell zur Reproduktion bei ausgestorbenen oviparen Amnioten, basierend auf bestehenden Zusammenhängen zwischen Körpergröße und verschiedenen masse-spezifischen Reproduktionsmerkmalen (Eigewicht, Gelegegewicht, jähr. Gelegegewicht) bei rezenten oviparen Amnioten, erarbeitet. Mit Hilfe dieses Modells und Informationen aus Fossilfunden wurde der Frage nachgegangen, wie diese Reproduktionsmerkmale bei Dinosauriern wahrscheinlich ausgesehen haben. Weiterhin erfolgte die Überprüfung der Hypothese, dass Dinosaurier, insbesondere Sauropoden, eine höhere Reproduktionskapazität hatten als gleich große landlebende Säugetiere, was ersteren im Vergleich zu letzteren ermöglicht haben soll so viel größer zu werden (Janis und Carrano 1992).

Die Untersuchungen der Zusammenhänge zwischen Körpergewicht und den masse-spezifischen Reproduktionsmerkmalen ergaben, dass das Körpergewicht immer stark mit den untersuchten Reproduktionsmerkmalen korreliert war. Große Vögel und große Reptilien unterscheiden sich in ihrem relativen Eigewicht (Eigewicht/Körpergewicht). Vögel haben relativ größere Eier. Betrachtet man das relative Gelegegewicht oder das relative jährliche Gelegegewicht so wird der Unterschied kleiner bzw. ist zwischen manchen Reptilien- und Vogelgruppen nicht mehr vorhanden. Dinosaurier hatten relative Eigewichte, die zwischen denen von Reptilien und Vögel liegen. Basale Dinosaurier, wie Prosauropoden, waren in ihrer Reproduktion eher reptilien-ähnlich, während vogel-ähnliche Theropoden eine Reproduktion hatten, die sich besser durch ein Vogelmodel beschreiben lässt. Die Reproduktion anderer Dinosaurier, wie Sauropoden und Hadrosaurier, lässt sich nicht eindeutig durch eines der beiden Modelle beschreiben und/oder die Modelle variierten in Abhängigkeit des betrachteten Merkmals. Trotzdem war es möglich für alle untersuchten Dinosaurier eine Abschätzung zur Gelegegröße und der Anzahl der jährlich gelegten Eier zu machen. Diese Schätzungen ergaben, dass die vermutete hohe Reproduktionskapazität von mehreren hundert Eiern pro Jahr nur für extrem große Sauropoden (70 t) haltbar ist.

Mit Ausnahme der Nagetiere fand ich die Unterschiede in der Reproduktionskapazität von Vögeln und Säugetieren, die Janis und Carrano (1992) postulierten, sogar auf der Ebene von Ordnungen. Dinosauriergelege waren größer als die Würfe von gleichgroßen (extrapolierten) Säugetieren während die Gelegegröße von gleichgroßen (extrapolierten) Vögeln ähnlich der von Sauropoden war. Da das Aussterberisiko häufig mit niedriger Reproduktionskapazität korreliert ist, impliziert dies ein geringeres Aussterberisiko großer Dinosaurier im Vergleich zu großen Säugetieren. Populationen sehr großer Dinosaurier, wie der Sauropoden, konnten vermutlich daher, über evolutionäre Zeiträume betrachtet, sehr viel länger existieren als Populationen großer Säugetiere.

7 Literatur

Bemerkung:
Aus den Referenzen mit hochgestellter Zahl vor dem ersten Autor wurden die Daten (Körpergewicht, Eigewicht, etc.) für die Analysen in Kapitel 3 gesammelt (siehe auch Table 1, Appendix A, im Anhang). Aus den Referenzen mit hochgestelltem „#“ wurden die Phylogenien entnommen aus denen die zusammengesetzte Phylogenie in „Figure 1“ (Anhang, Appendix B) erzeugt wurde.

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8 Anhang

Appendix A (Chapter 3)

Table 1. Body mass (BM), egg mass (EM), clutch mass (CM) and annual clutch mass (ACM) for the 154 extant and 16 extinct amniotic taxa used in this study. A = Anseriformes, C = crocodiles, D = dinosaurs, E = extinct flightless birds, G = Galliformes, T = Tortoises, S = Struthioniformes. For references, see corresponding numbered references in chapter 7 “Literatur”.

Species	group	BM (kg)	EM (kg)	CM (kg)	ACM (kg)	References
Tachyeres leucocephalus	A	3.194	0.132	0.609	0.609	21, 31, 47
Anhima cornuta	A	3.100	0.150	0.660	0.660	21, 31, 41,
Anseranas semipalmata	A	2.035	0.108	0.904	0.904	31, 47
Dendrocygna eytoni	A	0.924	0.035	0.380	0.380	31, 47
Dendrocygna arborea	A	1.150	0.049	0.455	0.455	31, 47
Dendrocygna autumnalis	A	0.777	0.044	0.605	0.605	21, 31, 47
Anser cygnoides	A	3.167	0.142	0.838	0.838	31, 47
Anser anser	A	3.200	0.165	1.020	1.020	21, 31, 47
Anser fabalis	A	3.201	0.146	0.759	0.759	21, 31, 47
Anser brachyrhynchus	A	2.788	0.123	0.504	0.504	21, 31, 47
Anser albifrons	A	2.289	0.128	0.663	0.663	21, 31, 47
Anser erythropus	A	1.860	0.103	0.515	0.515	21, 31, 47
Anser indicus	A	2.467	0.142	0.710	0.710	31, 47
Chen canagicus	A	2.718	0.120	0.564	0.564	21, 31, 47
Chen caerulescens	A	2.785	0.126	0.630	0.630	21, 31, 47
Chen rossii	A	1.447	0.092	0.381	0.381	21, 31, 47
Branta bernical	A	1.456	0.084	0.385	0.385	21, 31, 47
Branta ruficollis	A	1.242	0.078	0.429	0.429	21, 31, 47
Branta leucopsis	A	1.726	0.104	0.510	0.510	21, 31, 47
Branta canadensis	A	3.430	0.133	0.763	0.763	21, 31, 47
Branta sandvicensis	A	1.999	0.144	0.586	0.586	21, 31, 47
Coscoroba coscoroba	A	4.050	0.178	1.056	1.056	21, 31, 47
Cygnus olor	A	10.230	0.353	2.436	2.436	21, 31, 47
Cygnus buccinator	A	9.935	0.367	2.104	2.104	21, 31, 47
Cygnus columbianus	A	6.177	0.266	1.124	1.124	21, 31, 47
Cygnus cygnus	A	9.413	0.334	1.617	1.617	21, 31, 47
Cygnus atratus	A	5.662	0.267	1.789	1.789	21, 31, 47
Cygnus melanacorypha	A	4.550	0.247	1.367	1.367	21, 31, 47
Stictonetta naevosa	A	0.855	0.077	0.566	0.566	31, 47
Tadorna ferruginea	A	1.201	0.083	0.726	0.726	21, 31, 47
Cyanochen cyanopterus	A	1.520	0.097	0.669	0.669	21, 31, 47
Alopochen aegyptiacus	A	1.914	0.096	0.813	0.813	21, 31, 47
Chloephaga melanoptera	A	3.090	0.114	0.836	0.836	31, 47
Chloephaga picta	A	2.943	0.128	0.815	0.815	21, 31, 47
Chloephaga hybrida	A	2.183	0.142	0.724	0.724	21, 31, 47
Chloephaga rubidiceps	A	2.000	0.103	0.618	0.618	31, 47
Chloephaga poliocephala	A	2.222	0.097	0.485	0.485	31, 47
Hymenolaimus malacorhynchos	A	0.844	0.073	0.399	0.399	21, 31, 47
Tachyeres patachonicus	A	2.576	0.117	0.793	0.793	21, 31, 47
Tachyeres pteneres	A	4.566	0.147	0.957	0.957	21, 31, 47
Tachyeres brachypterus	A	3.680	0.145	1.018	1.018	21, 31, 47

Table 1 continued

Species	group	BM (kg)	EM (kg)	CM (kg)	ACM (kg)	References
Plectropterus gambensis	A	4.480	0.139	1.360	1.360	21, 31, 47
Cairina scutulata	A	2.568	0.089	0.860	0.860	21, 31, 47
Lophonetta specularioides	A	0.933	0.057	0.370	0.370	21, 31, 47
Anas sparsa	A	0.962	0.068	0.404	0.404	21, 31, 47
Anas poecilorhyncha	A	1.095	0.056	0.473	0.473	21, 31, 47
Anas undulata	A	0.917	0.052	0.416	0.416	21, 31, 47
Anas platyrhynchos	A	1.114	0.050	0.536	0.536	21, 31, 47
Anas rubripes	A	1.170	0.062	0.572	0.572	21, 31, 47
Netta rufina	A	1.104	0.057	0.544	0.544	21, 31, 47
Netta peposaca	A	1.051	0.058	0.554	0.554	21, 31, 47
Netta erythrophthalma	A	0.794	0.060	0.583	0.583	21, 31, 47
Aythya valisinera	A	1.199	0.071	0.639	0.639	16, 21, 31, 47
Aythya americana	A	1.002	0.063	0.579	0.579	21, 31, 47
Aythya ferina	A	0.913	0.068	0.596	0.596	21, 31, 47
Aythya australis	A	0.841	0.056	0.625	0.625	21, 31, 47
Oxyura australis	A	0.870	0.084	0.464	0.464	21, 31, 47
Tadorna cana	A	1.358	0.097	0.862	0.862	21, 31, 47
Tadorna variegata	A	1.415	0.088	0.835	0.835	21, 31, 47
Tadorna tadornoides	A	1.359	0.090	0.943	0.943	21, 31, 47
Tadorna radjah	A	0.852	0.058	0.520	0.520	21, 31, 47
Tadorna tadorna	A	1.064	0.081	0.678	0.678	21, 31, 47
Neochen jubata	A	1.250	0.065	0.537	0.537	31, 47
Sarkidiornis melanotos	A	2.043	0.064	0.761	0.761	21, 31, 47
Cairina moschata	A	2.106	0.079	0.834	1.668	3, 21, 31, 47
Anas superciliosa	A	1.022	0.054	0.488	0.488	21, 31, 47
Aix sponsa	A	0.453	0.024	0.284	0.569	18
Anas acuta	A	0.721	0.026	0.195	0.195	18
Anas americana	A	0.794	0.024	0.216	0.216	18
Anas clypeata	A	0.613	0.023	0.253	0.253	18
Anas crecca	A	0.344	0.015	0.150	0.150	18
Anas cyanoptera	A	0.411	0.018	0.182	0.273	18
Anas discors	A	0.420	0.018	0.183	0.183	18
Anas fulvigula	A	0.950	0.033	0.329	0.329	18
Anas laysanensis	A	0.500	0.026	0.099	0.099	18
Anas strepera	A	0.791	0.036	0.356	0.356	18
Aythya affinis	A	0.787	0.031	0.308	0.308	18
Aythya collaris	A	0.737	0.029	0.264	0.264	18
Aythya marila	A	0.929	0.046	0.417	0.417	18
Aythya valisineria	A	1.209	0.045	0.402	0.402	18
Branta bernicla	A	1.163	0.044	0.174	0.174	18
Bucephala albeola	A	0.400	0.024	0.190	0.190	18
Bucephala clangula	A	0.896	0.038	0.381	0.381	18
Chen canagica	A	2.148	0.082	0.401	0.401	18
Clangula hyemalis	A	0.872	0.025	0.175	0.175	18
Dendrocygna bicolor	A	0.737	0.027	0.351	0.351	18
Histrionicus histrionicus	A	0.561	0.033	0.197	0.197	18
Lophodytes cucullatus	A	0.634	0.031	0.341	0.341	18
Melanitta fusca	A	1.361	0.055	0.600	0.600	18
Melanitta nigra	A	1.052	0.043	0.389	0.389	18
Mergus merganser	A	1.445	0.046	0.462	0.462	18
Oxyura jamaicensis	A	0.542	0.043	0.344	0.344	18
Somateria mollissima	A	2.130	0.076	0.306	0.306	18

Table 1 continued

Species	group	BM (kg)	EM (kg)	CM (kg)	ACM (kg)	References
Phasianus colchicus	G	0.984	0.031	0.374	0.374	21, 31, 32
Meleagris gallopavo	G	4.111	0.091	1.043	1.043	2, 21, 31
Callipepla californica	G	0.138	0.006	0.084	0.084	18
Bonasa umbellus	G	0.532	0.012	0.132	0.132	18
Centrocercus urophasianus	G	1.930	0.031	0.214	0.214	18
Dendragapus obscurus	G	1.059	0.023	0.181	0.181	18
Francolinus francolinus	G	0.453	0.013	0.088	0.175	18
Lagopus lagopus	G	0.596	0.015	0.088	0.088	18
Lagopus leucura	G	0.326	0.013	0.077	0.077	18
Tympanuchus cupido	G	0.908	0.012	0.150	0.150	18
Tympanuchus phasianellus	G	0.908	0.013	0.154	0.154	18
Macrocephalon maleo	G	1.630	0.231	2.310	2.310	7, 24, 31
Casuarius casuarius	S	51.000	0.617	3.291	8.227	15, 21, 31
Dromaius novaehollandiae	S	35.400	0.550	8.067	12.100	21, 31
Struthio camelus	S	91.750	1.500	13.000	19.500	21, 31, 34
Rhea americana	S	22.667	0.600	14.229	14.229	16, 21, 31, 53
Pterocnemia pennata	S	18.500	0.623	12.709	12.709	4, 5, 13, 31, 42
Apteryx australis	S	2.817	0.430	0.860	0.860	21, 31
Apteryx owenii	S	1.340	0.301	0.452	0.452	21, 31
Homopus areolatus	T	0.229	0.009	0.025	0.050	8, 10, 29, 38, 46
Homopus femoralis	T	0.393	0.007	0.016	0.032	8, 11, 23 28, 29
Aldabrachelys gigantea	T	93.400	0.080	1.080	2.160	8, 22, 23, 46
Pyxis planicauda	T	0.573	0.018	0.023	0.070	8, 14, 44, 46
Astrochelys radiata	T	10.217	0.061	0.489	2.689	6, 8, 12, 23
Astrochelys yniphora	T	8.000	0.045	0.208	0.892	8, 23, 43, 46
Psammobates tentorius	T	0.487	0.013	0.023	0.080	8, 29, 36
Homopus boulengeri	T	0.177	0.011	0.011	0.033	8, 9, 23, 29
Chersina angulata	T	0.667	0.028	0.050	0.256	8, 28, 39, 46, 57
Chelonoidis carbonaria	T	2.000	0.042	0.238	0.833	8, 46, 49, 58
Chelonoidis nigra	T	221.000	0.120	1.366	4.552	8, 22, 23, 48, 51, 64
Geochelone elegants	T	4.850	0.028	0.132	0.339	8, 23, 46, 60
Geochelone sulcata	T	43.533	0.047	0.791	2.175	8, 25, 46, 54
Testudo marginata	T	1.756	0.018	0.133	0.319	8, 23, 26, 46, 63
Testudo graeca	T	2.612	0.014	0.081	0.258	8, 19, 23, 26, 46, 62, 63
Testudo horsfieldii	T	1.018	0.018	0.070	0.210	17, 23, 35, 46
Testudo hermanni	T	1.249	0.014	0.061	0.101	8, 23, 26, 40, 46, 61, 63
Indotestudo elongata	T	2.045	0.047	0.200	0.400	8, 23, 46
Manouria emys	T	21.700	0.057	2.299	2.299	1, 8, 23, 37

Table 1 continued

Species	group	BM (kg)	EM (kg)	CM (kg)	ACM (kg)	References
Gopherus agassizii	T	1.400	0.033	0.190	0.381	8, 23, 27, 56
Alligator mississipiensis	C	47.800	0.077	2.712	2.712	55
Alligator sinensis	C	14.600	0.048	1.239	1.239	55
Caiman crocodilus	C	10.900	0.063	1.535	1.535	55
Caiman latirostris	C	14.600	0.076	2.393	2.393	55
Melanosuchus niger	C	82.000	0.144	5.643	5.643	55
Paleosuchus palpebrosus	C	5.900	0.069	0.912	0.912	55
Paleosuchus trigonatus	C	7.500	0.067	1.015	1.015	55
Crocodylus acutus	C	76.700	0.113	4.016	4.016	55
Crocodylus cataphractus	C	50.500	0.146	2.847	2.847	55
Crocodylus intermedius	C	107.900	0.110	4.394	4.394	55
Crocodylus johnsoni	C	19.500	0.070	0.864	0.864	55
Crocodylus mindorensis	C	36.900	0.074	1.347	1.347	55
Crocodylus moreletii	C	31.700	0.080	2.401	2.401	55
Crocodylus niloticus	C	94.200	0.107	5.098	5.098	55
Crocodylus novaeguineae	C	39.900	0.089	2.602	2.602	55
Crocodylus palustris	C	42.700	0.100	2.328	4.657	55
Crocodylus porosus	C	78.700	0.109	5.220	5.220	55
Crocodylus rhombifer	C	57.500	0.104	2.649	2.649	55
Crocodylus siamensis	C	42.500	0.107	3.036	3.036	55
Osteolaemus tetraspis	C	18.800	0.055	0.677	0.677	55
Tomistoma schlegelii	C	119.000	0.140	4.449	4.449	55
Gavialis gangeticus	C	147.000	0.161	6.278	6.278	55
Euryapteryx curtus	E	24.000	0.637	0.956	0.956	20
Megalapteryx didinus	E	44.000	1.120	1.680	1.680	20
Anomalopteryx didiformis	E	44.000	1.378	2.067	2.067	20
Emeus crassus	E	68.000	1.928	2.892	2.892	20
Euryapteryx geranoides	E	90.000	2.503	3.755	3.755	20
Pachyornis elephantopus	E	94.000	3.146	4.719	4.719	20
Dinornis robustus	E	165.000	4.562	6.843	6.843	20
Aepyornis sp.	E	300.000	9.122	9.122	9.122	20
Troodoon formosus	D	43.700	0.357	8.211	8.211	59
Oviraptor philoceratops	D	39.000	0.269	8.070	8.070	59
Citipati osmolskae	D	79.000	0.450	9.900	9.900	59
Maiasaura peeblesorum	D	2500.000	1.023	16.368	16.368	30, 59
lambeosaurine	D	2500.000	4.737	104.214	104.214	30, 59
Massospondylus	D	137.000	0.128	0.768	0.768	45, 52
Megaloolithus patagonicus	D	5000.000	1.741	43.525	43.525	33, 50, 59
Megaloolithus siruguei	D	5000.000	5.211	46.899	46.899	33, 50, 59

Table 2. Common regression and borderline equations. The normalization constants of the borderlines were i±rs, where i is the normalization constant of the common regression model and rs is the maximal observed residual value. To calculate rs we used all available data points from an extant taxon including also those that were omitted in the regression analyses (see text). n.a. = not applicable.

	intercept	95% CI	Slope	95% CI
Egg mass vs. body mass				
Birds (N = 104)				
borderline (i-rs)	0.013	n.a.	0.94	n.a.
common regression	0.047	[0.045; 0.050]	0.94	[0.88; 1.02]
borderline (i+rs)	0.229	n.a.	0.94	n.a.
Reptiles (N =42)				
borderline (i-rs)	0.010	n.a.	0.38	n.a.
common regression	0.020	[0.016; 0.023]	0.38	[0.32; 0.45]
borderline (i+rs)	0.036	n.a.	0.38	n.a.
Clutch mass vs. body mass				
Birds (N = 104)				
borderline (i-rs)	0.125	n.a.	0.81	n.a.
common regression	0.363	[0.334; 0.392]	0.81	[0.72; 0.90]
borderline (i+rs)	1.555	n.a.	0.81	n.a.
Reptiles (N =42)				
borderline (i-rs)	0.023	n.a.	0.76	n.a.
common regression	0.076	[0.058; 0.099]	0.76	[0.66; 0.88]
borderline (i+rs)	0.312	n.a.	0.76	n.a.
Annual clutch mass vs. body mass				
Birds (N = 104)				
borderline (i-rs)	0.126	n.a.	0.8	n.a.
common regression	0.372	[0.345; 0.402]	0.8	[0.71; 0.9]
borderline (i+rs)	1.563	n.a.	0.8	n.a.
Reptiles (N =42)				
borderline (i-rs)	0.064	n.a.	0.76	n.a.
common regression	0.159	[0.120; 0.208]	0.76	[0.66; 0.88]
borderline (i+rs)	0.492	n.a.	0.76	n.a.

Table 3. Relative fits of extinct birds. Relative fits to the regression model (rF) were calculated as rF = 1 - $\text{resV}_{\text{extinct}}/\text{max\_resV}_{\text{extant}}$, where $\text{resV}_{\text{extinct}}$ is the residual value of the tested extinct species and $\text{max\_resV}_{\text{extant}}$ is the residual value of the extant species which is found on the same side of the common regression line as the extinct species and which had the maximum residual value. A relative fit of one corresponds to a perfect fit (100%) to the common regression line (residual value of the extinct species = 0) and a relative fit of zero means that the residual value of the tested extinct species equals the observed maximum residual value of the extant species. A negative relative fit indicates that the residual value of the tested extinct species is outside the observed range of residual values of the extant taxa. Its absolute value gives the degree of deviation from the maximum residual value of the extant species.

Regression	*Euryapteyx curtus*	*Megalapteryx didinus*	*Anomalopteryx didiformis*	*Emeus crassus*	*Euryapteryx geranoides*	*Pachyornis elephantopus*	*Dinornis robustus*	*Aepyornis sp.*
Egg mass vs. body mass	0.7135316	0.7093759	0.8673523	0.8114567	0.8095691	0.952656	0.8328143	0.9326132
Clutch mass vs. body mass	-0.5108742	-0.4419002	-0.2469483	-0.2627074	-0.2307689	-0.04887523	-0.1279807	-0.31304
Annual clutch mass vs. body mass	-0.4797453	-0.4062089	-0.2142276	-0.2257151	-0.1916674	-0.01214258	-0.08483206	-0.2615352

Table 4. Relative fits of dinosaurs for the bird and reptile model. Relative fits to the regression model (rF) were calculated as rF = 1 - $\text{resV}_{\text{extinct}}/\text{max\_resV}_{\text{extant}}$, where $\text{resV}_{\text{extinct}}$ is the residual value of the tested extinct species and $\text{max\_resV}_{\text{extant}}$ is the residual value of the extant species which is found on the same side of the common regression line as the extinct species and which had the maximum residual value. A relative fit of one corresponds to a perfect fit (100%) to the common regression line (residual value of the extinct species = 0) and a relative fit of zero means that the residual value of the tested extinct species equals the observed maximum residual value of the extant species. A negative relative fit indicates that the residual value of the tested extinct species is outside the observed range of residual values of the extant taxa. Its absolute value gives the degree of deviation from the maximum residual value of the extant species.

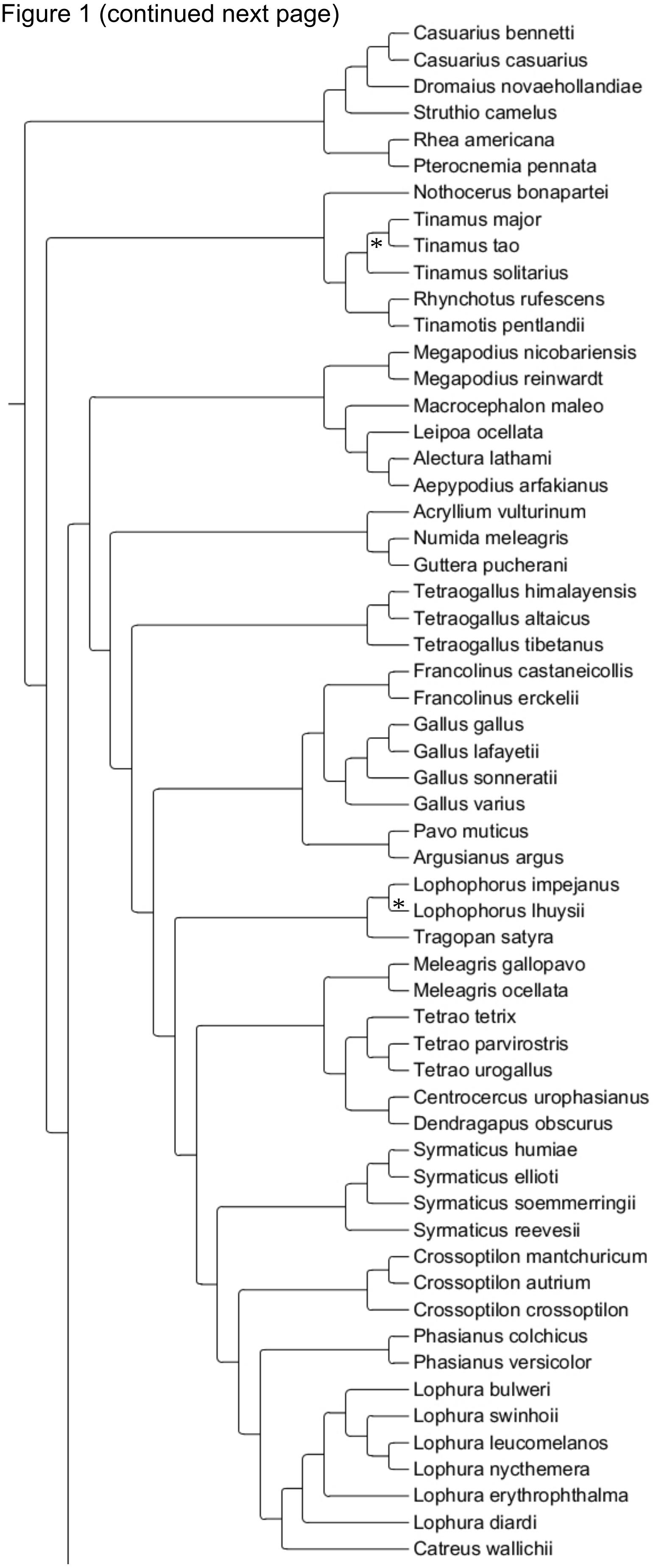
		Troodon formosus	*Oviraptor philoceratops*	*Citipati osmolskae*	*Maiasaura peeblesorum*	lambeosaurine	*Massospondylus*	*Megaloolithus patagonicus*	*Megaloolithus siruguei*
Egg mass vs. body mass									
	bird model	-0.1570118	-0.2911822	-0.4047253	-2.2535158	-1.085549	-1.757149	-2.344839	-1.509394
	reptile model	-1.4212196	-1.0268106	-1.4319339	-0.6234946	-3.144483	0.980093	-1.064845	-2.868104
Clutch mass vs. body mass									
	bird model	0.9594674	0.9080141	0.78033775	-1.378316	0.36250013	-2.0431891	-0.9865793	-0.9163672
	reptile model	-0.2828345	-0.3317521	-0.09684762	0.5280223	0.09525575	-0.1750987	0.9003028	0.9619026
Annual clutch mass vs. body mass									
	bird model	0.94868912	0.89737817	0.8028256	-1.290944	0.4233471	-1.97258	-0.8987571	-0.8296148
	reptile model	0.04960165	-0.01143916	0.2816813	-0.4448364	0.5213934	-1.385562	0.0532483	0.1356644

Appendix B (Chapter 4)

Table 1. Characteristics of dinosaurs used to test the hypothesis of Janis and Carrano (1992).

Species	Classification	Body mass (kg)	Clutch size	Reference(s)
Troodon formosus	Carnivore	43.700	23	Varricchio et al. 2008
Oviraptor philoceratops	Carnivore	39.000	30	Varricchio et al. 2008
Citipati osmolskae	Carnivore	79.000	22	Varricchio et al. 2008
Maiasaura peeblesorum	Herbivore	2500.000	16	Horner 1999; Varricchio et al. 2008
lambeosaurine	Herbivore	2500.000	22	Horner 1999; Varricchio et al. 2008
Massospondylus	Herbivore	137.000	6	Reisz et al. 2005; Seebacher 2001
Megaloolithus patagonicus	Sauropod	5000.000	25	Jackson et al. 2008; Sander et al. 2008; Varricchio et al. 2008
Megaloolithus siruguei	Sauropod	5000.000	9	Jackson et al. 2008; Sander et al. 2008; Varricchio et al. 2008

Figure 1 (continued next page)



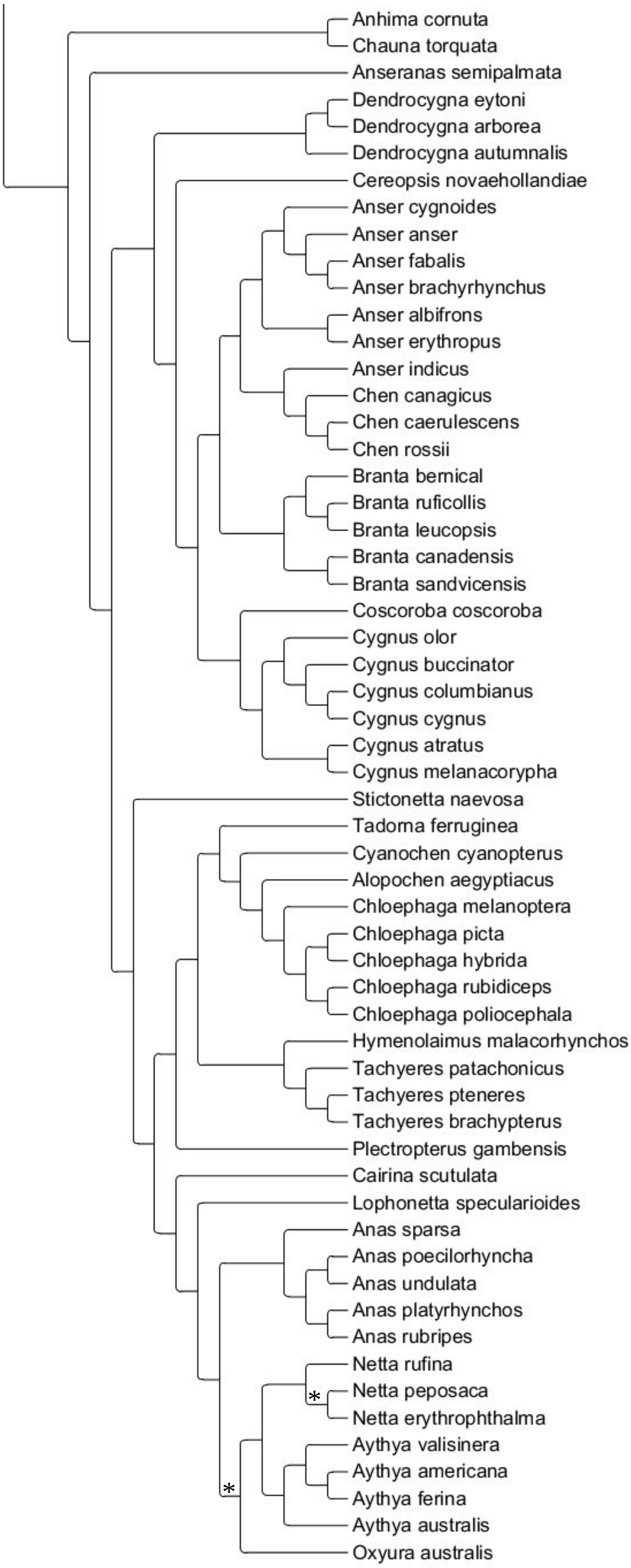


Figure 1. Phylogenetic tree used to control for phylogenetic effects in body size and reproductive parameters of birds (* indicates polytomies). For References, see “Literatur”.

9 Abbildungsverzeichnis

Anhang (Appendix B)

10 Tabellenverzeichnis

Anhang (Appendix A)

Anhang (Appendix B)

Erklärung

Hiermit erkläre ich, dass ich diese Arbeit selbständig angefertigt habe. Es wurden keine anderen als die angegebenen Hilfsmittel verwendet.

Mainz, den 2. August 2010

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Jan Werner

Lebenslauf