Investigation of the Growth Patterns of the Galagidae

by

Melissa K. Schaefer

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Leanne T. Nash, Chair
Mary W. Marzke
Gary T. Schwartz

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ABSTRACT

This study examined the ontogeny of body mass (i.e. "growth") of *Otolemur garnettii* and *Galago senegalensis*. Growth is a proximate causal mechanism for adult size variation and growth patterns themselves can be the target of selection with adult size being the end result. Therefore, growth patterns of species can be the result of adaptation to species-specific social system, ecology, and life-history. The goals of this study were to: (1) Assess whether interspecific body mass variation was due to differences in growth rate, growth duration, a combination of the two, or neither; (2) test the hypothesis that sexual size dimorphism is attained by differences in relative growth rate as predicted by sexual selection theory; and (3) test the hypothesis that frugivorous *O. garnettii* grow at a relatively lower rate than gummivorous *Go. senegalensis* as predicted by an ecological risk aversion hypothesis. Growth rates and durations of *Otolemur garnettii* and *Galago senegalensis* males and females were compared both interspecifically and intraspecifically. The hypotheses regarding the ontogeny of sexual size dimorphism and the risk aversion hypothesis were not supported. *O. garnettii* males and females grow at an absolutely higher rate and for a longer duration compared to *Go. senegalensis* males and females respectively. *O. garnettii* females grow at a relatively higher rate compared to *Go. senegalensis* females as well. This may relate to weaning habits. *O. garnettii* infants are weaned during the dry season when feeding competition would be presumably high making large mass at weaning advantageous. While the growth of females might be strongly influenced by natural selection and competition for resources following weaning, the growth of males may be more strongly influenced by sexual selection relating to contest competition for females. Sexual size dimorphism results from differences in growth duration in *O. garnettii* and from differences in both growth duration and growth rate in *Go. senegalensis*. The results of this study highlight the need for more data on the growth patterns, mating and social systems, feeding competition, and life history schedules for these and other galagids. Study of how and why growth patterns have diverged through evolution is important in discerning the evolutionary history of each species.

For Ben, Em, and Will

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Chapter 1: Studies of Growth in Body Mass in Primatology

INTRODUCTION

This study investigated the variability in the ontogeny of body mass ("growth" *sensu* Gould [1977]) within the Galagidae to assess the growth processes leading to adult mass variation and to test hypotheses linking growth and socioecological factors that have been generated from primarily haplorrhine models. These hypotheses have thus far not found support within strepsirrhines. Examination of galagids could help discern reasons for the discrepancy of results within primates. Galagid data also allow the testing of associations between growth and a gummivorous diet and between growth and a dispersed polygynous mating system. The association these socioecological factors have with growth is largely unknown to date.

Growth variability and its importance

The processes of ontogeny include growth (increase in size), development (differentiation), and maturation (biological aging) [Godfrey & Sutherland, 1995, 1996; Gould, 1977]. Growth, specifically a postnatal increase in body mass, was the focus here. Individual components of growth (rate of growth and duration of growth) are independent of each other and selection can operate on each component alone [Pereira & Leigh, 2003]. A species' growth pattern includes the entire growth process from conception to attainment of asymptotic size and includes growth parameters such as neonatal mass, growth rates (including changes in growth rates such as growth spurts), growth duration, and asymptotic (adult) mass. The growth patterns of species are likely the result of adaptation to species-specific ecology, social system and life-history [Bogin, 1999; Brizzee & Dunlap, 1986; Case, 1978; Garcia et al., 2009; Kappeler, 1996; Kirkwood & Mace, 1996; Leigh, 1992a, b; Plavcan, 1999; Taylor, 1997].

There has been a considerable amount of research published regarding adult body size variation as it relates to life history and to various socioecological factors such as predation, diet and social organization. However, until recently, less attention has focused on growth as a proximate causal mechanism for that variation. Selection can operate directly on growth thereby influencing adult size attained as a result [Pereira & Leigh, 2003] or selection can operate on adult morphology thereby influencing growth patterns as a result [Price, 1984; Price & Grant, 1985]. An understanding of the variability in growth patterns (i.e. the combinations of growth rates and growth durations) present both intraspecifically and interspecifically and of the association between specific growth patterns and socioecological conditions will lead to greater understanding of both the proximate and ultimate causes of specific growth patterns as well as the resulting adult size.

Growth patterns vary between species, between populations within a single species, and between individuals within a single population [Kirkwood, 1985; Mori, 1979; Scheuer & Black, 2000; Setchell et al., 2001]. These variations in growth pattern may yield differing, but sometimes similar adult body sizes [Case, 1978] highlighting the need to incorporate growth data into studies of adult size. For instance, adult female *Semnopithecus entellus* and *Hylobates* (*Symphalangus*) *syndactylus* are similar in mass, but *Semnopithecus* females grow faster and mature at least one year earlier compared to *Symphalangus* [Leigh, 1992a]. Clearly divergent growth patterns may result in convergent adult size. The social and ecological factors that favor accelerated growth (high growth rate) are likely different from those factors that favor prolonged growth [Badyaev, 2002; Shea, 1986]. Therefore, comparative studies of growth are needed to shed light on the ways in which specific socioecological factors influence a species' growth pattern.

The ultimate goal in studying growth is to identify causal relationships between socioecology, life history, and growth. For instance, high predation pressure on subadults may select for rapid growth [Case, 1978; Mitani & Watts, 1997], while seasonal scarcity of food (e.g. as might occur more often for frugivores than folivores) may select for slow growth [Janson, 2003; Janson & van Schaik, 1993]. Associations between a specific growth pattern and a specific socioecological condition provide an initial indication as to the potential adaptiveness of the growth pattern. Multiple cases of such association would provide stronger evidence, but demonstrating that a specific growth pattern is an adaptation requires data showing the growth pattern actually increases fitness within the specific socioecological condition and that it increases fitness more than an alternative growth pattern [Nunn & Barton, 2001; Ross et al., 2000]. The developmental basis of growth and its genetic underpinnings are also necessary to truly demonstrate an adaptive response in growth to socioecological selection pressures [Abzhanov et al., 2006; Abzhanov et al., 2004; Chiu & Hamrick, 2002;

Hamrick, 2001]. The comparative method and data from numerous and diverse species are imperative in this process.

While many species' growth patterns remain to be studied, growth research has rapidly increased since 1990. A review of PrimateLit database (http://primatelit.library.wisc.edu/ searched 10/9/2009) indicated almost twice as many studies have been published since 2000 as were published from 1980-1990. In fact, twice as many studies have been published in the last 20 years than were published in the entire 40 years prior.

Primates have low growth rates compared to other mammals [Kappeler & Heymann, 1996; Kirkwood & Mace, 1996; Mumby & Vinicius, 2008]. Within primates, strepsirrhines generally have the highest growth rate followed in order by platyrrhines, catarrhines, and hominoids [Kappeler & Heymann, 1996; Kirkwood, 1985; Mumby & Vinicius, 2008]. Most studies of primate growth have focused on large-bodied, diurnal haplorrhine primates and are concentrated within the callitrichids, cercopithecoids, and hominoids. Only recently have strepsirrhines been examined and those that have, e.g. some Malagasy lemurs [Blanco et al., 2009a; Godfrey et al., 2004; Godfrey et al., 2005; Leigh & Terranova, 1998], exhibit similarities in socioecology (for instance, large, multi-male/multi-female groupings, diurnality, large body size, etc.) with haplorrhines, but not always similar adaptations in growth. To test of the generality of these hypotheses for primates, data from additional species are needed. A wider sampling of strepsirrhines would broaden our understanding of the adaptive flexibility of growth within the Order Primates and would allow the examination of the influence of socioecological factors that are rare or absent among haplorrhines including, but not limited to, gummivorous diet, female dominance, post-partum estrus, or dispersed polygynous mating systems.

While studies of growth and its flexibility are important in and of themselves, the addition of growth data into studies of socioecology provides information that can explain paradoxes or decide between competing hypotheses. For instance, comparisons of adult size variation of *Propithecus* species could not distinguish between the hypotheses of resource quality and resource seasonality as selection factors on adult size. The resource quality hypothesis posits that larger species can survive on lower quality food, as assessed by a protein:fiber ratio, while smaller species require higher quality resources. Therefore, among closely related taxa, larger-bodied forms should be associated with poorer-quality habitats while smaller-bodied forms should be associated with higher quality habitats. The resource seasonality hypothesis suggests seasonality of resources, rather than resource quality itself, energetically constrains adult body size such that larger-bodied species should be associated with less seasonal habitats while smaller-bodied species should be associated with more seasonal habitats. Both hypotheses are supported by the pattern of adult size variation as the larger-bodied species are associated with poorer-quality less seasonal habitats. Using data from adult size alone was not sufficient to choose between the two competing hypotheses. Incorporating growth data provided support for the resource seasonality hypothesis over the resource quality hypothesis as the smaller-bodied *P. verreauxi*, which inhabits a more seasonal but higher quality habitat, grew at a slower rate than *P. diadema edwardsi*, which inhabits a steadier, but poorer quality habitat [Ravosa et al., 1993].

While the inclusion of growth data can resolve paradoxes between species, it can be used to resolve paradoxes within species as well. Varying patterns of sexual size dimorphism (SSD) are found among primates. Most often males are larger than females, but monomorphism and reverse SSD (females larger than males) are also present [Kappeler, 1990; Kappeler, 1991; Kappeler, 1997a; Plavcan & van Schaik, 1997]. Explanations for SSD range from phylogenetic inertia to diet to sexual selection and mating systems and studies of SSD are often contradictory in their findings [Leigh, 1992a, b]. These studies generally focus on adult traits as the ultimate target of selection and therefore, lack information on the proximate causes of SSD as they ignore the potentially important information on growth patterns [Badyaev, 2002]. This picture is changing as more studies are examining the ontogeny of SSD [e.g.Leigh, 1992a; Leigh, 1992b; Leigh, 1995; Leigh & Shea, 1995; Leigh & Terranova, 1998; O'Mara et al., in review; Shea, 1986]. The addition of growth data into studies of SSD may lead to better understanding of the adaptive nature of sexually differentiated growth [Badyaev, 2002; Leigh, 1992a; Shea, 1996].

For example, Leigh & Shea [1995] examine the growth patterns of African apes. Within the African apes, varying degrees of SSD are found. *Gorilla gorilla* exhibit the highest degree of SSD, followed by *Pan paniscus*; *P. troglodytes* exhibit the lowest degree of SSD within this group. Examining growth patterns of males and females, and both natural and sexual selection pressures can yield a comprehensive understanding of the pattern of SSD found within this group.

Like other folivores, both male and female *Gorilla* exhibit a high growth rate and SSD is attained primarily through differences in growth duration (i.e. bimaturism). Female *G. gorilla* cease growing earlier than expected for their body size, based on comparisons with *P. troglodytes*. This shortened female growth period is the biggest factor in the high degree of SSD for *Gorilla*. Adult females can "afford" to be small, as large size isn't needed for inter-female feeding competition as a result of the higher degree of folivory relative to the more frugivorous diet of chimpanzees. While male *Gorilla* don't need to compete for food, they do compete for females. Longer growth duration and a higher growth rate lead to increased male size, which is possible due to their folivorous diet, and necessary due to high intermale competition. Adult *Gorilla* SSD is, therefore, the result of natural selection on increased growth rate, early maturation for females and sexual selection for increased size for males [Leigh & Shea, 1995].

Similar to *Gorilla*, SSD in *P. paniscus* arises primarily through differences in growth duration. Females exhibit a high growth rate for a short duration reflecting the reliance on more folivorous foods (compared to *P. troglodytes*), also, fruits consumed occur in larger patches than foliage. Both these ecological factors lead to lower levels of feeding competition and favor high growth rates and lead to female growth patterns similar to that found in *Gorilla*. In contrast to *Gorilla*, there is little reported intermale competition, so large male size is unnecessary for this reason, and, indeed, *P. paniscus* exhibit lower levels of SSD compared to *Gorilla* [Leigh & Shea, 1995].

P. troglodytes females grow slowly to avoid starvation risk, but for a long period to better compete with other females as adults for food [Leigh & Shea, 1995]. Female dominance rank is significantly correlated with body mass [Pusey et al., 2005]. The degree of SSD is due more to rate differences than duration differences. While *P. troglodytes* live in multi-male/multi-female groups, male dominance is reportedly based more on coalitions than absolute size so it is not as beneficial for males to be large, resulting in lower levels of SSD within this species compared to other hominoids. Indeed male dominance rank is not correlated with body mass [Pusey et al., 2005]. As demonstrated by Leigh & Shea [1995], coupling growth data with detailed data on ecology, feeding competition and social relationships can yield a more complete understanding of patterns of adult SSD. This understanding of SSD within this taxon would be woefully incomplete without the inclusion of growth data.

Types of growth data

Though the majority of growth studies, including many of the studies mentioned above, have used growth data gathered from captive subjects [Lee, 1999], the question has been raised whether captive data are appropriate for testing adaptive hypotheses. Strum [1991] suggests that differences between wild and captive animals are no greater than differences between populations of a single species or differences within a single population during different years, a notion also proposed by Leigh [1994b]. Few studies have compared growth patterns between wild and captive subjects and those that have generally find that captive subjects exhibit a higher growth rate and/or longer growth duration (see, for instance, *Papio cynocephalus* [Altmann & Alberts, 1987], *Mandrillus sphinx* [Badyaev, 2002; Setchell & Dixson, 2002] *Macaca fascicularis* [Janson, 2003], *Callithrix jacchus* [Araújo et al., 2000]). Studies of adult size, the end product of growth, indicates that captive subjects may be larger than their wild counterparts, but generally not significantly so [Leigh, 1992b; Leigh, 1994b; Terranova & Coffman, 1997]. Fluctuations in adult size have also been found in captivity despite the constancy of food resources. Expectant male *Saguinus oedipus* gains approximately 3% of their body mass during the last three months of his mate's pregnancy [Rodríguez et al., 2008].

Additionally, both seasonal and age-related growth patterns are present in captive subjects despite continuously available food, indicating wild species-typical growth patterns are present even in captive subjects [Garber & Leigh, 1997; Hamada et al., 1999; Pereira, 1993]. Studies of captive *Lemur catta* demonstrated a seasonal growth pattern as growth rates decline during the fall even in the absence of seasonal food shortages [Pereira, 1993]. Seasonal fluctuations in adult mass, corresponding to fluctuations in wild adults, have been reported in other captive Malagasy primates though food supply remained unchanged [Petter-Rousseaux, 1980]. Growth of captive *Saimiri* ceases between 6-8 months, then resumes at 8 months of age in the absence of changes in food availability [Garber & Leigh, 1997]. Infant *L. catta* exhibit an accelerated growth rate during the fourth month and a reduction of growth rate during the eighth month regardless of varying levels of provisioning [Pereira, 1993]. Also, adolescent growth spurts are present in captivity [Hamada et al., 1999; Hamada & Udono, 2002; Leigh, 1995, 1996; Watts & Gavin, 1982]. The growth acceleration and deceleration of these species mirrors what is known of their wild counterparts therefore, it is reasonable to assume that captive subjects can be used for evolutionary studies and that adaptations to socioecological factors are present in captivity [Leigh, 1992b; Leigh & Shea, 1996].

Indeed, captive subjects have frequently been used for evolutionary studies of growth because collecting a large, longitudinal sample of known-age subjects is difficult, if not impossible ethically and logistically, in the wild. In captive studies, the age of individual subjects is usually known, often to the day, as is its nutritional history, health history, and pedigree. Measurements on captive subjects may be taken more frequently, as the subject's location is usually known, so individuals can be measured repeatedly and thus longitudinal data can be collected and larger sample sizes can be accumulated [Strum, 1991]. In short, captive studies can yield larger, more detailed and complete datasets.

Growth and an ecological risk aversion hypothesis

One comparative study relying on data from captive subjects sought a link between growth patterns and ecological risk as indicated by dietary category [Leigh, 1994a]. The ecological risk aversion hypothesis (RAH) suggests that juvenile primates, because they are group living, face greater starvation risk compared to other more solitary mammals as they must compete with larger, more experienced adults for food [Janson & van Schaik, 1993]. By growing more slowly, they reduce the amount of energy necessary for maintenance and growth. Folivory, on the other hand, would be associated with lower starvation risk compared to frugivory because of foliage's more reliable distribution. Using data from captive subjects, Leigh tested this hypothesis for 42 anthropoid primates. Results provided support for the RAH as folivorous species grew more rapidly than their similarly-sized frugivorous counterparts. Alternative explanations for rapid growth involving increased gut size, allocare and infanticide could not be ruled out by this study due, in part, to the common association between folivory and these factors, especially among the colobines which comprised the majority of the folivorous species included in the study [Leigh, 1994a]. Additional support for RAH has been found in studies of wild *Cercopithecus aethiops* populations inhabiting environments of varying quality and seasonality suggesting RAH may explain intraspecific as well as intraspecific growth variation [Whitten & Turner, 2009].

In a subsequent test of the RAH, Godfrey et al. [2004] compared mass growth of 22 species of (primarily captive) Malagasy lemuroids. Results of this sample were in direct contrast to those of Leigh's anthropoids. The frugivorous lemuroids grew faster than their similarly-sized folivorous counterparts. The authors suggest the differences in growth rates, coupled with differences in dental development and reproductive development are adaptations to the highly unpredictable environment found in Madagascar [Dewar & Richard, 2007; Wright, 1999]. In other words, selection pressures related to population maintenance, extreme unpredictability, growth, and development may override selection pressures related to resource availability alone. Calculation of growth rate constants indicated that lemurids exhibited a greater variability in growth than any other studied taxa [Mumby & Vinicius, 2008]. Clearly, more data from a wider sampling of both haplorrhine and strepsirrhine species are needed to fully explain the association between diet and growth [Leigh, 1994a].

These two large-scale contradictory studies demonstrate two important points. First, data from captive subjects can successfully be used to test evolutionary hypotheses as clear differences in growth were present in captive subjects who are not subjected to actual resource seasonality. Second, there is variability in both growth patterns and their adaptive explanations making studies of additional species imperative to uncovering relationships between growth and socioecology.

Utility of studies of growth in the Galagidae

In review, in some instances, growth can be limited by phylogeny [Kappeler, 1995; Kirkwood, 1985; Kirkwood & Mace, 1996]. In other instances, growth can be adapted to a species' unique social, ecological, and life history factors [e.g. Godfrey et al., 2004; Janson & van Schaik, 1993; Leigh, 1994a, 1995; Ravosa, 1998, 2007; Taylor, 1997]. Links between growth and specific socioecological conditions such as social organization and diet have been reported for many haplorrhines. Whether these associations can be generalized to all primates requires further study as examination of lemuroids sometimes finds contradictory results.

Galagidae are an important taxon for growth studies for several reasons. First, data from galagids could test competing hypotheses offered to explain differences between lemuriforms and haplorrhines in the pattern of association between growth patterns and socioecological conditions. These hypotheses include a strepsirrhine/haplorrhine dichotomy and phylogenetic constraints, possibly relating to the amount of growth variability present within each clade [Adkins et al., 2001; Kirkwood, 1985; Lee & Kappeler, 2003; Roberts, 1994; Wallis et al., 2001], and the unpredictability of Madagascar's environment leading to unique adaptations within the lemuriforms [Dewar & Richard, 2007; Jolly, 1984; Pereira, 1993; Richards & Nicoll, 1987; van Schaik & Kappeler, 1996; Wright, 1999]. In the first case, galagids would be expected to share similarities with lemuriforms while in the latter case galagids might be expected to share similarities with haplorrhines. Comparisons made in subsequent chapters of the dissertation will address this debate. Second, galagids can be used to test adaptive hypotheses for socioecological factors that are rare among many haplorrhine taxa, such as gummivory. Finally, galagids could be used to further test the generality within the Order Primates of socioecological models developed using haplorrhines, which the strepsirrhines studied to date contradict.

OBJECTIVES

The ultimate goal of this study was to investigate the diversity in growth patterns found within the Galagidae and to identify possible associations between socioecology and growth as a first step in identifying adaptive responses of growth to selection pressures. Species included in this study were *Galago* *senegalensis* and *Otolemur garnettii*. This study was designed around hypotheses generated from primarily haplorrhine studies which yielded four predictions:

1. **Prediction #1: A. Galagidae attain different adult mass through differences in growth rate; B. Galagidae attain different adult mass through differences in growth duration.** These predictions are investigated in chapter 2, which uses mixed longitudinal data for *Go. senegalensis* and *O. garnettii* to create growth curves for males and females of each species. Growth parameters including neonatal mass, age at growth cessation and adult mass were estimated. Growth rates were compared between species to assess whether interspecific mass variation results from differences in growth rates, differences in growth duration, a combination of the two, or neither. Some growth information from the literature on *Galagoides zanzibaricus*, *Go. moholi* and *O. crassicaudatus* were incorporated for comparison.
2. **Prediction #2: Sexual size dimorphism (SSD) in both species of galagids will be attained via differences in growth rate with males exhibiting a relatively higher growth rate compared to females.** This prediction is investigated in chapter 3 which compares relative growth rates of males and females within each species. Evidence suggests that both *Go. senegalensis* and *O. garnettii* form dispersed single-male/multi-female groups. Sexual selection theory suggests these males may be evicted from the group relatively early and abruptly, thus increasing the need for males to rapidly attain large size offset increased predation risk

and to successfully compete with other males for access to females and food.

3. **Prediction #3: Species consuming gum will grow more rapidly compared to those consuming fruit.** This prediction is investigated in chapter 4, which compares relative growth rates between gummivorous *Go. senegalensis* and nongummivorous *O. garnettii*. Limited data from two additional galagid species, *Go. moholi* and *O. crassicaudatus* [Rasmussen & Izard, 1988], were included in this comparison. Both species are reportedly gummivorous. This represents a novel interpretation of the ecological risk aversion hypothesis which posits a link between growth and diet such that species with more reliable food sources (i.e. gum) will grow at a higher rate compared to species with more seasonal food resources (i.e. fruit).

Chapter 2: Ontogeny of Species Size Differences in Galagids

ABSTRACT

The ontogeny of body mass of two species of Galagidae, *Otolemur garnettii* and *Galago senegalensis*, were compared to determine whether interspecific adult mass variability results from differences in growth rate, differences in growth duration, a combination of the two, or neither. Average neonatal and adult mass were estimated from mixed-longitudinal datasets of captive subjects. The duration of growth (age at growth cessation) was estimated from the first derivative of a pseudovelocity curve. Using only measurements from the growth period (those that precede the estimated age at growth cessation), ordinary least squares regression was used to estimate the growth rate (i.e. slope) of each sex of each species. These slopes were compared (*Otolemur* males with *Galago* males and *Otolemur* females with *Galago* females) using an F-statistic. Significant slope differences were found with *O. garnettii* males and females having higher slopes than *Go. senegalensis* males and females, respectively. Significant differences in the age at growth cessation were also found with *O. garnettii* growing for a longer duration than *Go. senegalensis*. Thus, interspecific differences in adult body mass are attained through differences in both the duration and the rate of growth. Body mass growth can be influenced by the specific niche a species inhabits. Therefore, it is likely that the growth patterns of these galagids have been altered by responses to differing socioecological pressures.

INTRODUCTION

In the biological world, size matters and much research has been done on the relationship between size and various metabolic and physiological variables, socioecological factors and life history [Calder III, 1984; Damuth & MacFadden, 1990; Schmidt-Nielsen, 1984]. Phyletic size differentiation among closely related taxa appears to be a common pattern in evolutionary change and niche partitioning [Brown et al., 2000; Calder III, 1984; Gould, 1975; Gould, 1977; Ravosa et al., 1993, 1995; Schluter, 2000; Shea, 2002; Weiner, 1994]. It has been stated that "… biological diversity is largely a matter of size. The variety of sizes plays a central role in the ability of organisms to make their living in so many different ways that they have literally covered the earth, exploiting nearly all of its environments." [Brown et al., 2000, p1]. Galagidae encompasses a mass range from 55 to 1130 grams [Nekaris & Bearder, 2007]. The purpose of this research was to investigate post-natal body mass growth of two species of galagids to determine whether interspecific mass differences result from differences in growth rate, differences in growth duration, a combination of the two, or neither with infants of both species being differently sized at birth and following a similar growth pattern post-natally. Taxonomy follows Groves [2001] and Grubb [2003]. To avoid generic confusion, *Galago* will be abbreviated *Go*. and *Galagoides* will be abbreviated *Gs*., after Masters & Brothers [2002].

Mass differentiation

Competitive exclusion theory holds that closely related sympatric species cannot coexist unless they differentiate themselves [Brown et al., 2000; Dayan &

Simberloff, 1998; Gause, 1937; Moll & Brown, 2008; Rastetter & Agren, 2002]. Mass differentiation may be a common theme in avoiding competition and frequently characterizes adaptive radiation and niche partitioning of clades [Calder III, 1984; Losos et al., 1997; Schluter, 2000; Shea, 2002; Weiner, 1994]. For example, Darwin's finches are a monophyletic clade that has undergone an extensive adaptive radiation since the founding population arrived in the Galápagos from Central or South America approximately 2.3 mya [Grant & Grant, 1979, 1982; Grant, 1966; Grant, 1984; Grant & Grant, 2008; Petren et al., 1999; Sato et al., 1999; Sato et al., 2001]. Small, medium, and large ground finches are found in sympatry while similar-sized species are often competitively excluded. This size differentiation allows them to consume different foods and presumably eliminates competition [Grant & Grant, 1982; Grant, 1966; Grant, 1984, 1986; Grant & Grant, 2008; Lack, 1945; Quammen, 1996; Weiner, 1994].

Similarly, mass differentiation characterizes the Galagidae with variably-sized galagids existing in sympatry in many places in Africa, especially on the east and west coasts [Bearder et al., 2003; Nash et al., 1989; Nekaris & Bearder, 2007] and similarly sized galagids existing parapatrically or only narrowly sympatrically as exemplified by *Galagoides cocos*, *Gs. zanzibaricus*, and *Gs. granti* in eastern Africa [Butynski et al., 2006; Honess, 1996]. Like Darwin's finches, extant galagids have traditionally been subdivided into three size categories: "large" galagos weighing more than 550 grams (e.g. *Otolemur*), "medium" weighing between 125 grams and 550 grams (e.g. *Galago*, *Sciurocheirus*, and *Euoticus*), and "small" galagos weighing less than 125 grams (e.g. *Galagoides*) [Nash et al., 1989] (Table I). However, recent identification of several additional galago species has blurred the line between the "small" and "medium" groups with several *Galagoides* species exceeding 125 grams [Butynski et al., 2006; Butynski et al., 1998; Groves, 2001; Grubb et al., 2003; Honess, 1996; Perkin, 2001; Perkin et al., 2002]. Grubb [2003] extends the range of *Galagoides* to 200 grams which overlaps the mass range of *Galago*. Additionally, it is noted that the monophyly of *Galagoides* has not been clearly established [Grubb et al., 2003] and some genetic studies indicate that *Galagoides* may be a polyphyletic group linked by symplesiomorphic traits [Masters et al., 2007].

When found in sympatry, species are often differentiated by size. Three galagids from two size classes are found in sympatry in Gabon (currently named *Euoticus*, *Sciurocheirus*, and *Gs. demidovii*) [Charles-Dominique, 1974]. Four species of galagids, two small (*Gs. demidovii and Gs. thomasi*) and two medium (*Sciurocheirus* and *Euoticus*), are found at a single site on Bioko Island [Ambrose & Perkin, 1999-2000]. Tanzania, has a total of 13 different species of galagids, and the geographic range of one of them *(Otolemur garnettii)* overlaps with the ranges of most others including the smallest and the largest galagid species (*Gs. orinus, Gs. rondoensis, Gs. demidovii, Gs. udzungwensis, Gs. cocos, Gs. granti, Gs. zanzibaricus, Go. senegalensis, Go. moholi, Otolemur crassicaudatus*) [Bearder, 1999; Bearder et al., 2003; Butynski et al., 1998; Honess, 1996; Lumsden & Masters, 2001; Nash et al., 1989; Nekaris & Bearder, 2007; Perkin, 2001]. In Kenya, *O. garnettii* is sympatric with *Gs. cocos*, *Gs. zanzibaricus* and

Go. senegalensis [Ambrose & Perkin, 1999-2000; Butynski et al., 2006; Butynski et al., 1998; Harcourt & Nash, 1986b; Muoria et al., 2003; Perkin, 2001]. Even species of the same genus can be differentiated by size. For instance, *O. crassicaudatus* is approximately one-third larger than *O. garnettii*. *Galagoides granti* is over twice as large as sympatric *Gs. rondoensis* [Bearder et al., 2003]. Size differentiation within the galagid clade is the focus of this study.

Mechanisms and Processes Underlying Mass Differentiation

Some authors suggest that mass differentiation is driven primarily by genetic and hormonal control (including growth hormone (GH), insulin-like growth factor (IGF-I), growth hormone binding protein (GHBP) and steroids) altering growth rates [Bernstein et al., 2007; Gould, 1971]. Growth hormone (GH) can influence linear skeletal growth, organ growth, and overall body growth [Bernstein et al., 2007]. While growth is a complex process, Bernstein et al. [2007] note that in lineages where selection is targeting overall size, a simple correlation between hormone levels and body size may be likely. Such a relationship is reported for several species of mammals. For instance, mice, rabbits, poodles, cervids, and human pygmies all show correlations between growth hormone levels and size variation within each group [Bernstein et al., 2007]. The underlying proximate mechanism for growth and size differentiation, especially in primates, warrants further study. Suffice it to say, theoretically, increase or decrease in size may be fairly simple to achieve via altering growth hormone levels.

Shea [2002] notes that closely related, but differently sized catarrhines tend to differ in growth rates, but not in growth duration and that alterations in the duration of growth may be more difficult to evolve. The opposite pattern tends to be found intraspecifically with sexual size dimorphism more often resulting from differences in duration (i.e. bimaturism) than from differences in growth rate [e.g.Leigh, 1992b; Leigh & Shea, 1995; Shea, 1986; Shea, 2002]. Interspecific growth rate differences, instead of growth duration differences might be more likely for species, such as those studied here, that breed seasonally as extension of the growth period may be too costly if it means an individual forfeits a breeding season [Leigh, 1992a]. This may partially explain the prevalence of duration differences intraspecifically as it might be more costly for females, with lower reproductive potential to begin with, to forgo a breeding season while males, with higher reproductive potential, may benefit even though losing a breeding season if reproductive success in subsequent seasons increases with increasing size. If this interspecific pattern holds for strepsirrhines, it would be expected that the galagids studied here will differ in growth rate. Since growth rate tends to increase with increasing body mass [Godfrey et al., 2004; Kirkwood, 1985; Leigh, 1994a], it would be expected that *O. garnettii* will exhibit a higher absolute growth rate compared to *Go. senegalensis*.

Alternatively, analyses of primate growth rates suggest that, while growth rates between higher-level taxa (e.g. Strepsirrhini versus Haplorrhini, Platyrrhini versus Catarrhini) are highly variable, within these clades, growth rates may be constrained [Kappeler, 1995; Kirkwood, 1985; Kirkwood & Mace, 1996].

Kappeler [1996] reports that lemurs and lorises had similar postnatal litter growth rates. Kirkwood suggests that at a lower taxonomic level, adaptive change in growth rate appears to be small [Kirkwood, 1985; Kirkwood & Mace, 1996]. Studies of growth hormones and their underlying genes show limited genetic variability in strepsirrhines compared to haplorrhines [Adkins et al., 2001; Li et al., 2005; Liu et al., 2001; Wallis et al., 2001; Ye et al., 2005] possibly suggesting limited variability in growth rates as well. For instance, studies of primate growth hormone (GH) genes show a single GH gene with little variability at the amino acid level in *Galago*, but five GH genes with high variability at the amino acid level in catarrhines [Adkins et al., 2001]. Following these studies, it would be expected that growth rate variability is limited in Galagidae and that the species studied here will exhibit similar growth rates. If similar growth rates are found in *Go. senegalensis* and *O. garnettii*, then subsequent tests of hypotheses positing alteration of growth rates as an adaptive response to socioecological factors would be precluded.

The current study initiated investigation of mass differentiation within the Galagidae to assess whether interspecific mass variation was due to differences in growth rate and/or growth duration. Size, as represented by body mass, ranges from *Gs. orinus* averaging 55 grams to *Otolemur crassicaudatus* averaging 1131 grams [Honess, 1996; Nash et al., 1989] and may be partially responsible for the successful adaptive radiation of this clade. Other measures of size, such as linear measurements, are currently unavailable for most species of galagids.

While the monophyly of Galagidae is well accepted, based on both molecular and morphological characters [DelPero et al., 2000; Masters et al., 2005; Masters et al., 2007; Masters & Brothers, 2002; Roos et al., 2004; Yoder et al., 2001], numerous phylogenetic analyses have not yielded a consensus as to the specifics of the galagid phylogeny. Regardless, this clade represents a fairly successful radiation as galagids are found across much of Africa [Bearder, 1999]. In fact, galagids are the most widely distributed African primate [Bearder et al., 2003]. Monophyly coupled with size differentiation makes this clade ideal for studies of the processes underlying interspecific body mass variability.

MATERIALS AND METHODS

Datasets

O. garnettii subjects included 43 females and 38 males with known dates of birth. A captive colony was maintained by the Duke Lemur Center (formerly the Duke University Primate Center) [Izard, 1989]. Housing was indoor and consisted of cages 0.5 m x 0.5 m x 2 m high furnished with partitions, ledges, and nestboxes; light cycle was constant (12:12 LD) or fluctuated mimicking the local (North Carolina) photoperiod [Coffman, 1995; Izard, 1989; Izard & Pereira, 1994; Izard & Simons, 1986b]. Diet included fruits, vegetables, Purina High Protein Monkey Chow, Purina Cat Chow, and crickets [Izard & Simons, 1986b]. Body mass data available were collected between February 1980 and September 1996. Some subjects were measured multiple times and some were measured only once creating a mixed longitudinal dataset [Coelho, 1985] ranging from 0 days to approximately 7.5 years of age. Subjects measured multiple times were measured sporadically and the number of measurements per individual during the growth period ranged from 1 to 19. There was an average of five mass measurements per female and 6 mass measurements per male. Only subjects with known dates of birth were included in the current study. In some instances, pregnancy was noted and these measurements were removed from the current analysis. In most cases, delivery dates were unknown so no prior measurements were removed as was done with the *Galago* dataset (see below). The data were divided by sex and mass was measured to the nearest gram.

Go. senegalensis subjects included 36 laboratory-born individuals, 19 males and 18 females with known dates of birth. These individuals were part of a captive colony maintained at Arizona State University. Data were collected between July 1976 and March 1992. Housing consisted of varying cage sizes ranging from 2.4 m x 1.4 m x 2.4 m high to 2.4 m x 2.4 m x 2.4 m high and enriched with multiple perches, branches, panels, and nestboxes. A 12:12 LD cycle was maintained. Diet included fruit, vegetables, Purina High Protein Monkey chow and occasionally mealworms. For further description, see [Nash & Flinn, 1978; Schaefer & Nash, 2004]. Subjects were weighed within a day of birth and then up to twice per week until approximately 7 weeks of age and then once per week until death creating a longitudinal dataset for each subject. Over 60 mass measurements are available for most subjects during the growth period. Mass was measured to the nearest gram, but neonates may have had mass measured to the nearest tenth of a gram. Gestation length of *Go. senegalensis* is estimated to be 142 days [Izard & Nash, 1986; Izard & Nash, 1988; Nash et al., 1989]. All mass data for adult pregnant females that were recorded 142 days prior to parturition were removed from the dataset. While this dataset is longitudinal for each subject, not all subjects were measured at the same age.

Additionally, published data from *Go. moholi* and *O. crassicaudatus* were incorporated [Rasmussen & Izard, 1988]. Their sample size was 10 male and 10 female *Go. moholi* and 10 male and 10 female *O. crassicaudatus*, all captive-born at Duke Lemur Center. Husbandry is similar to that summarized above for *O. garnettii* [Coffman, 1995; Izard, 1989; Izard & Pereira, 1994; Izard & Simons, 1986b]. Subjects were weighed at weekly or biweekly intervals for the first few months and at longer intervals afterwards. Data are mixed longitudinal and only individuals surviving to adulthood were included.

Limited growth data are available for one additional galagid, possibly *Galago senegalensis zanzibaricus* (currently considered *Galagoides zanzibaricus*) [Groves, 2001; Grubb et al., 2003]. Gucwinska and Gucwinski [1968] provide mass measurements for a captive sample of "*Galago senegalensis zanzibaricus*", but include no details regarding the original source of the population. Sample size was three infants, one which lost weight and died prior to 39 days. Mass measurements from 1 to 39 days of age were taken sporadically and infant sex was not recorded [Gucwinska & Gucwinski, 1968]. Citing Gucwinska & Gucwinski, Zullinger [1984] provides a growth rate constant for "*Galago senegalensis*". Six data points were used to estimate this. Zullinger notes that adult mass was fixed at 229 grams. This mass is higher than reported adult mass for *Galagoides zanzibaricus* (104-203 grams [Olson & Nash, 2002-2003], 118-183 grams [Harcourt & Nash, 1986b]; 133-154 grams [Courtenay & Bearder, 1989]). However, it is noted that captive subjects tend to be heavier than their wild counterparts [Leigh, 1994b; Terranova & Coffman, 1995; Terranova & Coffman, 1997]. A citation for this adult mass was not provided.

Analysis

Growth parameter estimation

Species average and standard error of the mean were estimated for neonatal mass, adult mass, and age at growth cessation (AGC). Unless otherwise noted, males and females were always analyzed separately. For some estimates, resampling techniques were used [Roff, 2006]. Since the goal of the research was to investigate how interspecific variability in adult body mass arises, no attempt was made to control for body size differences and absolute growth rates and durations were compared.

Male and female neonatal mass were estimated as the average of mass measurements taken within two days of birth. For each subject measured more than once within the first 2 days, only the measurement at the youngest age was used. Generally, intersexual mass differences between males and females are lacking at birth [Badyaev, 2002; Leigh, 1992a; Smith & Leigh, 1998] and the same is true for both species studied here [Izard & Nash, 1988] (also see Chapter 3). For this parameter, male and female data were pooled.

Adult mass was estimated as the average mass at approximately 3.5 years of age. This age was selected as it is substantially after the reported age at sexual maturity for both species which is 9-15 months for *Go. senegalensis* and 12-18 months for *O. garnettii* [Horn & Eaton, 1979; Izard & Nash, 1988; Nash, 1993]. However, it is noted that in many primate species, growth continues past the age at sexual maturity [Altmann et al., 1981; Bercovitch, 2000; Bercovitch et al., 1998; Coelho, 1985; Maggioncalda et al., 2002; Setchell & Dixson, 2002; Setchell et al., 2001; Smith & Jungers, 1997]. Estimating adult size at an age well past sexual maturity increases the likelihood of capturing true adult size. Also, visual inspection of scatterplots of mass by age for each sex of each species indicates that the growth curve subsequent to 3.5 years is fairly horizontal rather than increasing and that growth has therefore ceased (Fig. 1). For each subject, the first measurement taken after 1280 days was used as this criterion maximized available samples for each sex of each species, though several *O. garnettii* subjects were not measured in adulthood so sample sizes are smaller than those for estimated AGC.

Adult mass could have been estimated as the mass at the age at growth cessation (see below). However, using this method could lead to a biased estimate as mass would always either be underestimated (when age at growth cessation was underestimated) or correctly estimated (when age at growth cessation was correctly estimated and when it was over estimated). In no case would mass be overestimated and the resulting species average would likely underestimate adult mass.

Mass often fluctuates throughout an animal's lifetime. Growth cessation is defined here as the point at which regular increase in mass ceases. Local regression (LOESS) curves were fit to each of the datasets (males and females of each species) using the loess function (R2.10.0, Base Package) (Fig. 1). A span of 0.3 was selected by visual inspection as the smoothing parameter that accounted for all prominent features of the data without undue noise [Cleveland, 1979; Cleveland & Devlin, 1988] (Appendix A). Once a smoothing parameter was selected, bootstrapping was used to estimate the age at growth cessation (AGC) (programming code can be found in Appendix B). One thousand datasets of the same size as the original dataset were created by sampling with replacement from the original dataset [Roff, 2006]. A 95% confidence interval was calculated for comparison of AGC (growth duration).

When resampling, the standard error of the mean (SEM) decreases as the number of replications increases, therefore too many replicates can render the confidence intervals estimated from bootstrapped estimates too small to make comparisons between estimates entirely reliable [Potvin & Roff, 1993]. Bootstrapped estimates of the age at growth cessation (AGC, see below) were collected from 200, 1000, 2000, and 5000 iterations (Appendix C). The number of replications had little effect on the estimated mean of AGC, but it did influence the SEM which decreased with the number of replications. Roff [2006] recommends 1000 replicates for estimating confidence intervals. This lower number of replicates produces larger confidence intervals so it was selected to provide greater confidence in the results.

The first local maximum of the growth curve was collected from each bootstrapped sample. The first local maximum of the growth curve is equivalent to the first time the first derivative of the growth curve with respect to age (i.e. a pseudovelocity curve) is equal to zero. This first local maximum represents the first point of the growth curve where there is no size increase [R Development Core Team, 2009; Venables & Ripley, 2003] and estimates the age at growth cessation. Pseudovalues for age at growth cessation were collected from each bootstrapped sample. The mean and variance were estimated from these pseudovalues for each sex of each species.

Growth variability

Once AGC was estimated, the dataset was truncated at this point and data preceding AGC used for tests of growth rate differences. Data were natural log-transformed (Appendix D) and Ordinary Least Squares regression (OLS) was fit to each truncated dataset. The slopes of the OLS were compared (*Otolemur* males with *Galago* males; *Otolemur* females with *Galago* females) using a likelihood ratio test with an exact F-statistic. This compares the sum of squares when a common slope is fitted to pooled data and when a separate regression line is fitted to each sex separately [Sokal & Rohlf, 1995; Warton et al., 2006] using an ANOVA function (R2.10.0, Base Package) [R Development Core Team, 2009]. This method is robust to non-normality and does not assume equal variance between groups [Warton, 2007; Warton et al., 2006]. Growth durations (AGC) were compared using 95% confidence intervals.

Gompertz model

To increase the number of species compared, the methods in Rasmussen & Izard [1988] were replicated so comparable growth rate constants could be estimated for *Go. senegalensis* and *O. garnettii*. Rasmussen & Izard replicated the method used in Zullinger [1984]. This method involved fitting the individual data to a sigmoidal curve by using iterative least-squares method; the NLIN feature of SAS was used. A Gompertz model, $(M_t) = Ae^{-e^{-k(t-I)}}$ was used to estimate growth parameters including a growth rate constant (k), asymptotic mass (A), and age at the inflection point (I). (M_t) equals the mass at age(t). A separate curve was fit for each subject and species' values were the means of the individual curves [Rasmussen & Izard, 1988; Zullinger et al., 1984].

The Gompertz-estimated growth rate constant K is highly correlated with body mass so K is not directly comparable between species [Zullinger et al., 1984]. However, the growth rate constant can be converted into a linear growth rate in grams per day by multiplying the growth rate constant (K) by the mass at the inflection point (I). The inflection point for the Gompertz equation is at 37% of adult mass [Zullinger et al., 1984]. Therefore, comparable linear growth rates could be estimated for five galagid species - three using published data (*O. crassicaudatus*, *Go. moholi*, and *Gs. zanzibaricus*) and two using raw data (*O. garnettii* and *Go. senegalensis*). This portion of the study is limited by the data available and the previous methods used. For statistical comparison between the growth rates of *O. garnettii* and *Go. senegalensis* and those of *O. crassicaudatus* and *Go. moholi*, and *Gs. zanzibaricus*, raw growth data for the latter species are needed.

RESULTS

Growth parameters and variability

Both scatterplots and loess fits for each of the four groups (*Go. senegalensis* males, *Go. senegalensis* females, *O. garnettii* male*s, and O. garnettii* females) indicate that early growth is fairly linear, followed by deceleration and finally growth cessation. However, considerable individual fluctuation is obvious throughout adulthood, especially for *O. garnettii* males (Fig. 1). *O. garnettii* neonates are about 2 ½ times larger than *Go. senegalensis* neonates. *O. garnettii* neonates average 51.72 ± 2.38 grams (n = 9) and *Go. senegalensis* neonates averaged 19.6 ± 0.37 grams (n = 35) (Table II). These results are comparable to published neonatal mass estimates [Izard & Nash, 1988; Smith & Leigh, 1998].

O. garnettii adults are larger than *Go. senegalensis* adults. *O. garnettii* males average 1221.4 ± 36.4 grams (n=14), *O. garnettii* females average 1064.2 ± 40.74 grams (n = 11), *Go. senegalensis* males averaged 338.3 ± 20.19 grams (n = 12), *Go. senegalensis* females averaged 253.1 ± 11.23 grams (n = 15). Captive primates tend to be heavier than their wild counterparts, though generally not significantly so [Leigh, 1994b; Terranova & Coffman, 1995; Terranova & Coffman, 1997]. Similarly, average masses for these captive subjects are higher than those reported for wild subjects. Nash et al. (1989) report wild-caught weights as follows: *O. garnettii* males 829 grams, *O. garnettii* females 720 grams, (range 550-1040 grams), *Go. senegalensis* males 225 grams, and *Go. senegalensis* females 200 grams (range 112-300 grams).

Bootstrapped estimates for AGC are as follows: *O. garnettii* males 783 (± 11.72) days; *O. garnettii* females 557 (± 3.78) days; *Go. senegalensis* males 717 (± 4.99) days; and *Go. senegalensis* females 484 (± 2.94) days. Confidence intervals show that *O. garnettii* males and females grow for a longer duration than *Go. senegalensis* males and females respectively. Datasets were truncated at these ages and OLS regression fit to the remaining log-transformed data (Fig. 2). Likelihood ratio tests for common slope (comparing *O. garnettii* males with *Go. senegalensis* males and *O. garnettii* females with *Go. senegalensis* females) show the rate of growth of the two species to be significantly different for both males ($F(3,2) = 2837$, $p<0.001$) and females ($F(3,2) = 3076.8$, $p< 0.001$) (Table III).

Gompertz model

Replicating the Gompertz methods used by Rasmussen & Izard [1988] provided growth rate constants of 0.010 for *O. garnettii* males, 0.012 for *O. garnettii* females, 0.010 for *Go. senegalensis* males, and 0.013 for *Go. senegalensis* females. Reported growth rate constants from Rasmussen & Izard were 0.020 for *Go. moholi* and 0.019 for *O. crassicaudatus.* Zullinger [1984] records a growth rate constant for *Go. senegalensis zanzibaricus* as 0.017 (Table IV).

Converting the growth rate constant (K) into a linear “grams per day” growth rate (K*mass(I)) yields linear growth rates as follows: (*O. crassicaudatus* 7.6 grams/day; *O. garnettii* 4.7 grams/day; *Go. senegalensis* 1.2 grams/day; *Gs. zanzibaricus* 1.4 grams/day; and *Go. moholi* 1.1 grams/day. Ordinary least squares regression of (ln) growth rate on (ln) adult mass shows that the linear growth rate increases with increasing adult mass (Fig. 3).

DISCUSSION

The purpose of this study was to ascertain whether interspecific size differences in galagids result from differences in growth rate, growth duration, a combination of the two, or neither. Shea [2002] reports that for catarrhines, growth variation is more likely due to rate differences than to duration differences. Conversely, mass growth rate and growth hormone gene variability appear to be constrained at lower taxonomic levels [Adkins et al., 2001; Kappeler, 1995; Kirkwood, 1985; Li et al., 2005; Liu et al., 2001; Wallis et al., 2001; Ye et al., 2005]. Results of this study show that, for *O. garnettii* and *Go. senegalensis*, interspecific adult size variation results from both rate and duration differences. *O. garnettii* grows at a higher absolute rate and for a longer period of time compared to *Go. senegalensis*.

O'Mara et al. [in review], also using data from Duke Lemur Center, estimated age at growth cessation for *O. garnettii* as 444.5 days for females and 529.0 days for males (Fig. 4). O'Mara et al. estimated age at growth cessation iteratively by first dividing the data into two segments – a growth segment and an adult segment. A quadratic model was fit to the growth segment. Age at growth cessation was the point which maximized the sum of squares of residuals of the two piece regression. This method would underestimate the age at growth cessation if the latter part of the growth process was slowed to such a degree that its slope is closer to zero (the expected slope of the adult portion of the growth curve) than to the relatively high slope associated with the earlier part of growth. Visually, O'Mara et al.'s Fig. 1 shows that more data points fall above the horizontal line marking adult size than fall below it for *Otolemur* males. This suggests that both adult size and AGC are underestimated by this model.

Conversely, the current study estimated AGC indirectly from loess regression. The loess fit for *O. garnettii,* especially the males, appears to continuously increase thus estimating AGC from this regression may overestimate AGC. Whether the continuously increasing growth curve is an artifact of captivity or whether *O. garnettii* males, like *Pongo* males exhibit indeterminate growth [Kappeler, 2002; Leigh, 1992b; Leigh, 1994b] requires data from wild subjects. As indeterminate growth is rare among primates, this seems unlikely. The pattern of increasing mass makes estimating both age at growth cessation and adult size difficult and may partially explain the disparity, as might different methods used. Estimated adult mass for *O. garnettii* were 983 grams for females and 1162 grams for males [O'Mara et al., in review]. These estimates are lower than those of the current study. O'Mara et al. estimated adult size as the size at the estimated AGC which, as noted above, may underestimate adult size. The current study's estimates of adult size accord with those of Kappeler [1991].

Gompertz model and linear growth rates of galagids

Using the Gompertz equation and previously published data, linear growth rates were calculated for five galagid species. While statistical comparison of the growth rates is not possible with current data, it is clear that both *Otolemur* species have considerably higher growth rates compared to the smaller *Galago* and *Galagoides* species. Visually, the linear growth rates of both *Otolemur* species are more similar to each other than they are to the other galagid species (Fig. 5). Data are lacking for statistical comparison of growth durations.

The utility of the Gompertz model for galagids is problematic. Zullinger [1984] notes that for all primate species examined, the van Bertalanffy equation fit the data better than the Gompertz equation. Further, for most mammalian species examined, Gompertz over estimated neonatal mass. Adult mass of older individuals was also consistently overestimated [Zullinger et al., 1984]. Rasmussen & Izard [1988] note that Gompertz underestimated adult mass for both *O. crassicaudatus* and *Go. moholi*. Superimposing the growth curve predicted by the Gompertz (as estimated by linear growth rate = K * Mass(I)) (Fig. 6) demonstrates that a linear growth rate does not adequately describe the growth curves of either species, but appears to fit better during the early part of growth than the later part of growth. Since the Gompertz model fits better during the early, more rapid phase of growth than the later, slower phase of growth, average growth rates using Gompertz will be overestimated. O'Mara et al. [in review] estimated growth rates as ((adult mass – neonatal mass)/growth duration) and reports 2.10 grams/day for both *O. garnettii* males and females, 0.526 grams/day for *Go. moholi* males and 0.557 grams/day for *Go. moholi* females. Both these estimated growth rates and those estimated as the slopes of the regression (1.96 grams/day for both *O. garnettii* males and females, 0.479 for *Go. moholi* males and 0.512 for *Go. moholi* females) are considerably lower than those estimated from the Gompertz model. As the Gompertz model may not provide the best fit or the best estimate of growth rate, raw data from additional species of galagids is needed to adequately compare growth rates between species.

Growth variability among galagids

The growth pattern of at least one of the species studied here has diverged from the ancestral pattern. Examination of both fossil and extant species suggests that primitive galagids were small-bodied [Martin, 1979; McCrossin, 1992; Walker, 1978, 1987; Wesselman, 1984, 1995]. The earliest fossil galagids tend to be small in size, but within the size range of extant species, with larger species only appearing more recently [McCrossin, 1992; Seiffert et al., 2003] (Table I). The complete size range encompassed within extant galagids is not present until 3 million years ago (mya) [Wesselman, 1995].

The earliest fossil species that is morphologically similar to the larger-bodied *Otolemur* dates to approximately 3 mya and is smaller than extant *Otolemur* species [Wesselman, 1984, 1995]. This fossil suggests that *Otolemur* diverged within the galagid clade by 3 mya and that a size increase has occurred within the *Otolemur* lineage. Further support for this size increase is found in the molecular study of Masters et al. [1988] which indicates that the larger *O. crassicaudatus* diverged from the smaller *O. garnettii* approximately 2 mya. The body size of *Go. senegalensis* appears closer to the primitive condition for galagids suggesting that body size increase, as indicated by body mass, has occurred in the galagid lineage. Whether the interspecific complexity of growth patterns found here, with differences in both growth rate and growth duration, characterizes Galagidae as a whole remains unknown. The current study is limited in both the number of species examined and in the size range represented. Conclusions would be strengthened if data for other species, including the smallest galagids such as *Gs. demidovii* were available.

O'Mara et al., [in review], though focusing on intraspecific comparisons between males and females, provides evidence that *O. garnettii* and *Go. moholi* have significantly different growth rates and durations as well, paralleling the results found here. Direct comparison of O'Mara et al.'s results with this study is not possible as different methods were used to estimate slope. While Shea [2002] suggests that interspecific variation in growth duration, if it is linked to reproductive maturity and other life history variables for seasonally breeding species [Leigh, 1992a], may be limited. Neither this study nor that by O'Mara et al. [in review] supports his assertion as duration differences were found both between *O. garnettii* and *Go. senegalensis* and between *O. garnettii* and *Go. moholi*. For comparison between *Go. senegalensis* and *Go. moholi*, similar methods would need to be used for both datasets. Not only is growth duration variable within the galagid clade, but age at sexual maturity is variable as well. For instance, *Go. moholi* reaches sexual maturity at 258 days and *Go. senegalensis* reaches sexual maturity at 372 days [Izard & Nash, 1988] indicating greater variability than that suggested by Shea.

While prenatal growth data are unavailable, gestation length coupled with neonatal mass data indicate that *O. garnettii* grow at a higher rate prenatally as well. *O. garnettii* is born weighing 52 grams after 130 days of gestation while *Go. senegalensis* is born weighing 20 grams after 142 days of gestation [Izard & Nash, 1986; Izard & Nash, 1988; Nash et al., 1989]. Estimates combining gestation length and neonatal mass for other galagid species suggest that galagid prenatal growth rates vary considerably, growth durations vary less (Fig. 7). Prenatal growth rates increase with increasing adult body mass, but gestation lengths do not (Figs. 8 and 9). Prenatal growth data would be needed to support these assertions. This crude estimate of prenatal growth rate assumes that zygotes are similarly sized, that prenatal growth rate is linear, and that sex differences in gestation length are negligible. All assumptions have some support within the literature [Conrad et al., 1995; Corradini et al., 1998; Jaquish et al., 1995; Jolicouer, 1985; Lee & Kappeler, 2003; Leigh & Shea, 1996; McKim et al., 1972; Warton et al., 2006].

Growth variability among strepsirrhines

The presence of both growth rate and duration differences within this clade accords with more recent and fine-grained studies of primate growth which indicate that growth patterns may vary considerably within lower taxonomic levels. Growth patterns may vary between species, between populations within a single species, and between individuals within a single population [Kirkwood, 1985; Mori, 1979; Scheuer & Black, 2000; Setchell et al., 2001]. Though strepsirrhines may have low variability in growth rate hormones and their underlying genes, considerable variability in mean growth rates and durations is present both within strepsirrhines as a whole and at lower taxonomic levels (e.g.

Lemuroidea vs Lorisoidea, Lorisidae vs Galagidae) [O'Mara et al., in review]. The growth patterns of species are considered to be the result of adaptation to species-specific ecology, social system and life-history [Bogin, 1999; Brizzee & Dunlap, 1986; Case, 1978; Kappeler, 1996; Kirkwood & Mace, 1996; Leigh, 1992a, b; Plavcan, 1999; Taylor, 1997]. Indeed, growth patterns seem to be highly responsive to differing socioecological pressures these groups may face and adaptations to unique socioecological conditions may override phylogeny [Jungers & Cole, 1992]. Several strepsirrhine primate studies support this.

Ecogeographic size variation among sifakas has been related to differences in resource seasonality each species faces [Ravosa & Daniel, 2010; Ravosa et al., 1993, 1995]. Progressively larger species are found in poorer quality, but less seasonal habitats. These studies point out the usefulness of growth data in socioecological studies - adult size distribution fit both hypotheses of forage quality and of resource seasonality (specifically, dry season constraint) as selective factors. The forage quality hypothesis proposes that larger body size, with longer gut transit times, is an adaptation to poor forage quality. The resource seasonality hypothesis proposes that resource seasonality places constraints on body size such that small body size is an adaptation to seasonal unavailability of food resources. Sifakas are distributed such that larger bodied forms are found in regions with poor food quality (as measured by the ratio of protein to fiber in mature leaves) and smaller forms are found in regions with high seasonality of resources. Extending these hypotheses to growth rates, the forage quality hypothesis predicts that slow growth rate will be associated with poor quality food and the resource seasonality hypothesis predicts that slow growth rate will be associated with high seasonality of food resources. The addition of growth data suggested that resource seasonality is the primary selective factor explaining size differentiation as the species with the lowest growth rate were associated with the most seasonal habitats and those with the highest growth rate were associated with the poorest quality habitats. This suggests that seasonality of food resources constrains not only adult size, but growth rates as well. Growth durations were similar for all species [Ravosa et al., 1993, 1995].

Bergman's Rule links body mass and climate such that mammalian species living in colder climates will be heavier compared to species living in warmer climates. A high volume to surface area ratio allows improved conservation of body heat [Blackburn et al., 1999; James, 1970]. Size differentiation among African lorisids follows patterns predicted by Bergmann's rule, (with climate inferred by elevation), coupled with character displacement wherever *Potto* is sympatric with *Arctocebus*. Similar patterns are found among Asian lorisids with the larger species inhabiting higher latitudes [Gomez, 1991; Gomez, 1992; Ravosa, 1998]. In the case of the African lorisids, size differentiation appears to arise through differences in growth rate while differences in growth duration explains the size differentiation in the Asian lorisids [Ravosa, 1998, 2007].

Whether similar patterns of ecogeographic size variation are found among Galagidae warrants further study. However, it is noted that on Bioko Island, which hosts four species of galagids, one of the smallest species, *Galagoides* *thomasi* is found at the highest elevation (Butynski, pers. comm.). Likewise, in eastern Africa, *Gs. orinus* is found at higher elevation than larger sympatric galagid species [Butynski et al., 1998]. The smaller *Go. moholi* is found in more southerly latitudes than its larger *Galago* counterparts and is smaller than *Go. senegalensis* which appears to be it's ecological equivalent [Nash et al., 1989]. Patterns of ecogeographic variation and size distribution of this clade clearly require further study to determine if exceptions such as these to Bergman's Rule, which appears to hold interspecifically more often than not [Blackburn et al., 1999; Harcourt & Schreier, 2009], are rare in galagids.

The presence of growth rate and duration differences found here indicate that body mass growth patterns of strepsirrhines can be divergent among closely related taxa and differences in growth patterns are likely associated with each species' unique socioecology. Galagidae exhibit considerable variability in body mass and shape, socioecology and life history [Nash et al., 1989]. Body size within this family ranges from 55 grams to 1130 grams (Table I) [Nash et al., 1989]. Shape differences are indicated by intermembral indices which range from 52-70 [Fleagle, 1999]. Galagids inhabit a wide variety of habitats from the east to the west coast of Africa including primary and secondary rain forests, riverine and montane forests, thorn scrub and acacia woodlands, forest edges, and savannah. They range at different elevations and altitudes. Diets vary between species and include exudates, insects and small animals, seeds, and fruit. The number of offspring per litter ranges from one to three and number of litters per year ranges from one to two. Species are generally solitary foragers with varying amounts of association between individuals both during active time and during sleeping time; matriarchies are not uncommon [Bearder, 1987; Bearder et al., 1995; Nash et al., 1989; Nekaris & Bearder, 2007]. Each of these sociological and life history factors have potential implications for growth so it is not surprising that *O. garnettii* and *Go. senegalensis* do not share a common growth pattern, instead their growth patterns may have responded to each species' unique socioecology and life history.

The variability that characterizes the Galagidae is present in the species in this study. *O. garnettii* is nearly three times as large as *Go. senegalensis*. *O. garnettii* produces a single litter per year while *Go. senegalensis* can produce two litters [Izard & Nash, 1988; Nash et al., 1989]. *O. garnettii* weans infants during the dry season while *Go. senegalensis* weans infants during the rainy season [Nash, 1983, 1986a]. *O. garnettii* lives in coastal and riverine forests while *Go. senegalensis* inhabits more open woodland [Nash et al., 1989]. *O. garnettii* consumes fruit and insects and *Go. senegalensis* consumes gums and insects [Harcourt & Nash, 1986b; Nash, 1986a; Nash, 1986b; Nash, 1989; Nash & Harcourt, 1986; Nash & Whitten, 1989]. Any and all of these socioecological factors could influence the growth patterns of the species examined in this study. Much more information regarding the distribution of galagid species, each species ecological niche, body size variability, life history, and ontogeny is needed to unravel patterns linking socioecology, life history and growth and to shed further light on the adaptive radiation of this clade.

TABLE I. Body mass of extant and fossil (in bold) Galagidae (sorted by increasing mass)

Species	Mass (grams)	Age	Source
Galagoides orinus	55	Extant	[Honess, 1996]
Galagoides rondoensis	60	Extant	[Groves, 2001]
Galagoides demidovii	70	Pliocene to extant	[Nash et al., 1989; Wesselman, 1995]
Galagoides thomasi	99	Extant	[Nash et al., 1989]
Wadilemur elegans	**112**	**Eocene**	**[Seiffert et al., 2005]**
Saharagalago misrensis	**122**	**Eocene**	**[Seiffert et al., 2003]**
Galagoides udzungwensis	136	Extant	[Groves, 2001; Honess, 1996]
Komba minor	**141**	**Miocene**	**[McCrossin, 1992]**
Galagoides cocos	144	Extant	[Butynski et al., 2006]
Galagoides granti	150	Extant	[Butynski et al., 2006]
Galagoides zanzibaricus	145	Extant	[Butynski et al., 2006; Nash et al., 1989]
Galago moholi	158	Extant	[Nash et al., 1989]
Galago senegalensis	206	Pleistocene - extant	[Nash et al., 1989; Simpson, 1965; Wesselman, 1995]
Galago. sadimanensis	**Similar to *Go. senegalensis***	**Pliocene**	**[Walker, 1987]**
Galago matschiei	210	Extant	[Nash et al., 1989]
Euoticus pallidus	182-210	Extant	[Nekaris & Bearder, 2007]
Sciurocheirus gabonensis	260	Extant	[Nekaris & Bearder, 2007]
Euoticus elegantulus	293	Extant	[Nash et al., 1989]
Komba robustus	**344**	**Miocene**	**[McCrossin, 1992]**
Sciurocheirus alleni	350	Extant	[Grubb et al., 2003]
Galago howellii	**Between *S. alleni* and *O. garnettii***	**Pliocene**	[Wesselman, 1984, 1995]
Otolemur garnettii	767	Extant	[Nash et al., 1989]
Otolemur crassicaudatus	1131	Extant	[Nash et al., 1989]
Komba winamensis	**1138**	**Miocene**	**[McCrossin, 1992]**

TABLE II. Summary of growth parameters

	Neonatal Mass (SEM) (grams)	Adult Mass (SEM) (grams)	AGC (SEM) (days)	95% CI
O. garnettii males	54.0 (3.70) (n = 5)	1221.4 (36.4) (n = 14)	783.2 (11.73) (n = 38)	759.74 – 806.66
O. garnettii females	48.9 (2.53) (n = 4)	1064.2 (40.74) (n = 11)	557.0 (3.78) (n = 43)	549.44 – 564.56
O. garnettii pooled	51.7 (2.38) (n = 9)	1152.3 (30.98) (n = 35)	714.0 (8.29) (n = 81)	697.42 – 730.58
Go. senegalensis males	19.6 (0.95) (n = 19)	338.3 (20.19) (n = 12)	717.4 (4.99) (n = 19)	707.42 – 727.38
Go. senegalensis females	19.6 (0.55) (n = 17)	253.1 (11.23) (n = 15)	484.0 (2.94) (n = 18)	478.12 – 489.88
Go. senegalensis pooled	19.6 (0.37) (n =36)	287.4 (13.55) (n = 27)	710.1 (3.70) (n = 37)	702.7 – 717.5

TABLE III. Ordinary least squares regression of slope ((ln) mass (grams) on (ln) age (days)) of males and females for each species

	Slope (SEM)	**95% CI**	**r^2**	**Significance**
O. garnettii males	0.522 (0.011)	0.500 – 0.544	0.906	P>.001
Go. senegalensis males	0.488 (0.005)	0.478 – 0.498	0.883	
O. garnettii females	0.536 (0.010)	0.516 – 0.556	0.921	P>.001
Go. senegalensis females	0.455 (0.004)	0.447 – 0.463	0.895	

TABLE IV. Growth rate constant estimated using Gompertz model

Species	K (SEM)	Adult Mass (grams)	Linear Growth Rate (K*M(I)) (Grams/day)	Source
O. crassicaudatus (n = 10)	0.019 (0.005)	1120 [1]	7.6	[Rasmussen & Izard, 1988]
O. garnettii females (n = 43)	0.012 (0.006)	1004 [1]	4.7	Current study
Go. senegalensis females (n = 18)	0.013 (0.004)	242 [1]	1.2	Current study
Gs. zanzibaricus (n = 3)	0.017 (0.003)	229 [2]	1.4	[Zullinger et al., 1984]
Go. moholi (n = 9)	0.020 (0.004)	149 [1]	1.1	[Rasmussen & Izard, 1988]
Go. senegalensis males (n = 19)	0.010 (0.004)	330[1]	1.2	Current study
O. garnettii males (n = 38)	0.010 (0.005)	1270[1]	4.7	Current study

[1] Asymptotic mass estimated from Gompertz model

[2] Asymptotic mass fixed

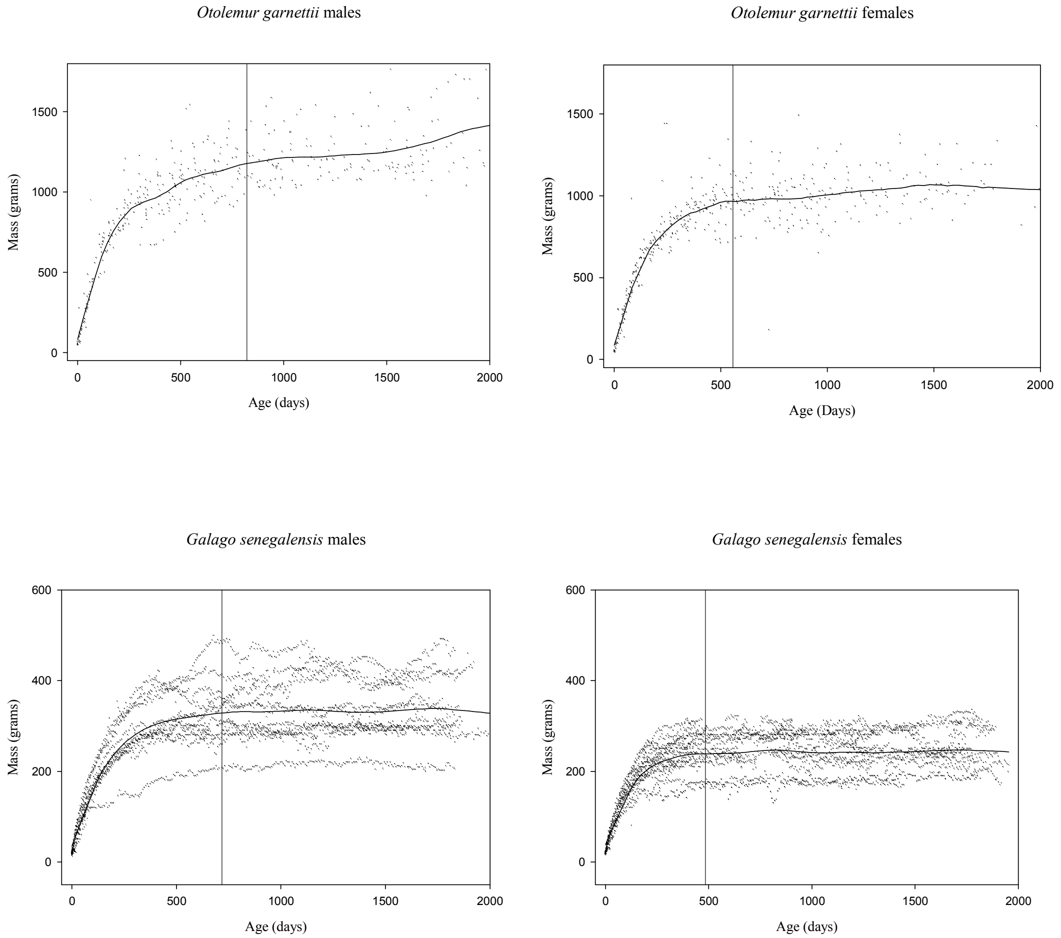
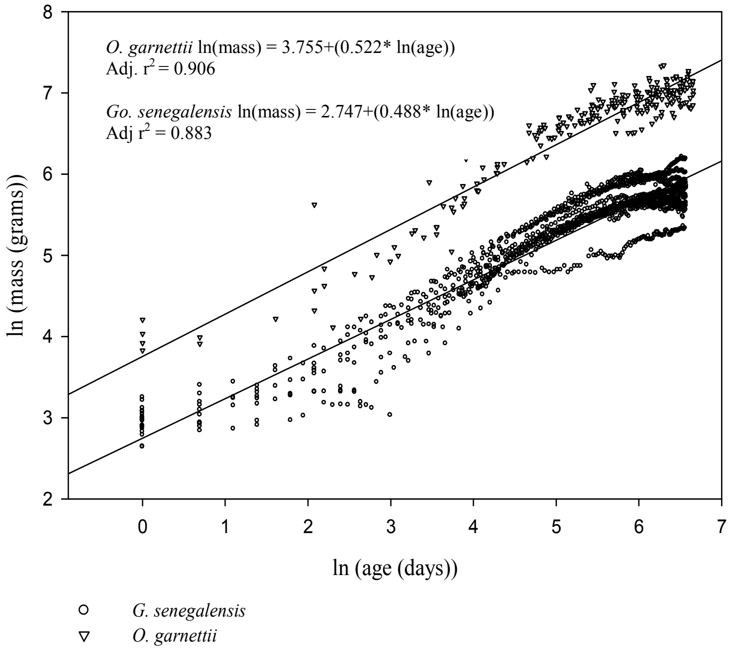


Fig. 1. Loess estimated growth curves fit for male and female galagids. Vertical lines are placed at the bootstrapped estimated age at growth cessation (AGC).

Galagid Males



Galagid Females

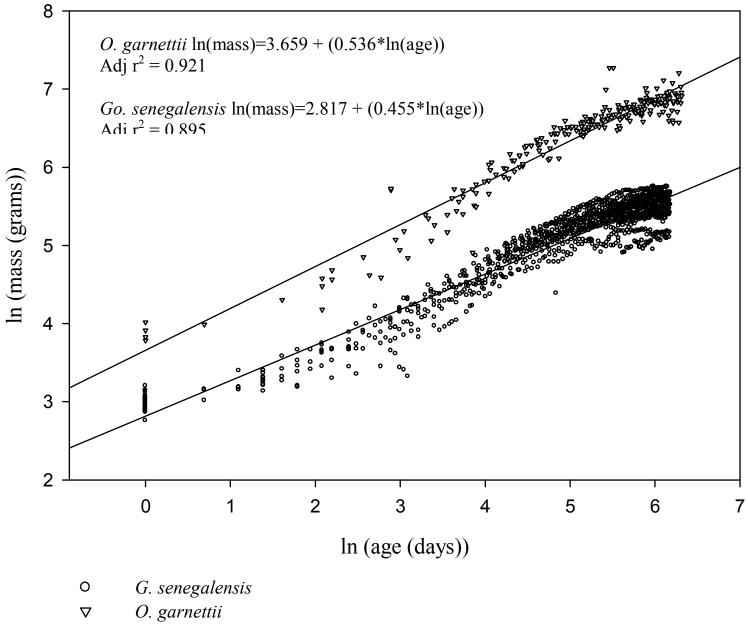


Fig. 2. Ordinary least squares regression for male and female galagids. Note: Only data preceding the age at growth cessation included.

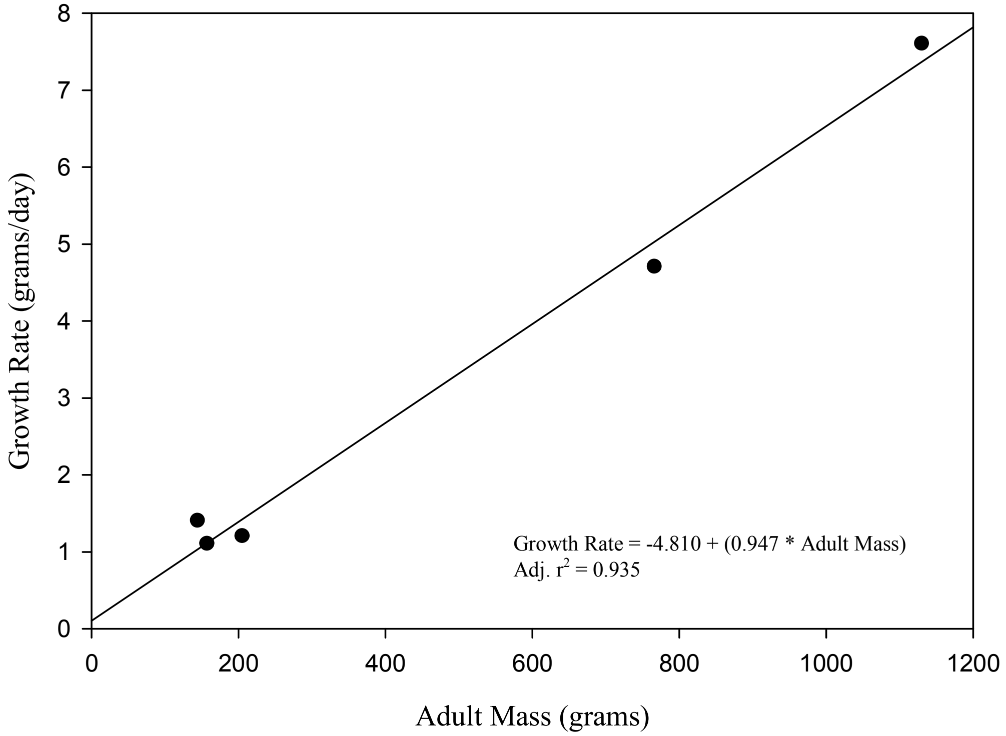
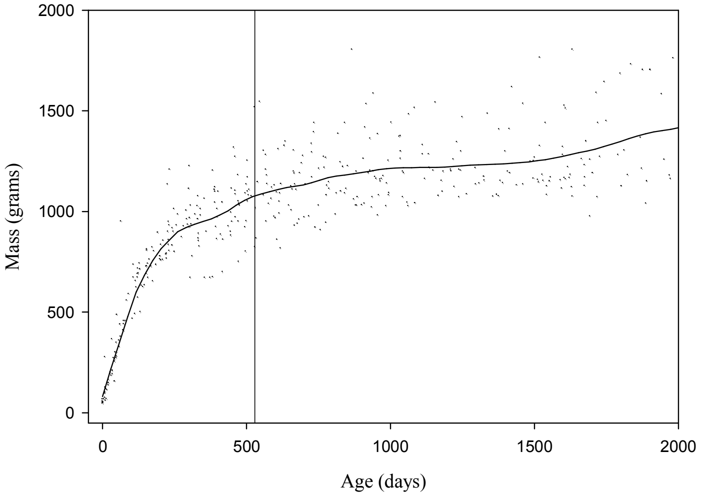
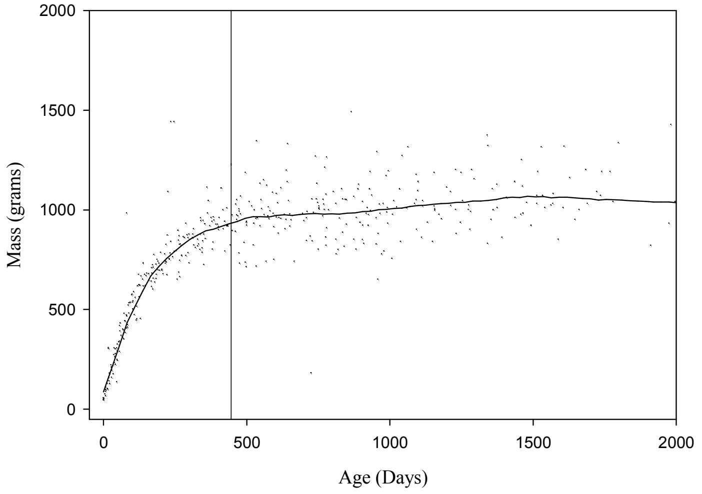


Fig. 3. Linear growth rate (estimated as K*Mass(I)) regressed onto adult mass. (Data from Table IV)



O. garnettii males



O. garnettii females

Fig. 4. Loess regression of growth data with vertical reference line at age at growth cessation (529 days for males, 445 days for females) as estimated by O’Mara et al. [in review].

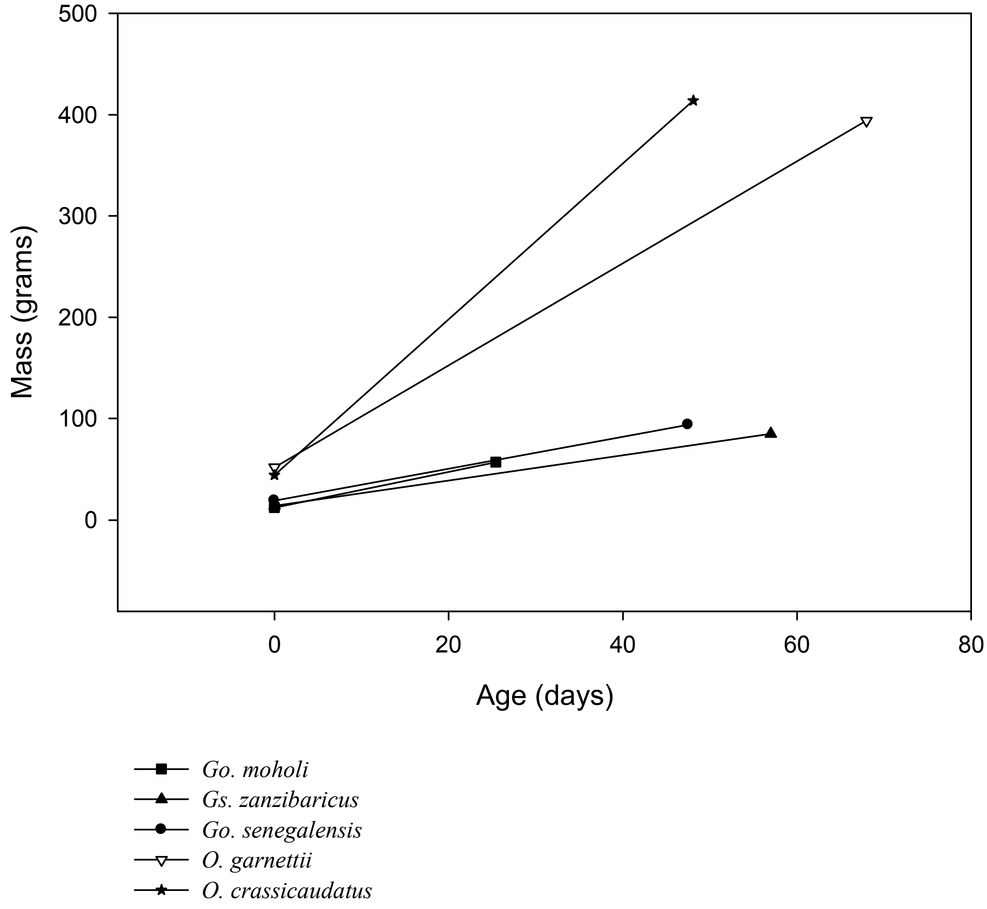
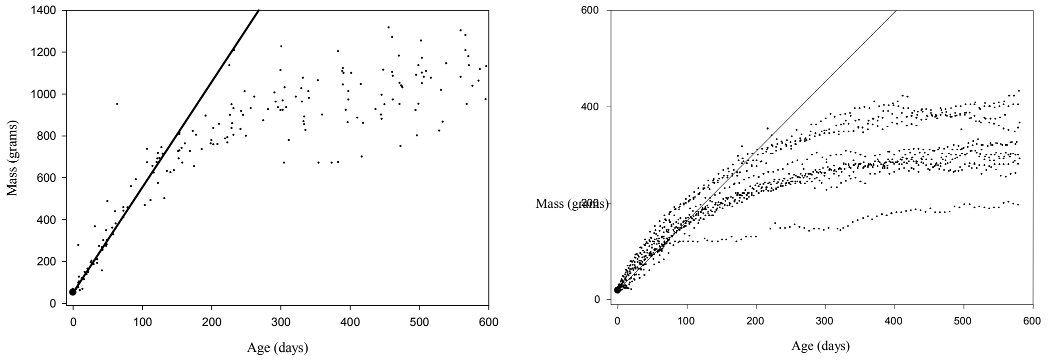


Fig. 5. Growth from birth to the inflection point as estimated from the Gompertz model.

O. garnettii males *G. senegalensis* males



O. garnettii females *G. senegalensis* females

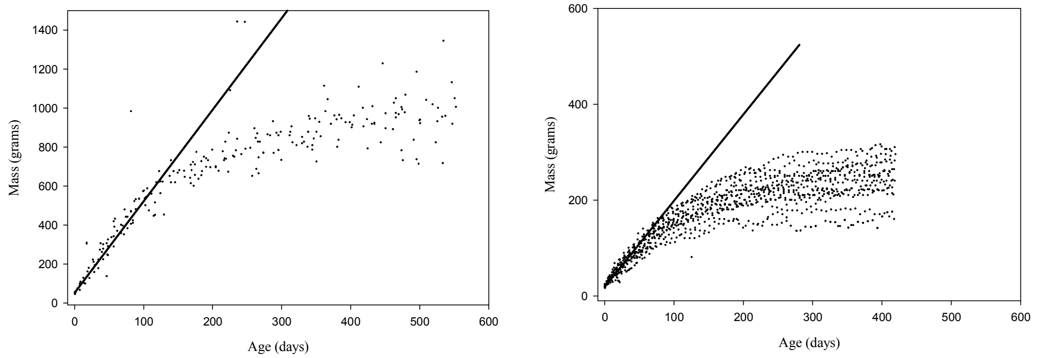


Fig. 6. Linear growth curve estimated by the Gompertz model superimposed onto a scatterplot of mass by age.

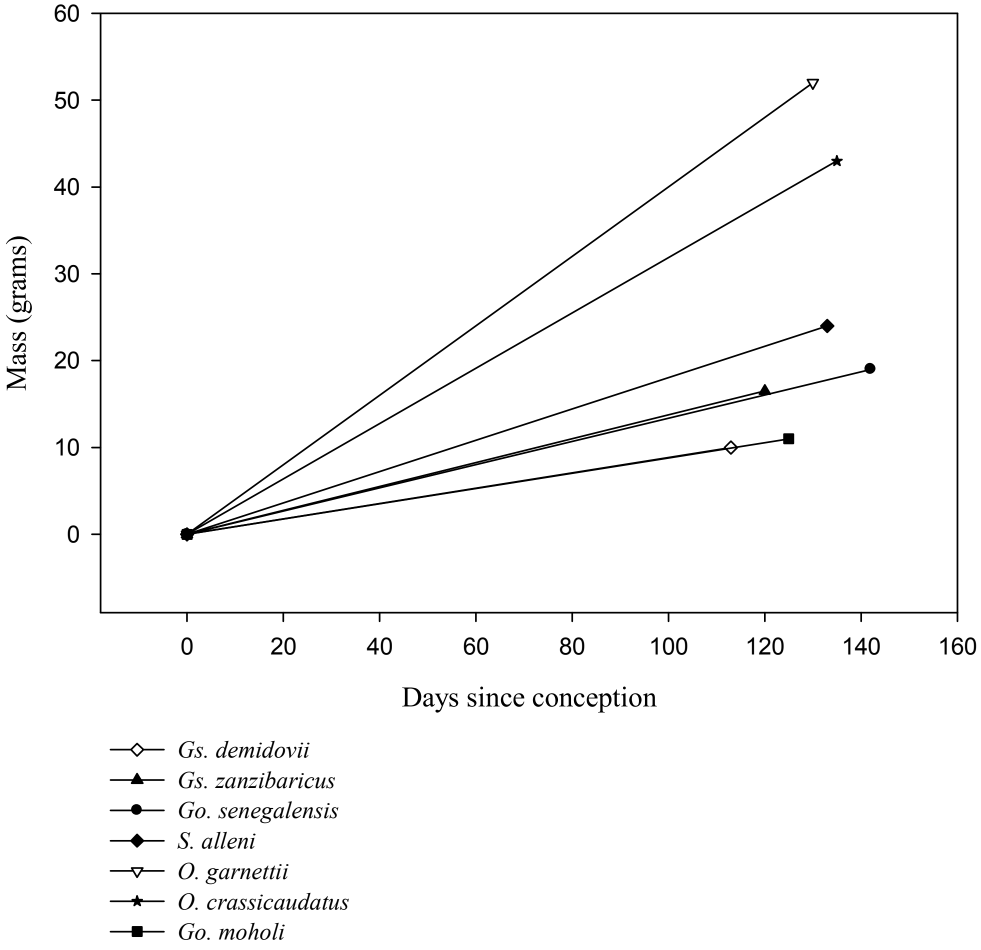


Fig. 7. Linear prenatal growth curves for galagid species. (Gestation length from [Nash et al., 1989]; neonatal mass from [Smith & Leigh, 1998]).

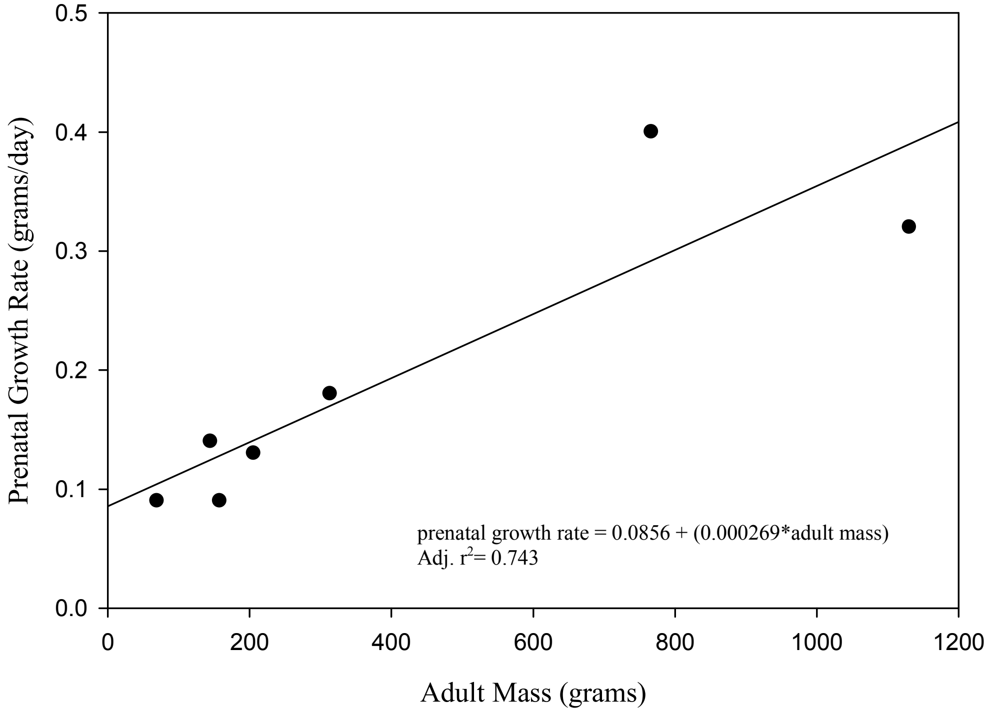


Fig. 8. Prenatal growth rates for galagid species regressed onto adult body mass. (Growth rate calculated as neonatal mass/gestation length). (Gestation length and adult mass from [Nash et al., 1989]; neonatal mass from [Smith & Leigh, 1998]).

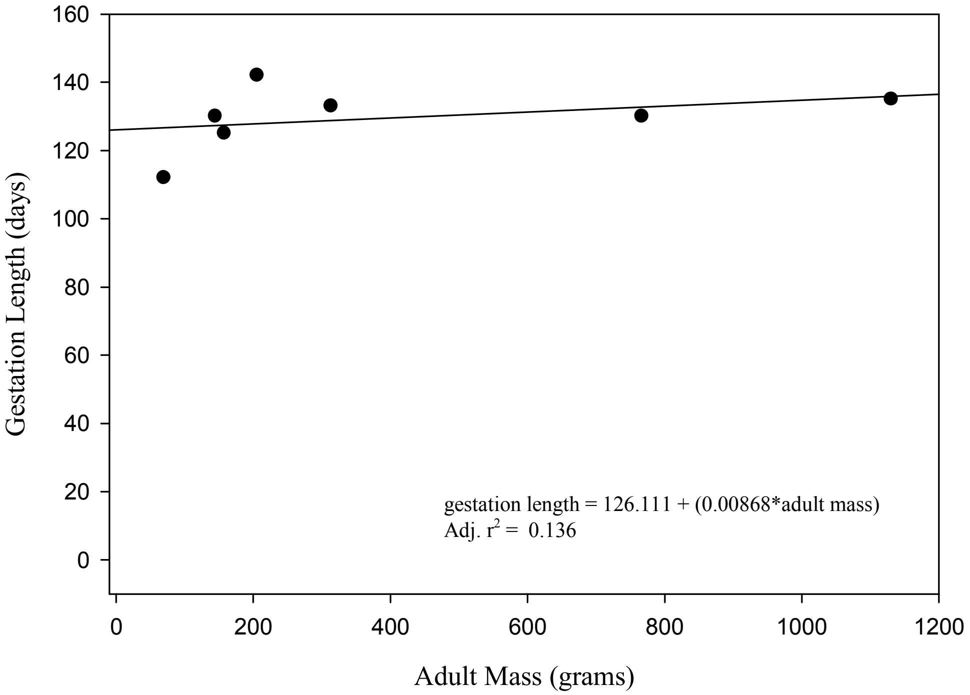


Fig. 9. Gestation length for galagid species regressed onto adult body mass. (Gestation length and adult mass from [Nash et al., 1989]).

Chapter3: Ontogeny of Sexual Size Dimorphism in Galagidae

ABSTRACT

Sexual size dimorphism (SSD) characterizes most mammals in which males use contest competition with other males for mating rights. Across different species, similar degrees of SSD may result from different growth patterns. Even closely related species attain sexual dimorphism through varying ways. Among haplorrhine primates, the ontogeny of SSD is correlated with social organization. Males in species forming single-male/multi-female groups attain larger size primarily through higher growth rate while males in species forming multi-male/multi-female groups attain larger size through longer growth duration (i.e. bimaturism). While SSD is rare among strepsirrhines in general, it is common among galagids. This study examines the ontogeny of SSD in two species of galagids, *Otolemur garnettii* and *Galago senegalensis*. Both species are sexually dimorphic in body mass and reportedly form single-male/multi-female groups. Therefore if galagids follow a pattern similar to that found in haplorrhines, then males of both species should attain larger size through a higher growth rate compared to females. The relative growth rates of males and females of each species were compared using a likelihood ratio test calculating an F-statistic. Raw mass measurements were converted to proportion of adult mass by dividing each individual's mass by its adult mass. Growth rate was then estimated as the proportion of adult mass gained over time. *Go. senegalensis* males exhibit a significantly higher relative growth rate compared to females. No significant difference was found in growth rate for male and female *O. garnettii*. Differences

in growth duration were present in both species with males growing for a longer time than females. The hypothesis is thus not strongly supported for this clade. Possible explanations include the complexity of social interactions of galagids or that selection from other socioecological pressures, such as resource competition, overrides that associated with intrasexual competition.

INTRODUCTION

Sexual selection and sexual size dimorphism

Sexual selection theory posits that intrasexual competition selects characteristics that improve successful contest for mates and leads to sexual dimorphism [Darwin, 1871]. Measures of sexual selection vary. Frequency and intensity of male-male contest, the ability of males to monopolize access to females, as well as inter- and intra-sexual competition for food are all factors that influence the amount of sexual selection and sexual dimorphism a species exhibits [Plavcan, 1999; Plavcan, 2001; Plavcan & van Schaik, 1997]. Sexual dimorphism among primates may be manifested in canine size, coloring or adornments, or, most commonly, body size (sexual size dimorphism or SSD) [Leutenegger & Kelly, 1977]. At its most basic, sexual selection theory posits that mammalian sexual size dimorphism (SSD) is related to male-male contest competition such that increased competition leads to SSD as the larger (e. g. heavier) male has an advantage in agonistic competition [Jarman, 1983; Leigh, 1995; Plavcan, 1999; Plavcan, 2001; Plavcan & van Schaik, 1997]. The ontogeny of SSD in two species of galagids, *Otolemur garnettii* and *Galago senegalensis* was the focus of this study.

Among primates, SSD is relatively common among haplorrhines and rare among strepsirrhines with the exceptions of galagids [Kappeler, 1991; Leigh, 1995; Leigh & Terranova, 1998; Lindenfors & Tullberg, 1998; Plavcan, 2001]. Varying patterns of SSD are found within the primates, most often males are larger than females, rarely, females are larger than males and sometimes males and females are the same size [Badyaev, 2002; Cheverud et al., 1985; Gaulin & Sailer, 1984; Kappeler, 1993; Leigh, 1992b; Leigh, 1995; Leutenegger & Cheverud, 1985; Plavcan, 1999; Plavcan & van Schaik, 1997; Smith & Leigh, 1998]. Additionally, some species exhibit seasonally fluctuating SSD with males being heavier one season but females being heavier another [Dietz et al., 1994; Fietz, 1998]. In *Microcebus murinus*, a seasonal increase in male body mass is correlated with an increase in testes size which is likely related to male-male competition in the form of sperm competition [Fietz, 1998].

Most primates are not sexually dimorphic at birth, but acquire sexual dimorphism postnatally [Badyaev, 2002; Leigh, 1992a, b; Watts, 1985] though this is not universal [Bercovitch et al., 2000]. Processes leading to SSD include differences in rate or length of growth or a combination of the two and may alter male and/or female growth patterns [Watts, 1985]. The ecological and selective factors that favor accelerated growth (high growth rate) are likely different from those factors that favor prolonged growth, and the selective factors that affect male growth are likely different from those factors that affect female growth+ [Leigh, 1992a, b; Leigh, 1995]. Though a simplistic view, generally, female ontogeny is influenced by competition for food while male ontogeny is influenced by competition for mates [Leigh, 1992a, b; Leigh, 1995; Müller & Thalmann, 2000; Wrangham, 1979]. Examination of each of these components contributing to SSD is crucial to understanding the adaptive nature of SSD [Badyaev, 2002; Shea, 1986].

Across different species, similar degrees of SSD may result from very different growth patterns. Even closely related species attain sexual dimorphism through varying ways [Leigh, 1992a, b; Leigh & Shea, 1995; Shea, 1986]. Interestingly, monomorphism may also result from differing growth patterns. While most often monomorphic males and females exhibit similar growth patterns, among some monomorphic species, males may have a higher growth rate, but cease growing earlier compared to females [Leigh, 1992a, b; Leigh & Shea, 1995]. Though rare, this has been reported for *Cercopithecus mitis* [Leigh, 1992a, b].

Socioecological factors and life history variables will influence growth of males and females, possibly in different ways. Studies of haplorrhine primates have suggested that species which form multi-male/multi-female groups (subsequently referred to as multi-male groups) primarily attain SSD via duration differences while those which form single-male/multi-female groups primarily attain SSD through rate differences, with an adolescent growth spurt among males being common[Leigh, 1992a; Leigh, 1995]. When living in multi-male/multi-female groups, it may be adaptive for a male to grow slowly thus delaying intrasexual competition for mates and increasing the time available for learning social skills needed to successfully compete and move up the dominance hierarchy. Conversely, males in single-male groups may be evicted from the group relatively early and abruptly thus increasing the need for males to rapidly attain large size to successfully compete with other males for access to females and food [Leigh, 1992a, b; Leigh, 1995; Plavcan, 2001]. Additionally, males in some species that form single-male/multi-female groups leave the natal group as adolescents and might be, for a time, solitary and exposed to greater predation pressure [Dunbar, 1987; Plavcan, 2001; Pusey & Packer, 1987]. Rapid growth may provide protection from predators as individuals will then be larger when exposed to predation pressures. As females are more often philopatric [Pusey & Packer, 1987], they do not face the same predation pressures as males, and thus do not exhibit as high a growth rate [Leigh, 1992a, b].

A different pattern is found among the strepsirrhines, primarily lemurids, so far studied. SSD is rare within this clade regardless of social system [Kappeler, 1990; Kappeler, 1991; Leigh & Terranova, 1998; Lindenfors & Tullberg, 1998]. For instance, lemurids live in large multi-male/multi-female groups which, among haplorrhines, are often associated with SSD, yet in lemurids they are not. Leigh & Terranova [1998] suggest lemurids lack SSD because they have a short growth period (due to constraints of high seasonality of food) that precludes SSD due to bimaturism. Lemuriforms are faced not only with seasonal unavailability of food resources, but also larger environmental unpredictability as well [Dewar & Richard, 2007; Godfrey et al., 2004; Godfrey et al., 2003; Wright, 1999]. Food resources in Madagascar are extremely irregular being affected by drought, cyclones, and frost. The forests are characterized by longer periods without fruits and other food sources compared to mainland African forests [Dewar & Richard, 2007; Wright, 1999]. Additionally, most lemurids exhibit seasonally synchronized reproduction, so growing for a longer period of time would shorten a male's reproductive lifespan, which would be disadvantageous.

The authors suggest high metabolic costs may prevent rate differences and that it is simply too expensive to grow at any higher a rate. While SSD is generally rare among lemuriforms, there is greater variability in SSD among strepsirrhines than previously thought [Kappeler, 1991]. It is common among galagids (Table V), as well as some lorises (i.e. *Nycticebus pygmaeus*) and cheirogaleids (i.e. *Cheirogaleus major, Microcebus murinus*) [Fietz, 1998; Kappeler, 1991; Nash et al., 1989].

Galagid social organization

Galagids are generally classified as solitary foragers with varying amounts of association between individuals which can include sleeping associations and ranging overlap [Bearder, 1999; Bearder & Doyle, 1974a; Bearder & Martin, 1980b; Charles-Dominique, 1977; Harcourt, 1986c; Harcourt & Nash, 1986a; Honess, 1996; Nash et al., 1989; Nash & Harcourt, 1986; Off et al., 2008; Pullen et al., 2000]. Matriarchies, where an adult female shares her range with her fully adult daughters, appear relatively common [Bearder, 1999; Charles-Dominique, 1979; Nash et al., 1989]. Females tend to be aggressive towards unrelated females and males tend to be aggressive towards other adult males [Charles-Dominique, 1979; Nekaris & Bearder, 2007]. In some instances, males may be tolerant of smaller (presumed younger) males [Bearder, 1999; Bearder & Doyle, 1974a; Harcourt & Nash, 1986a; Nash & Harcourt, 1986; Pullen, 2000; Pullen et al., 2000]. In many cases, males have ranges that are separate from, but overlap the ranges of females in a dispersed social organization [Bearder, 1999; Bearder et al., 1995; Bearder & Martin, 1980b; Charles-Dominique, 1977; Charles-

Dominique, 1979; Müller & Thalmann, 2000]. A male may approach and sniff females within his range, but these associations tend to be brief unless the female is in estrus [Charles-Dominique, 1979]. Female home ranges are generally more stable and focus on food sources while male home ranges are larger, more variable, and dependant on female home ranges [Bearder, 1999; Bearder & Doyle, 1974b; Bearder & Martin, 1980b; Charles-Dominique, 1979; Clark, 1978; Clark, 1985; Doyle & Bearder, 1977; Harcourt, 1986c; Harcourt & Bearder, 1989; Harcourt & Nash, 1986a; Nash, 1984; Nash & Harcourt, 1986; Pimley, 2009; Pimley et al., 2005].

The galagids studied here are *Otolemur garnettii* and *Galago senegalensis*. *O. garnettii* exhibits a dispersed single-male/multi-female social organization where a male's range is larger and overlaps the smaller ranges of multiple females [Fleagle, 1999; Nash & Harcourt, 1986]. The range of a fully adult male rarely overlaps the ranges of other fully adult males [Nash & Harcourt, 1986; Nekaris & Bearder, 2007]. Sleeping groups are generally either solitary or include an adult female and her offspring, rarely, a sleeping group may include an adult male [Nash & Harcourt, 1986].

Little detailed information on social organization exists for wild *Go. senegalensis*. However, field surveys suggest individuals are most often solitary and when encountered in larger groups, only rarely do these groups include more than a single adult male [Haddow & Ellice, 1964]. In recent field surveys, *Go. senegalensis* was found solitary 80% of the time. The age and sex of individuals when found in pairs were not noted [Off et al., 2008]. A captive study of group formation found that aggression and displacement were more common intrasexually as males directed aggression and displacement towards other males and females directed aggression and displacement towards other females [Nash & Flinn, 1978]. These results would be expected in species forming dispersed single-male/multi-female groups. There are data for wild *Go. moholi*. *Go. moholi* and *Go. senegalensis* are comparable in body mass and socioecology and genetic analysis indicates great similarity and a very recent divergence between the two [Masters, 1998; Masters et al., 1994; Nash et al., 1989]. *Galago moholi* was considered a subspecies of *Go. senegalensis* and only fairly recently has *Go. moholi* been detached from *Go. senegalensis* and elevated to species status [Groves, 2001; Grubb et al., 2003; Izard & Nash, 1986; Izard & Nash, 1988]. Like *O. garnettii*, *Go. moholi* exhibit a dispersed single-male/multi-female social organization [Bearder, 1987; Bearder, 1999; Pullen, 2000; Pullen et al., 2000]. Because of the similarities between *Go. sen*egalensis and *Go. moholi*, a similar mating system is assumed for *Go. senegalensis*.

Ontogeny of sexual size dimorphism

Sexual size dimorphism is common in haplorrhine species which are not pair-bonded including both single-male/multi-female and multi-male/multi-female groups. Sexual size dimorphism is absent in lemurids and indriids forming similar social groups. A large sampling of haplorrhines finds that males forming single-male/multi-female groups attain SSD via differences in growth rate while males forming multi-male/multi-female groups attain SSD via differences in growth duration [Leigh, 1992a, b; Leigh, 1995].

Sexual size dimorphism is not entirely lacking among Malagasy primates. Some cheirogaleids exhibit similarities with galagids including nocturnality, dispersed social organization, ranging and sleeping association, and are sexually dimorphic. *Microcebus murinus* tends to spend foraging time solitary, but may sleep in fairly large groups. Except for during the breeding season, these sleeping groups are comprised of females and their offspring. Males can be found in sleeping association when females are in estrus [Martin, 1972b; Martin, 1973]. Unlike many galagids, spatial monopolization of females by males was not evident [Martin, 1972b; Radespiel, 2000; Radespiel et al., 1998; Radespiel et al., 2003]. Little is known of the ontogeny of SSD of cheirogaleids though Blanco et al. [2009b] note there is ontogenetic variation as the smaller *Microcebus* spp. reaches adult mass within one year while *Cheirogaleus* spp. exhibit a reduction in growth rate during hibernation and don't reach adult mass until the second year. Female *M. murinus* mate with multiple males [Radespiel, 2000; Radespiel et al., 1998; Radespiel et al., 2001, 2003]. If a haplorrhine pattern of differences in growth duration leading to SSD in species forming multi-male/multi female groups is present in cheirogaleids, then it is predicted that SSD in this group would be attained via differences in the duration of growth.

As appropriate data for cheirogaleids are largely lacking, galagids, which aren't subject to such environmental harshness, provide an alternate test for the generality of sexual selection theories linking growth patterns and social organization. If selection pressures for dispersed single-male/multi-female groups are similar to those for gregarious single-male/multi-female groups then, for both species studied here, SSD should be attained via differences in growth rate with males exhibiting a higher growth rate than females.

MATERIALS AND METHODS

Datasets

O. garnettii subjects included 43 females and 38 males with known dates of birth. Neonatal masses have been previously estimated as 54.0 grams for males and 48.9 grams for females yielding a pooled average of 51.7 grams (Table VI). Average adult male mass has been previously estimated as 1221.4 grams and adult female mass averages 1064.2 grams. Age at growth cessation (AGC) has previously been estimated as 783 days for *O. garnettii males*, 557 days for *O. garnettii* females (Table VI, Fig. 10). Only measurements prior to the age at growth cessation were used in this analysis. *Go. senegalensis* subjects included 37 laboratory-born individuals, 19 males and 18 females with known dates of birth. Average neonatal masses were previously estimated as 19.9 grams for males and 19.6 grams for females yielding a pooled average of 19.8 grams; adult male mass averages 338.3 grams and adult female mass averages 253.1 grams [Izard & Nash, 1988]. Age at growth cessation (AGC) has previously been estimated as 717 days for *Go. senegalensis* males, and 484 days for *Go. senegalensis* females (Fig. 10). Only measurements prior to the average age at growth cessation were used in this analysis. See Chapter 2 for further description.

Analysis

Intersexual mass differences

SSD has been previously noted for adults of both study species, but absent in neonates [Izard & Nash, 1988; Kappeler, 1991; Nash et al., 1988]. However, Hager and Welker [2001] note that adult body mass of a small sample of captive *O. garnettii* was variable, but not significantly different. The presence (in adults) or absence (in neonates) of SSD was tested using a Mann-Whitney Wilcoxon Rank Sum test on individual mass measurements. For neonatal comparisons, only measurements taken on subjects less than three days old were used. For adult comparisons, the first mass measurement taken after each individual was 3.5 years old was used.

Larger-bodied species tend to grow faster (gain more grams per day) than closely related smaller-bodied species on an absolute scale [Godfrey et al., 2004; Leigh, 1994a] and the same is likely true intraspecifically where males are larger than females. To compensate for intersexual mass differences, each individual's mass measurements were divided by its adult mass and the growth rate calculated as the proportion of adult mass gained per day. For individuals lacking adult mass measurements, species averages were used.

Linear regression

Once raw mass measurements were converted to proportions, data were natural log-transformed and fit with ordinary least squares (OLS) regression of ln(proportion) of adult mass on ln(age) [Smith, 2009; Sokal & Rohlf, 1995; Warton et al., 2006]. Ordinary least squares regression was used as measurement error is asymmetrical and is greater for the mass measurements than for the age measurements [Warton et al., 2006]. A likelihood ratio test using an exact F-statistic was used to compare the sum of squares when a common slope was fitted to pooled data and when a separate regression line was fitted to each sex separately [Sokal & Rohlf, 1995; Warton et al., 2006] using R2.10.0 [R Development Core Team, 2009]. Specifically, comparisons were made between *Otolemur* males and females and between *Galago* males and females.

Piecewise regression

When comparisons were significant, two-segment piecewise regression function in Sigmaplot 11.0 was used to investigate growth differences further. Piecewise regression separates each growth trajectory into two parts at an inflection point. This inflection point is the crossing point where the r^2's of the preceding and succeeding lines are maximized**.** After dividing the data into early growth (data preceding the inflection point) and late growth (data succeeding the inflection point), the F-statistic was used for comparison of sex differences in relative growth rates within each phase for each species. Early growth rates were compared between *Otolemur* males and females and between *Galago* males and females and then late growth rates were compared between *Otolemur* males and females and between *Galago* males and females.

Growth duration

To examine duration differences, 95% confidence intervals were constructed for AGC. Potvin [1993] notes that confidence intervals estimated for bootstrapped estimates may be too small to make comparisons between estimates entirely reliable. Using a smaller number of iterations will yield a larger confidence interval yielding more reliability to the test therefore, 1000 replications were used [Roff, 2006].

RESULTS

Intersexual mass differences

A Mann-Whitney Wilcoxon Rank Sum test of *O. garnettii* male and female neonatal mass found that the sexes are not significantly different in mass ($P < 0.286$, $W_x = 15$, $n = 5, 4$). The same is true of neonatal *Go. senegalensis* males and females (($P < 0.80$, $W_x = 323$, $n = 19, 17$). Comparisons of adult males and females does find significant differences for both *O. garnettii* ($P < 0.009$, $W_x = 95$, $n = 14,11$) and *Go. senegalensis* ($P < 0.001$, $W_x = 238$, $n = 15, 12$). In both species adult males are heavier than adult females.

Linear regression

The test for common slope finds no significant differences between *O. garnettii* males and females in proportional growth rates ($F = 1.8536$, $P<0.1740$), but *Go. senegalensis* males grow proportionately faster than conspecific females ($F = 79.263$, $P<0.001$) (Table VII, Fig. 11).

Piecewise regression

The differences for both species were investigated further using piecewise regression function in Sigmaplot 11.0**.** The inflection points separating early and late growth were 179.4 ± 10.07 days for *O. garnettii* males, 185.4 ± 9.4 days *O. garnettii females*, 177.1 ± 2.4 days for *Go. senegalensis* males, and 139.2 ± 2.8

days for *Go. senegalensis* female. Thus, with the exception of *Go. senegalensis* females, rapid early growth decelerates at approximately the same age while *Go. senegalensis* females begin decelerating considerably earlier (see chapter 4 for further discussion and figures).

Separating the data into early and late growth phases (with the dividing point between the early and late growth phases being the age at the inflection point) and repeating the analysis finds that *Go. senegalensis* males are growing significantly faster than females during the early growth phase (male slope = 0.519 ± 0.012, female slope = 0.457 ± 0.008; F = 38.78, $P < 0.001$), but there is no significant difference found during the late growth phase (male slope = 0.251 ± 0.034, female slope = 0.214 ± 0.024; F = 1.2367, $P < 0.2663$). While no significant rate differences were found for *O. garnettii* when comparing the entire growth period, a significant difference was found during the early phase of growth with *O. garnettii* males growing faster than *O. garnettii* females (male slope = 0.584 ± 0.021, female slope 0.554 ± 0.019; F = 5.5636, $P < 0.019$). No significant difference was found for the *O. garnettii* late growth phase (male slope = 0.234 ± 0.049, female slope = 0.249 ± 0.041; F = 0.096, $P < 0.75$). The later growth phase for *O. garnettii* males is longer than that for females which would lower the slope of the regression line for the overall growth period. This may explain the lack of significant differences in the overall growth period. Early growth is considerably faster and less variable compared to the late growth rate for both *O. garnettii* and *Go. senegalensis*. Variability is not a result of sample size as there are at least twice as many measurements for the late growth period than for the early growth period for both males and females.

Growth duration

For both species, the average male AGC falls outside of the 95% CI for females and the average female AGC falls outside of the 95% CI for males. Growth duration differences are present for both *O. garnettii* and *Go. senegalensis* with males growing for a longer period of time than females.

In sum, SSD is absent in neonates and present in adults of both species. There are no significant differences between male and female *O. garnettii* in the proportion of adult mass gained per day. *Go. senegalensis* males grow proportionately faster than females, especially during the early stages of growth. Differences in growth duration are present in both species.

DISCUSSION

Previous results for haplorrhine species suggest that SSD in species forming single-male/multi-female groups arises via differences in growth rates with males growing at a higher rate compared to females. These results are not entirely corroborated by the current study of galagids. Though both species are dimorphic as adults, significant overall relative growth rate differences were found for *Go. senegalensis*, but not for *O. garnettii*. The higher growth rate in *Go. senegalensis* was present during the early rather than the late growth phase. A higher male growth rate during the early growth phase was present for *O. garnettii* as well. This pattern is contrary to that reported for haplorrhines where females had slightly higher early growth rates compared to males [Leigh, 1992a; Leigh, 1995]. It is noteworthy that Leigh's analysis compared absolute growth. However, the same intersexual pattern is found for *O. garnettii* and *Go. senegalensis* whether comparing absolute mass gained (see Chapter 2, Table 3) or comparing proportion of adult mass gained. In both comparisons (absolute rate and relative rate), no rate differences are found for *O. garnettii* but male *Go. senegalensis* grow at a significantly higher rate than females. This suggests that the mass difference between males and females does not significantly impact rates of growth.

Growth duration differences, with males growing for a longer duration than females, were present in the two galagid species studied here. Both growth patterns, SSD arising from bimaturism alone and SSD arising from a combination of duration and rate differences are found in haplorrhines with the latter pattern being more common [Leigh, 1992a, b]. The hypothesis linking social organization with intersexual growth differences is not, therefore, clearly supported.

Neither *Go. senegalensis* or *O. garnettii* are sexually dimorphic at birth. For *Go. senegalensis*, these results corroborate those of Izard & Nash [1988]. Both species are sexually dimorphic as adults so SSD arises post-natally, a pattern common for primates [Badyaev, 2002; Leigh, 1992b; Watts, 1985]. The commonly used practice of calculating SSD as female mass as a proportion of male mass (female mass/male mass) shows that, on average, *O. garnettii* females are 87.1% and *Go. senegalensis* females are 74.8% of their male counterparts. The degree of SSD usually scales with body mass for anthropoids [Leutenegger &

Cheverud, 1982; Lindenfors & Tullberg, 1998; Ravosa et al., 1993; Rensch, 1959; Smith & Cheverud, 2002], but not strepsirrhines [Kappeler, 1991; Smith & Cheverud, 2002]. A similar pattern is found here as the larger *O. garnettii* is less sexually dimorphic than *Go. senegalensis*.

Leigh [1992a; 1992b] notes that for haplorrhines in general, the length of primate female growth period is about 90% of the length of the male growth period and that for dimorphic species, female growth duration is about 80% of the male growth duration. For these galagids, on average, the length of the female growth period is about 71% of the length of the male growth period for *O. garnettii* and 68% of the length of the male growth period for *Go. senegalensis*. Leigh's [1992a; 1992b] method of assessing duration differences was subtracting female AGC from male AGC. Using this method, duration differences are present for both *O. garnettii* (males grow approximately 7.5 months longer than females) and *Go. senegalensis* (males grow approximately 7.8 months longer than females). Comparison of the 95% confidence intervals for age at growth cessation (AGC, estimated in Chapter 2) shows that the durations are significantly different between sexes of each species. These results accords with many previous studies on the ontogeny of SSD which note that bimaturism is common among primates [see, for instance Leigh, 1992a; Leigh, 1992b; Leigh, 1995; Leigh & Terranova, 1998; Leutenegger & Cheverud, 1982; Ravosa & Daniel, 2010; Ravosa et al., 1995; Shea, 1983; Shea, 1986; Taylor, 1997; Watts, 1985].

Social Organization

Though initially galagids were often described as “solitary” with the assumption that their social organization was less complex than that of gregarious species [Bearder & Doyle, 1974a], it is now understood that “solitary” does not accurately describe their social organization. Instead, a variety of social organizations are reported within the galagid clade including dispersed pairs, dispersed single-male/multi-female groups, and dispersed multi-male/multi-female groups [Bearder, 1999; Bearder et al., 2003; Harcourt, 1986c; Harcourt & Nash, 1986a; Müller & Thalmann, 2000; Nash & Harcourt, 1986; Nekaris & Bearder, 2007; Pullen et al., 2000]. While there is a general correspondence between a species’ social organization and its mating system, greater complexity exists and social and spacing systems do not always reveal mating systems [Kappeler, 2002].

Correlating social organization with growth may be an oversimplification as there are several components to social organization. Social systems, including behavior and relationships within the group, spacing and ranging patterns, sleeping associations, and mating systems all contribute to a species’ social organization [Sterling et al., 2000; Sterling & Radespiel, 2000]. Social organizations are difficult to establish for these small nocturnal species and many studies have relied on examination of ranging patterns and sleeping associations to assess social organization [Sterling et al., 2000]. Social systems, ranging patterns and sleeping associations have been described for several galagids (Table V) [Bearder & Martin, 1980b; Charles-Dominique, 1974, 1977; Charles-

Dominique, 1979; Clark, 1978; Clark, 1985; Harcourt, 1986c; Harcourt & Bearder, 1989; Harcourt & Nash, 1986a, b; Kappeler, 1997b; Nash & Harcourt, 1986; Pullen & Bearder, 2004; Pullen et al., 2000]. While these methods are useful for examining the social and spacing systems, they shed little light on the mating system which would require data on reproductive behaviors and paternity [Bearder et al., 2003; Müller & Thalmann, 2000; Nekaris & Bearder, 2007]. These data are largely lacking for most galagids.

Paternity data are available for only one species, *Go. moholi* [Pullen & Bearder, 2004; Pullen et al., 2000], though mating systems for other species have been inferred through examination of relative testes size. Across primates, species in which females mate with multiple males (promiscuous mating system *sensu* [Kappeler, 2002; Kappeler, 1997a, b]) have relatively large testes compared to species in which females mate with a single male [Dixson, 1987; Dixson & Anderson, 2004; Harcourt et al., 1995; Harcourt et al., 1981; Kappeler, 1997b; Radespiel et al., 2001]. Kar Gupta [2008]reports that paired *Loris tardigradus* males have larger testes compared to unpaired males and roaming males, but notes that this may reflect post-copulatory sperm competition and extra-pair copulation with roaming males. Galagids with relatively large testes include *Galagoides demidovii*, *Go. moholi*, *Go. senegalensis*, *O. garnettii*, and *O. crassicaudatus* [Dixson & Anderson, 2004; Harcourt et al., 1995] suggesting a promiscuous mating system and a lack of exclusive mating rights by the resident male.

A primary assumption of this study was that both species, like many galagids, have a dispersed single-male/multi-female social organization as field studies report that adult males rarely have overlapping territories [Charles-Dominique, 1977; Clark, 1985; Harcourt, 1986c; Harcourt & Nash, 1986a; Honess, 1996; Nash et al., 1989; Nash & Harcourt, 1986] and that a hypothesis linking social organization and growth could be tested. Strong association between single-male/multi-female groups and higher male growth rate has been demonstrated for haplorrhines. However, it is clear that the social organization of galagids is highly complex and that factors other than ranging patterns and whether or not male territories overlap will influence mating success.

One complicating factor is that several galagid species (e.g. *Gs. demidovii*, *Gs. cocos*, *Go. moholi*) reportedly have two types of adult males: larger "A" males and smaller, presumed younger, "B" males. B males may be tolerated by an A male, but other A males are aggressively excluded [Bearder, 1987; Bearder & Doyle, 1974a; Bearder & Martin, 1980b; Charles-Dominique, 1977; Harcourt & Nash, 1986a; Nash, 1983; Pullen & Bearder, 2004; Pullen, 2000; Pullen et al., 2000].

The assumption of intrasexual contest competition for mates is that larger males have an advantage in physical combat and therefore larger males have higher reproductive success. This has clear implications for the link between growth patterns and social organization. *Galago moholi* A males had a higher number of copulations compared to the B males [Pullen et al., 2000]. However, the smaller B males may pursue an alternate scramble competition reproductive strategy where the male that first locates a receptive female would have a "finder's advantage" [Alcock, 1980; Sussman & Garber, 2007]. Since B males are tolerated within resident A male ranges, they could mate opportunistically when the A male is in a different part of his range [Pullen, 2000; Pullen et al., 2000]. Sleeping associations also have implications for scramble competition especially for species in which a female's window of receptivity is very small. In a study of *Go. moholi*, a small (95 gram) B male fathered the most offspring [Pullen, 2000] though he was never observed copulating with any females.

This calls into question the assumption underlying sexual selection theory that bigger males are often more reproductively successful. Whether such a high reproductive success for smaller males is an artifact of the small sample size of Pullen' work, the one study with paternity data from the field for a galagid, or is common requires further studies of paternity. Field studies of *O. garnettii* note that larger, older males tolerate younger smaller males, a situation similar to A and B males [Nash & Harcourt, 1986].

An additional complicating factor is that adult female galagids may share either territories or adjacent territories with their adult daughters such that a male's territory, if it overlaps these matriarchal territories, might include his adult daughters [Müller & Thalmann, 2000], assuming he lives long enough to have reproductively active daughters. This may be a poor assumption in some species. It is possible that the tolerance of other adult males may be related to incest avoidance. A male can increase his reproductive success if non-related males are tolerated and allowed to mate with a "resident" male's daughters. Such a scenario blurs the line between single-male/multi-female and multi-male/multi-female groups. Further study is warranted to gain a clear understanding of the social, spatial, and mating structure of this diverse clade with the focus being on mating systems.

If the mating system of *O. garnettii* is better described as promiscuous or multi-male/multi-female (as implied by relative testes size [Dixson, 1995]), then SSD via bimaturism would be expected for this species. As female *Go. moholi* mate with both A and B males, multi-male/multi-female best describes their mating system. Sexual size dimorphism in *Go. moholi* also arises through bimaturism rather than absolute rate differences [O'Mara et al., in review]. This lack of absolute rate differences corroborates results from haplorrhines with similar promiscuous systems. *Go. senegalensis* attains SSD via rate (both absolute rate and relative rate) and duration differences. In haplorrhines, rate differences are found in species with single-male/multi-female mating systems. While field observations and paternity data for *Go. senegalensis* are largely lacking, the relatively large testes size of this species suggest a promiscuous mating system [Harcourt et al., 1995] and the results of this study are unexplained by a hypothesis of social organization as it pertains to mating system.

Predation Risk

The hypothesis linking growth and social organization references not only intrasexual competition for mates, but predation risk as well. The hypothesis holds that males in single-male/multi-female groups would benefit from rapidly attaining adult size as they experience a sudden increase in intrasexual competition and rapid expulsion from the group upon reaching adulthood (see, for instance, [Dittus, 1979; Rajpurohit & Sommer, 1991; Rajpurohit & Sommer, 2002; Robinson, 1988]). Once expelled, they are solitary and thus face a sudden increase in predation risk [Rajpurohit & Sommer, 2002]. Rapid growth could offset this increased predation risk and, therefore, be adaptive [Leigh & Shea, 1996]. If both species face similar predation risk, then results from this study are mixed.

Predation is size-specific and smaller-bodied species face greater predation risk than larger-bodied species. Estimated predation rates of less than 5% of the population are common for larger-bodied primates compared to rates of greater than 15% of the population for smaller primates [Cheney & Wrangham, 1987]. While data on predation rates on galagids are limited, the largest galagid, *O. crassicaudatus*, is not heavily predated possibly due to its large body size compared to other lorisoids [Clark, 1985]. Nash & Harcourt [1986] note that "… larger body size and consequent protection from many predators …" may partially explain differences in sociality between sympatric *O. garnettii* and *Gs. cocos* (formerly *zanzibaricus*).

Following this logic, it could be hypothesized that *O. garnettii*, being less susceptible to predation compared to the smaller *Go. senegalensis*, do not face the same selection pressures leading to rapid increase in size to offset predation risk. The smaller *Go. senegalensis*, if facing greater predation risk, would benefit from rapidly attaining larger size prior to emigrating. Results of this study are consistent with this scenario as differences in growth rate are found for *Go.*

senegalensis, but not *O. garnettii* males compared to females. Data on predation rate, predation risk, and predation schedules, are needed to test this. *Go. moholi*, which is smaller than *Go. senegalensis*, exhibits a pattern like *O. garnettii* where SSD is attained by duration rather than absolute rate differences in growth [O'Mara et al., in review] suggesting that predation risk is an insufficient explanation for the differences in growth rate for *Go. senegalensis*.

Predation risks and schedules for diurnal gregarious haplorrhines are likely very different from the predation risks and schedules for nocturnal solitary galagids. Haplorrhine infants are carried clinging to their mothers and as adults, live in cohesive social groups [Kappeler, 1998; Ross, 2001]. Solitary time is generally limited to emigration thus, for haplorrhine species, predation risk varies throughout the life cycle in a pattern suggested by the hypothesis linking social organization and growth as it relates to predation risk. Haplorrhine males exhibit higher growth rates, compared to females, near the time of male emigration suggesting a link between an increase in growth rate and an increase in predation risk [Leigh, 1992a; Leigh, 1995]. *Go. senegalensis* growth rates differ during the early phase of growth rather than during the later phase of growth. Also, galagids spend a good deal of time solitary throughout the lifecycle [Kappeler, 1995; Kappeler, 1996; Kappeler, 1998; Kappeler & Heymann, 1996; Ross, 2001] making it unlikely that predation risk increases significantly during emigration.

During night time activity, most galagid infants are parked while their mother forages alone [Kappeler, 1995; Kappeler, 1996; Kappeler, 1998; Kappeler & Heymann, 1996; Ross, 2001]. She may make frequent visits to nurse the infant, and may move the infant several times during the night, but for the most part, infants are solitary during the active period [Bearder, 1987]. As the infants age, they may follow their mothers during foraging, but begin to forage farther and farther away from her [Bearder, 1987]. During the day, most galagids seek protection by sleeping in hidden or protected sites such as nests, tree hollows, or within thorny leaves [Bearder et al., 2003; Kappeler, 1998]. As adults much of their active foraging time is spent solitary. During the night, galagids rely on anti-predation strategies such as crypsis, vigilance and rapid escape, and more rarely, mobbing [Bearder, 1987; Cheney & Wrangham, 1987; Nash, 2007]. Solitary foraging, promoting crypsis, itself may be an anti-predation strategy for these smaller, nocturnal species [Wrangham, 1987].

None of these anti-predation strategies rely on increased size and instead, decreased size may be more beneficial (for instance with crypsis as a strategy). If the assumption that the rapid increase in predation pressure is what drives the rapid growth of males among haplorrhines forming single-male/multi-female groups, a similar pattern would not necessarily be expected for galagids nor for other nongregarious nocturnal species.

Dietary Considerations

The pathway to SSD varies between these closely related species. Both species exhibit differences in growth duration, but *Go. senegalensis* also exhibits rate differences while *O. garnettii* does not. This suggests that sexual selection theory relating social organization and growth is not generally applicable to this clade and that other socioecological factors may override, or act in concert with, sexual selection pressures. One possible explanation is found in the study of the ontogenetic correlates of diet by Leigh [1994a; 1995] which examined growth of 45 species of haplorrhines. Results showed that diet was correlated not only with differences in growth rates between species, but also with differences in growth rates between sexes within species.

Because foliage is a reliable food source compared to fruit, both in space and in time, there is little feeding competition, both intersexually and intrasexually, so there is less advantage to growing larger [Janson, 2003; Leigh, 1992a; Leigh, 1994a, 1995; Taylor, 1997]. Sexual dimorphism among folivores should arise by rapid growth and early cessation of growth of females due to the reduction of feeding competition. Males, driven by sexual selection, will continue to grow for a longer period of time [Janson & van Schaik, 1993; Leigh, 1995; Leigh & Shea, 1995; Taylor, 1997]. It is suggested that generally, variation in female growth patterns is largely the product of natural selection and resource variability while variation in male growth patterns may be largely the product of sexual selection with minor role for natural selection [Leigh, 1992b; Leigh & Shea, 1995; Wrangham, 1979]. Such a pattern has been found in a large, diverse sampling of haplorrhines.

For example, like other folivorous haplorrhines, both male and female *Gorilla* exhibit a relatively high growth rate compared to more frugivorous hominoids. SSD is attained through both growth duration and absolute growth rate differences, specifically, a male adolescent growth spurt [Leigh, 1995; Leigh & Shea, 1996; Shea, 1986]. Female *G. gorilla* cease growing earlier than expected for their body mass, based on comparisons with *P. troglodytes*. This shortened female growth period is the biggest factor in the high degree of SSD for *Gorilla*. Adult females can 'afford' to be small as large size isn't needed for interfemale feeding competition as a result of folivory. While male *Gorilla* don't need to compete for food, they do need to compete for females. Extended growth duration and a higher growth rate lead to increased male size, which is possible due to their folivorous diet, and necessary due to high intermale competition. Adult *Gorilla* SSD is, therefore, the result of natural selection on increased growth rate, early maturation for females and sexual selection for increased size for males [Leigh & Shea, 1995; Leigh & Shea, 1996; Plavcan, 2001]. A similar pattern might be seen in galagids.

Gums are similar to foliage in that both are a comparatively constant food resource (see Chapter 4). *Go. senegalensis* are gummivorous while *O. garnettii* are frugivorous. Like *Gorilla* females compared to *Pan* females, *Go. senegalensis* females appear to cease rapid growth, (as indicated by the inflection point separating high early growth from decelerating later growth), relatively early compared to *O. garnettii*. Growth differences between *Go. senegalensis* and *O. garnettii* are similar in pattern to those between folivorous *Gorilla* and more frugivorous *P. troglodytes* as *Go. senegalensis*, with a presumably more reliable food source, shows a greater level of SSD (*Go. senegalensis* females are 74.8% of male mass while *O. garnettii* females are 87.1% of male mass) and females possibly cease growing relatively earlier. Also, like gorillas, *Go. senegalensis*

SSD arises through both duration and rate differences. Both growth and rate differences are responsible for SSD in *Pan* as well.

Growth patterns of *Go. moholi*, which is gummivorous, are more similar to *O. garnettii* than to *Go. senegalensis*. Females are 86% of male mass and SSD is attained through bimaturism only [O'Mara et al., in review].

The lack of similarity of ontogeny of SSD for *Go. senegalensis* and *Go. moholi* is puzzling. These species are similar in body mass and in many social, ecological, and life history variables [Izard & Nash, 1988; Nash et al., 1989]. One notable difference is litter size. *Go. moholi* regularly produces twins while singletons are more common for both *Go. senegalensis* and *O. garnettii* [Izard & Nash, 1988; Izard & Simons, 1986a; Nash & Harcourt, 1986]. The effects of litter size on growth rate for galagids is largely unknown and previous studies of the effects of litter size on individual growth rates for haplorrhine primates have yielded differing results, sometimes within a single species. In some instances twins had a higher individual growth rate compared to singletons and in some instances the opposite pattern was found [Benirschke & Miller, 1981; Ellsworth & Andersen, 1997; Jaquish & Tardif, 1993; Jaquish et al., 1997; Tardiff et al., 2001]. For *Callithrix jacchus*, maternal size was an interacting factor as twins of smaller mothers had lower individual growth rates compared to singletons while twins of larger mothers had higher individual growth rates compared to singletons [Tardif et al., 2002]. Intersexual growth rate differences for *Go. senegalensis* were found in the early growth phase when infants were nursing. It is possible *Go. moholi* mothers simply cannot support a high growth rate for two infants and that early growth rates are therefore constrained. Following this assumption, gummivory may be generally associated with high growth rate, especially for males, but energetic constraints of twins limits its expression in *Go. moholi*. This limited sampling of galagids indicates that *Go. senegalensis*, with SSD arising through both growth rate and duration differences, is unusual. Much more data from additional galagid species are needed to fully test this assertion.

This study sought to uncover an association between growth and social organization for galagids and hypothesized that both species would attain SSD via higher growth among males. Wide support for such a link is found among haplorrhines, but not lemurids. Results are mixed for galagids. The hypothesis tested here postulates that slow growth is advantageous for males in multi-male/multi-female groups to delay intrasexual competition and that rapid growth is advantageous for single-male/multi-female groups to offset intrasexual competition risk and predation risk. However, slow growth may be beneficial for males in single-male/multi-female groups as well when these smaller, peripheral males are tolerated by the resident males.

As hypothesized, *Go. senegalensis* attained SSD via differences in growth rate, but *O. garnettii* did not. Clearly divergent reproductive strategies cloud the purported link between growth and social organization as does the lack of clear correspondence between spatial systems, social systems, and mating systems within species. Also, differences in these systems between species make it difficult to disentangle possible causal factors of growth differences. Whether these results are due to the complexity of social interactions for these species, whether galagids face different selection pressures related to intrasexual competition or predation, or whether other socioecological pressures, such as those related to diet, are overriding pressures related to sexual selection will require further study. The final possibility is examined in greater detail in the following chapter.

TABLE V. Summary of galagid sociality characteristics.

Species	Ranging Patterns	Sleeping Association	Matriarchies	% Time Social	A and B males	SSD	Citation
Gs. orinus		At least 1-3		10			[Honess, 1996; Honess & Bearder, 1996]
Gs. rondoensis		At least 3		16			[Honess, 1996; Honess & Bearder, 1996]
Gs. demidovii	MM overlap FF overlap MF overlap (central M overlaps one or more F; other M may have access to F)	2-10 F with offspring M often sleep alone	Present	25	Present	Present	[Charles-Dominique, 1977; Kappeler, 1991]
Gs. thomasi	MM overlap FF overlap MF overlap	1-5		25			[Charles-Dominique, 1977]
Gs. udzungwensis		MF pair with offspring		8			[Honess, 1996; Honess & Bearder, 1996]
Gs. cocos	MM overlap (slight) FF overlap MF overlap	M sleeps with 1-2 F and offspring	Present		Present?	Present	[Harcourt, 1986a; Harcourt, 1986c; Harcourt & Bearder, 1989; Harcourt & Nash, 1986a; Nash, 1984]
Gs. granti		4-5 individuals		8			[Honess, 1996; Honess & Bearder, 1996]
Go. moholi	MM overlap FF overlap MF overlap	FM (M never together, but with 2 or more F offspring)	Present	6-18	Present	Present	[Bearder & Doyle, 1974a, b; Bearder & Martin, 1980b; Doyle & Bearder, 1977; Harcourt & Bearder, 1989; Pullen & Bearder, 2004; Pullen et al., 2000]
Go. senegalensis	Groups of 1-3	Up to 3	Present	19		Present	[Haddow & Ellice, 1964; Nash et al., 1989; Off et al., 2008]
E. pallidus		At least 1-4					[Nekaris & Bearder, 2007]
S. gabonensis	FF overlap MF overlap	2-4?	Present	15			[Charles-Dominique, 1977]
E. elegantulus		1-7 (F sleep in groups; sometimes M sleep with F)	Present	24			[Charles-Dominique, 1977]

Species	**Ranging Patterns**	**Sleeping Association**	**Matriarchies**	**% Time Social**	**A and B males**	**SSD**	**Citation**
S. alleni	FF overlap (58%) MF overlap (31%) MM 'extremely aggressive' towards each other	At least 1-3 (Adults usually sleep alone; sometimes F sleep together)		.6-30			[Pimley, 2009; Pimley et al., 2005]
O. garnettii	MM overlap (different age classes) FF overlap (different age classes) MF overlap (extensive overlap)	1-4 Adults may sleep alone or MF with offspring	Present	Up to 20		Present?	[Bearder & Doyle, 1974a; Harcourt & Nash, 1986a; Honess, 1996; Nash, 1984; Nash & Harcourt, 1986]
O. crassicaudatus	MF overlap M probably exclude other M (age-graded tolerance) F probably exclude other Fs	1-4 MF and offspring	Present	20		Present	[Bearder & Doyle, 1974a; Clark, 1985; Doyle & Bearder, 1977; Honess, 1996]

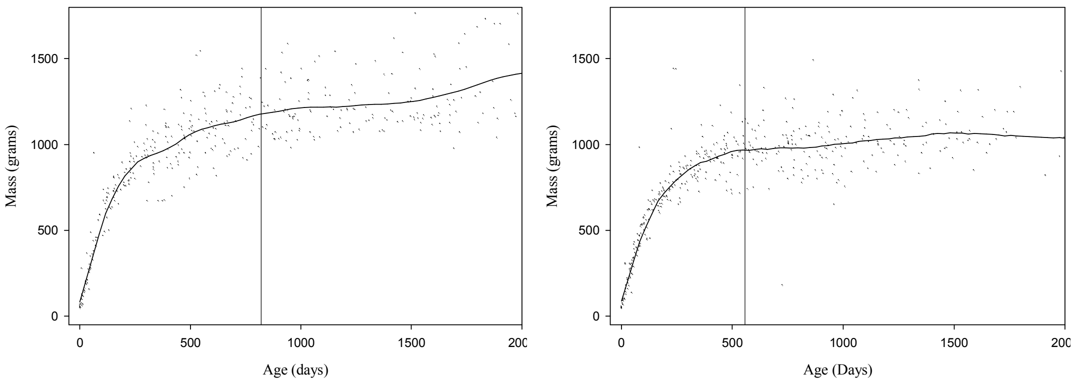
TABLE VI. Summary of growth parameters (See Chapter 2).

	Neonatal Mass (SEM) (grams)	Adult Mass (SEM) (grams)	AGC (SEM) (days)	95% CI
O. garnettii males	54.0 (3.70) (n = 5)	1221.4 (36.4) (n = 14)	783.2 (11.73) (n = 38)	759.74 – 806.66
O. garnettii females	48.9 (2.53) (n = 4)	1064.2 (40.74) (n = 11)	557.0 (3.78) (n = 43)	549.44 – 564.56
O. garnettii pooled	51.7 (2.38) (n = 9)	1152.3 (30.98) (n = 35)	714.0 (8.29) (n = 81)	697.42 – 730.58
Go. senegalensis males	19.6 (0.95) (n = 19)	338.3 (20.19) (n = 12)	717.4 (4.99) (n = 19)	707.42 – 727.38
Go. senegalensis females	19.6 (0.55) (n = 17)	253.1 (11.23) (n = 15)	484.0 (2.94) (n = 18)	478.12 – 489.88
Go. senegalensis pooled	19.6 (0.37) (n =36)	287.4 (13.55) (n = 27)	710.1 (3.70) (n = 37)	702.7 – 717.5

TABLE VII. Ordinary least squares regression comparing the slope of males and females for each species. Slope = regression of ln (proportion) of adult mass on ln (age).

	Slope (SEM)	**95% CI**	**r^2**	**Significance**
O. garnettii males	0.504 (0.008)	0.488 - 0.519	0.905	NS
O. garnettii females	0.499 (0.008)	0.482 - 0.515	0.934	
Go. senegalensis males	0.515 (0.009)	0.498 - 0.533	0.954	P>.001
Go. senegalensis females	0.473 (0.009)	0.455 - 0.491	0.935	

Otolemur garnettii males *Otolemur garnettii* females



Galago senegalensis males *Galago senegalensis* females

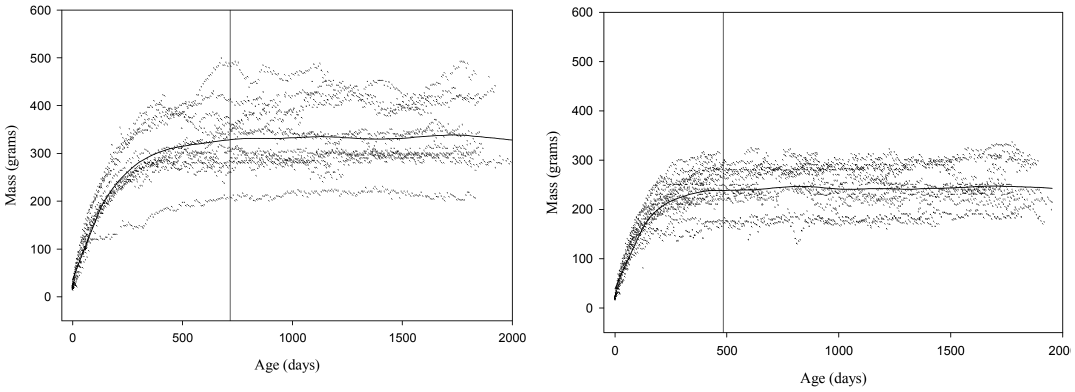
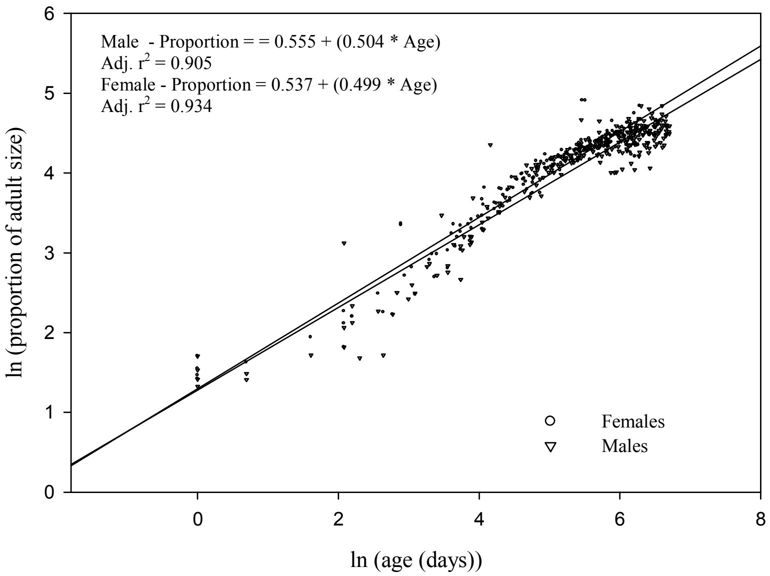


Fig. 10. Loess estimated growth curves fit for male and female galagids. Vertical lines are placed at the bootstrapped estimated age at growth cessation (AGC).

O. garnettii



Go. senegalensis

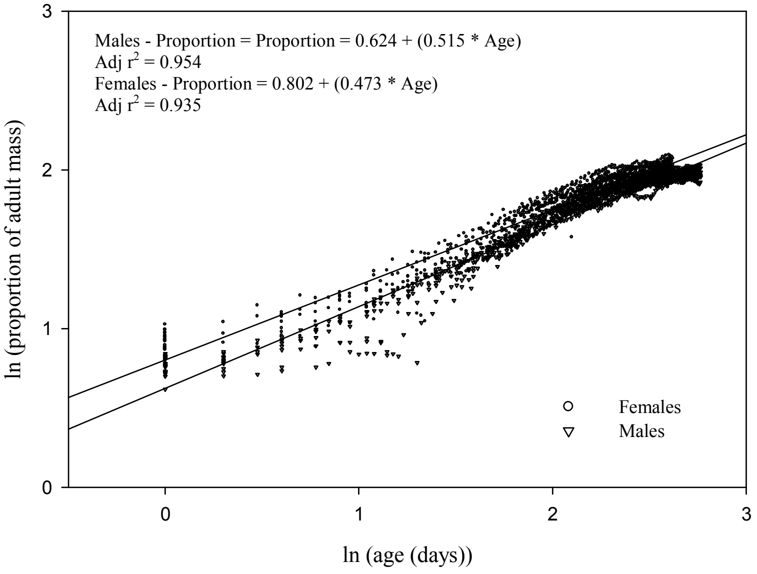


Fig. 11. Ordinary least squares regression comparing males and females.

Dissertation Chapter 4: Ecological Risk Aversion Hypothesis and Gummivory

ABSTRACT

This study compares the relative growth rates of *Galago senegalensis* and *Otolemur garnettii* as a test of the ecological risk aversion hypothesis (RAH). The RAH suggests that the low growth rate in primates, as compared to other mammals, is an adaptation offsetting starvation risk that is associated with seasonal food shortages. Thus, since foliage is less seasonal and therefore generally available year-round, species relying of foliage should grow faster than species relying on more seasonal resources such as fruit. Studies of the growth patterns of numerous haplorrhine species have provided support for this hypothesis while studies of lemuriforms have not. As gums, like foliage, are generally available year-round, the RAH posits that gummivorous galagid species will grow faster than frugivorous galagid species. This hypothesis was tested by comparing the relative (proportional to adult mass) growth rates of *Galago senegalensis*, a gummivore, with the growth rate of *Otolemur garnettii*, a frugivore. Tests for common slope found no significant growth rate differences between *Go. senegalensis* males and *O. garnettii* males, but that *Go. senegalensis* females have a lower growth rate compared to *O. garnettii* females thus the ecological risk aversion hypothesis is not supported. *O. garnettii* infants are weaned during the dry season when competition for resources is presumably high while *Go. senegalensis* infants are weaned during the wet season when food is abundant. The results of the current study might be explainable when integrating both natural and sexual selection theories. As *Go. senegalensis* females

experience low feeding competition both at weaning and, presumably during adulthood, they can grow slowly and cease growing at a relatively smaller mass. *O. garnettii* females face greater competition for food both during weaning during the dry season and as adults relying on a more seasonal food resource. Under these conditions, selection for rapid growth to attain larger mass at weaning could be advantageous.

INTRODUCTION

Primate diets

Primates consume a wide variety of foods including fruit, nuts, seeds, leaves, stems, flowers, roots, bark, fungi, invertebrates, vertebrates (including other primates), gum, and sap [Fleagle, 1999; Lambert, 2007; van Schaik & Brockman, 2005]. Diet has extensive repercussions for an animal's biology. Diet is related to an animal's morphology (e.g. body size, tooth and jaw morphology, gut morphology, etc.), life history (e.g. age at sexual maturity, litter size, interbirth interval, etc.) and socioecology (e.g. social organization, group size, density, range size, etc.) as well as ontogenetic and developmental patterns [Fleagle, 1999; Harding, 1981; Hladik, 1979; Kay & Covert, 1984; Lambert, 2007; Oates, 1987; van Schaik & Brockman, 2005]. Variation in diet occurs not only between species, but within species as well. Intraspecifically, diet may vary by season, between populations, between individuals of different sexes, and between individuals of different age-categories [see, for instance, Altmann, 1991, 1998; Boinski & Fragaszy, 1989; Chapman et al., 2003; Cords, 1986; Gautier-Hion, 1980; Harcourt, 1986b; Harding, 1981; Hemingway & Bynum, 2005; Herrera & Heymann, 2004; Lambert, 2007; Leigh, 1994a; Masters et al., 1988; Nakagawa et al., 1996; Overdorff et al., 1997; Ravosa, 2007; Whitten, 1983]. This study examined associations between variation in dietary category and growth rates for two species of galagids, *Otolemur garnettii* and *Galago senegalensis*.

Most primates are omnivorous and consume a variety of food making it difficult to assign any specific primate species to a single dietary category

[Harding, 1981; Kay & Covert, 1984; Lambert, 2007]. However, broad primate dietary categories, relying on the proportion of food types consumed, include frugivory, folivory, and insectivory. Recent and more fine-grained analyses find that these dietary categories often obscure the dietary variability present, yet at the same time, are often associated with other aspects of socioecology and life history.

Ripe fruit is considered a "high quality" food because it is easily digested and high in carbohydrates and thus, calories [Fleagle, 1985; Lambert, 2007]. However, fruit is low in protein and primarily frugivorous primates tend to supplement their diet with insects or leaves, depending on their body size. Foliage is considered a low-quality food partially due to the structural components which are difficult to digest and to secondary compounds [Hemingway & Bynum, 2005; Leigh, 1994a]. Consequently, large quantities of leaves must be consumed to ensure sufficient nutrition. Folivorous primates exhibit morphological dietary adaptations to processing and digesting leaves including high shearing crests on molars, sacculated stomachs, and enlarged cecum and colon leading to increased gut capacity and gut transit time [Fleagle, 1999; Hemingway & Bynum, 2005; Hladik, 1978; Leigh, 1994a]. Similar to foliage, insects have an exoskeleton that requires shearing to process. Insects are also high in protein. While insects are high in nutrition, they are small in size and are sparsely and unpredictably distributed compared to foliage. Additionally, some insects are noxious or poisonous which pose other problems for consumption and digestion [Fleagle, 1985; Lambert, 2007].

Feeding proficiency

Feeding proficiency varies throughout the life cycle. Infant resources are provided by the lactating mother so selection pressures operating on her feeding proficiency are important during this phase of the lifecycle. Following weaning, these sub-adults need to successfully obtain and process food on their own [Altmann & Alberts, 1987; Ross, 2003]. Reports are mixed as to foraging efficiency and competency of subadults. Janson & van Schaik [1993] note that juveniles spend more time foraging and are less successful compared to adults. For instance, reduced foraging success for juveniles compared to adults was reported for *Cercocebus* [Waser, 1977], *Callicebus* [Kinzey, 1977], *Tarsius* [Roberts, 1994], *Trachypithecus* [Ossi-Lupo & Koenig, 2010], and *Pongo* [Jaeggi et al., 2010]. Additionally, juvenile orangutans appear to have reduced digestive efficiency compared to adults [Knott, 2010] adding another dimension to the obstacles faced by juveniles as they try to acquire sufficient nutrition. Reduced foraging proficiency may be due to skill constraints if food is difficult to process, or size constraints if strength is required to process it [Fragaszy & Bard, 1997; Tan, 2009]. Food toughness was the biggest factor limiting foraging ability for *Trachypithecus*. Young juveniles had the lowest rates of intake followed by older juveniles and adults indicating size was important [Ossi-Lupo & Koenig, 2010]. Adult *Hapalemur simus* forage more efficiently for bamboo shoots and culm piths. Juveniles, possibly mechanically constrained by smaller size, spend more time scavenging for scraps discarded by adults [Tan, 2009].

In contrast, Watts [1988] reports that juvenile gorillas forage for the same amount of time as adults. Juvenile *M. fuscata* spend the same amount of time feeding as adults [Hashimoto, 1990; Hashimoto, 1991] and young *Saimiri*, *Cebus* and *Cercopithecus* forage as competently as adults well before adulthood [Joffe, 1997]. While more information regarding foraging proficiency of juveniles is needed, for many species, during times of food scarcity, more juveniles die than either infants or adults suggesting they lack the foraging skills of adults [Bogin, 1999]. Gibbons (*Hylobates lar*) had the highest mortality rate immediately after weaning compare to earlier and later parts of the life cycle supporting this [Savini et al., 2008]. Strategies leading to survival of juveniles would be highly advantageous.

Diet, growth and the Ecological Risk Aversion Hypothesis

Diet is related to growth, both as a proximate causal mechanism by which calories and other nutritional requirements necessary for growth are obtained, and as an ultimate causal mechanism when selective forces lead to an adaptive response [Lambert, 2007]. Growth pattern (including both rate and duration of growth) appears to be one of these adaptive responses. Among mammals, primates have an unusually low growth rate [Kirkwood, 1985; Kirkwood & Mace, 1996]. One explanation for this is the ecological risk aversion hypothesis (RAH) proposed by Janson & van Schaik [1993]. The RAH proposes that a low growth rate is an adaptation to offset ecological (i.e. starvation) risk faced by species consuming seasonally available food such as fruit. A lower growth rate translates to lower daily energetic and nutritional requirements. While fruit may be more nutritious and easy to digest compared to leaves, fruit is not uniformly available year-round [Hemingway & Bynum, 2005; Lambert, 2007; Radespiel et al., 2006; van Schaik & Pfannes, 2005]. Therefore, extending this logic, the RAH suggests that folivorous species, with a presumably more reliable food source will grow more rapidly compared to frugivorous species as they aren't constrained by limited food availability. However, Ganzhorn [2003] finds the nutritional content of leaves highly seasonally variable, and Harris [2010] finds that even folivorous primates experience feeding competition.

Among haplorrhines, frugivorous species generally grow more slowly compared to similarly sized folivorous species [Leigh, 1994a]. Comparisons of growth rates of 42 species of primates found consistent association between folivory and relatively high growth rate thus providing support for the RAH. Results were consistent with numerous other hypotheses addressing both proximate and ultimate causation. Leigh's study was unable to support any one hypothesis to the exclusion of other (see below).

Among lemuroid species, the reverse pattern was found. Frugivorous lemuroids grew at a higher rate compared to folivorous lemuroids [Godfrey et al., 2004]. This study examined not only growth in body mass, but dental development as well. In contrast to body mass growth, dental development was faster in folivorous lemuroid. These results suggest that rapid dental development may provide a competitive advantage in juvenile feeding competition providing an alternate strategy for coping with seasonality of food resources. Multiple adaptive responses are possible for selective pressures associated with obtaining food resources.

It is possible that the RAH, focusing on seasonal food availability, is generally correct, but is an insufficient explanation for lemuriform growth variation as lemuriforms are faced not only with seasonal availability of food resources, but also larger environmental unpredictability [Dewar & Richard, 2007; Godfrey et al., 2004; Godfrey et al., 2003; Wright, 1999]. Food resources in Madagascar are extremely irregular being affected by drought, cyclones, and frost, and, compared to mainland African forests, the forests are characterized by longer periods without fruits or other food sources [Dewar & Richard, 2007; Wright, 1999]. Consequently, lemuriforms may not provide an adequate test for the generality of the RAH because of the additional pressure of resource unpredictability. As galagids do not incur the costs of extreme resource seasonality and instability found in Madagascar, they provide an alternative test of the RAH from a different strepsirrhine clade.

The RAH focuses on distribution of resources as the selective pressure influencing growth. Fruit availability is correlated with annual rainfall such that fruit is more available during wet seasons and less available during dry seasons [Janson & Chapman, 1999; Lambert, 2007]. Though foliage may be considered low quality food, it is readily abundant and available, being more reliable in both space and time compared to fruit [Janson & Chapman, 1999; Lambert, 2007; Leigh, 1994a; Saj et al., 2007; van Schaik & Brockman, 2005].

Gummivory and the Ecological Risk Aversion Hypothesis

Like the structural components of foliage, gums are complex beta-linked polysaccharides which cannot be digested by mammalian digestive enzymes and likely require fermentation for digestion [Hemingway & Bynum, 2005; Power, 2010]. Some gummivores exhibit expansion of the cecum and colon, which may be associated with fermentation, and longer gut transit time. These traits are similar to those found in folivores [Nash, 1986a; Nash, 1986b; Nash, 1989; Power, 2010]. Gummivores are hind-gut fermenters while some folivores (e.g. colobines) are fore-gut fermenters [Power, 2010]. Also, both gum and foliage are more reliable in space and time compared to fruit [Bearder & Martin, 1980a; Charles-Dominique, 1974; Garber & Porter, 2010; Génin, 2008; Génin et al., 2010; Nash, 1986a] and, being more readily available, may be a fallback food for some primates species during the season of low fruit availability [Bearder & Martin, 1980a; Garber, 1993; Génin, 2003, 2008; Isbell, 1998; Joly-Radko & Zimmermann, 2010; Nash, 1986a; Nash & Burrows, 2010; Porter & Garber, 2006; Power, 2010; Radespiel et al., 2006; Smith, 2010; Swapna et al., 2010]. Gums consist of varying amounts of minerals and carbohydrates and are generally low in protein, lipids, and vitamins [Power, 2010]. While gum composition may be variable [Anderson & Pinto, 1980; Corbeisier et al., 2001; Douglas, 2006; Génin et al., 2010; Heymann & Smith, 1999], Gaulin [1979] ranks gums as a "high quality" food resource for primates, second only to insects. This ranking likely reflects the high carbohydrate content of gums. Much of the nutritional composition of gums (e.g. protein, fiber) were not included in Gaulin's analysis and the sample size was limited (i.e. one gum sample). Gums, as a “high quality” food source is questionable. They are likely consumed mainly for their energy (carbohydrate) and possibly mineral content and are difficult to obtain and digest [Nash & Burrows, 2010; Power, 2010].

While haplorrhine data provide support for RAH, they do not do so to the exclusion of other hypotheses for the growth patterns found. Galagids generally lack infanticide and allocare which confound results reported for haplorrhine primates [Leigh, 1994a]. Galagids also do not face the extreme seasonality found in Madagascar which may confound results reported for lemuroid [Godfrey et al., 2004]. Comparisons of gummivorous and nongummivorous *Galago* species provide a novel test of the RAH. Because of gum’s less seasonal distribution [Bearder & Martin, 1980a; Charles-Dominique, 1974; Génin, 2008; Nash, 1986a], the RAH would predict that species consuming gum would grow more rapidly compared to those consuming fruit. Support for this is found within Leigh’s study of haplorrhine primates. *Erythrocebus patas*, classified as a frugivore in Leigh’s [1994a] study, grows as fast as comparably-sized folivorous species. Isbell [1998] reports that, at least at one site, patas monkeys consume a considerable amount of gum, thus supporting the hypothesis being tested. Specifically, this study predicts that gummivorous *Go. senegalensis* will grow at a higher rate, relative to body size, compared to nongummivorous *O. garnettii*.

MATERIALS AND METHODS

Datasets

O. garnettii subjects include 43 females and 38 males with known dates of birth. A captive colony was maintained by the Duke Lemur Center (formerly the Duke University Primate Center) [Izard, 1989]. Housing was indoor and consisted of cages 0.5 m x 0.5 m x 2 m high furnished with partitions, ledges, and nestboxes; light cycle was constant (12:12 LD) or fluctuated mimicking the local (North Carolina) photoperiod [Coffman, 1995; Izard, 1989; Izard & Pereira, 1994; Izard & Simons, 1986b]. Diet included fruits, vegetables, Purina High Protein Monkey Chow, Purina Cat Chow, and crickets [Izard & Simons, 1986b]. Growth data available were collected between February 1980 and September 1996. Some subjects were measured multiple times and some were measured only once creating a mixed longitudinal [Coelho, 1985] dataset including measurements from 0 days to approximately 7.5 years of age. Subjects measured multiple times were measured opportunistically. The number of measurements per individual during the growth period ranged from 1 to 19. There was an average of five mass measurements per female and 6 mass measurements per male. Only subjects with known dates of birth were included in the current study. In some instances, pregnancy was noted and these measurements were removed from the current analysis. In most cases, delivery dates are unknown so no prior measurements were removed as was done with the *Galago* dataset (see below). The data are divided by sex and mass was measured to the nearest gram. Neonatal masses have been previously estimated as 54.0 grams for males and 48.9 grams for females yielding a pooled average of 51.7 grams (Table VIII) (See Chapter 2). Average adult male mass has been previously estimated as 1221.4 grams and adult female mass averages 1064.2 grams. Age at growth cessation (AGC) has previously been estimated as 783 (± 11.72) days for *O. garnettii* males, 557 (± 3.78) days for *O. garnettii* females (Fig. 12). Only measurements prior to the age at growth cessation were used in this analysis.

Go. senegalensis subjects include 36 laboratory-born individuals, 19 males and 18 females with known dates of birth. These individuals were part of a captive colony maintained at Arizona State University; data were collected between July 1976 and March 1992. Housing consisted of varying cage sizes ranging from 2.4 x 1.2 m high to 2.4 m to 2.4 m x 2.4 m x 2.4 m high and enriched with multiple perches, branches, panels, and nestboxes; a 12:12 LD cycle was maintained. Diet included fruit, vegetables, Purina High Protein Monkey chow and occasionally mealworms. For further description, see [Nash & Flinn, 1978; Schaefer & Nash, 2004]. Subjects were weighed within a day of birth and then up to twice per week until approximately 7 weeks of age, and then once per week until death creating a longitudinal dataset for each subject. Over 60 mass measurements are available for most subjects during the growth period. Mass was measured to the nearest gram, but neonates may have mass measured to the nearest tenth of a gram. Gestation length of *Go. senegalensis* is estimated to be 142 days [Izard & Nash, 1986; Izard & Nash, 1988; Nash et al., 1989]. All mass data for adult pregnant females that were recorded 142 days prior to parturition were removed from the dataset. While this dataset is longitudinal for each subject not all subjects were measured at the same age. Average neonatal masses were previously estimated as 19.9 grams for males and 19.6 grams for females yielding a pooled average of 19.8 grams; adult male mass averages 338.3 grams and adult female mass averages 253.1 grams (Table VIII). Age at growth cessation (AGC) has previously been estimated as 717 (± 4.99) days for *Go. senegalensis* males, and 484 (± 2.94) days for *Go. senegalensis* females (Fig. 12). Only measurements prior to the average age at growth cessation were used in this analysis.

Applicability of captive data

Theoretically, data from wild subjects may be better suited for studies of the adaptive significance of growth patterns because the very factors of interest in these studies are actually operating on these subjects. They are not buffered from the effects of selection (e.g. seasonality of resources). Wild growth data for galagids are currently nonexistent. Collecting a large, longitudinal sample of known-age subjects is difficult, if not impossible ethically and logistically, in the wild. Captive studies can yield larger, more detailed and complete datasets [Strum, 1991]. Captive subjects may be larger than their wild counterparts and growth rates and durations may be higher in captivity, but generally not significantly so [Leigh, 1992b; Leigh, 1994b; Terranova & Coffman, 1997]. Species-typical seasonal and age-related growth patterns as well as seasonal fattening patterns are present in captive subjects despite continuously available food suggesting that species-typical growth patterns are present even in captive subjects [Garber & Leigh, 1997; Génin et al., 2005; Hamada et al., 1999; Pereira, 1993; Petter, 1978].

Research into the diet of captive *Go. senegalensis* finds that this species retains other presumed adaptations to gummivory, (e.g. fermentive digestion as indicated by extended gut transit time compared to similar-sized nongummivorous species and the presence of DAPA, a bacteria associated with fermentation in other species), even in captivity and in the absence of gum in the diet. Furthermore, when captive subjects were fed gums, gut transit time increased even more [Nash, 1986a; Nash, 1986b; Nash, 1989]. For the purpose of this research, it will be assumed that captive subjects can be used for evolutionary studies and that adaptations to socioecological factors are present in captivity [Leigh, 1992b; Leigh & Shea, 1996].

Analysis

Linear regression

R.2.2 was used for statistical analyses. Larger-bodied species tend to grow faster (gain more grams per day) than closely related smaller-bodied species on an absolute scale [Godfrey et al., 2004; Leigh, 1994a]. This pattern is seen with these the species studied here. Both *O. garnettii* males (1221 grams) and females (1064 grams) are larger than *Go. senegalensis* males (338 grams) and females (253 grams) respectively (Table VIII). Previous research shows that *O. garnettii* grows at a significantly higher absolute rate compared to *Go. senegalensis* as well (see Chapter 2). To take into account absolute differences in mass between these species, each individual's mass measurements were divided by its adult mass (mass/adult mass) and the growth rate calculated as the proportion of adult mass gained per day. For individual subjects that do not have adult mass measurements, species averages were used. To statistically control for differences in growth rate that are due to differences in mass, a wider sampling of galagid species would be needed [Smith, 1984, 2005; Smith & Jungers, 1997].

Once raw mass measurements were converted to proportions, data were natural log-transformed and fit with Ordinary Least Squares (OLS) regression of ln (proportion) on ln (age). As measurement error was not symmetrical, OLS is appropriate [Smith, 2009]. A likelihood ratio test using an F-statistic (ANOVA package) was used to compare the sum of squares when a common slope was fitted to pooled data and when a separate regression line was fitted to each species separately [Sokal & Rohlf, 1995; Warton et al., 2006]. Specifically, comparisons were made between *Otolemur* males and *Galago* males and between *Otolemur* females and *Galago* females.

Piecewise regression

When comparisons were significant, two-segment piecewise regression function in Sigmaplot 11.0 was used to investigate growth differences further. Piecewise regression iteratively separates each growth curve (plotted as proportion by age) into two parts at an inflection point. This inflection point is the crossing point where the r^2's of the preceding and succeeding lines are maximized**.** After dividing the data into early growth (data preceding the inflection point) and late growth (data succeeding the inflection point), the F-statistic was used for comparison.

RESULTS

Linear regression

The RAH predicted that gummivorous *Go. senegalensis* would grow at a relatively higher rate compared to the frugivorous *O. garnettii*. Neither male nor female *Go. senegalensis* grow at a significantly higher rate compared to *O. garnettii* males and females respectively. Therefore, the hypothesis that gummivory is associated with a higher growth rate is rejected. The test for common slope finds that there are no significant proportional growth rate differences between *O. garnettii* and *Go. senegalensis* males (F = 1.7342, P< 0.1881), but contrary to the prediction, *O. garnettii* females grow proportionately faster than *Go. senegalensis* females (F = 11.254, P< 0.001) (Table IX, Fig. 13).

Piecewise regression

Investigating the growth differences for females further, two-segment piecewise regression was used to identify an inflection point at which the growth curve changes and growth begins to slow. The inflection points separating early and late growth were 179.4 ± 10.07 days for *O. garnettii* males, 177.1 ± 2.4 days for *Go. senegalensis* males, 185.4 ± 9.4 days *O. garnettii females*; and 139.2 ± 2.8 days for *Go. senegalensis* females. *O. garnettii* males and females and *Go. senegalensis* males begin growth deceleration at similar ages while *Go. senegalensis* females begin deceleration earlier. As indicated by AGC, *Go. senegalensis* females also cease growing earlier than *Go. senegalensis* males and both *O. garnettii* males and females. While the inflection point is similar for these other groups, AGC is not with *O. garnettii* males growing the longest followed by *Go. senegalensis* males, *O. garnettii* females and finally *G. senegalensis* females.

Separating the data into early and late growth phases (with the dividing point between the early and late growth phases being the age at the inflection point) and running the same analysis (comparing slopes with a F-statistic) finds that there are significant differences in early growth rate for females (*O. garnettii* slope = 0.554 ± 0.019, *Go. senegalensis* slope = 0.457 ± 0.008; $F = 13.316$, $P < 0.001$), but there are no significant differences in late growth (*O. garnettii* slope = 0.249 ± 0.041, *Go. senegalensis* slope = 0.214 ± 0.024; $F = 0.0700$, $P < 0.792$). This parallels results in the previous chapter which found that when overall significant growth rate differences were present between the sexes, significant differences were found in early, but not late growth. This suggests either that late growth rates are so variable as to overlap when comparing either between species or between sexes within species, or that early growth is more responsive to selection pressures.

Both the early and late growth phases were compared for males as well. No significant slope difference was found for males in either early growth (*O. garnettii* slope = 0.584 ± 0.021, *G. senegalensis* slope = 0.519 ± 0.012; $F = 0.182$, $P < 0.670$) or in late growth (*O. garnettii* slope = 0.234 ± 0.049, *G. senegalensis* slope = 0.251 ± 0.034; $F = 2.583$, $P < 0.108$). This accords with the comparison of overall growth of males as no significant differences were found.

DISCUSSION

The RAH predicts that species consuming a less reliable food resource, such as fruit, will grow relatively slowly to offset starvation risk [Janson & van Schaik, 1993]. Previous studies have reported conflicting results with folivorous haplorrhines growing more rapidly than frugivorous haplorrhines [Leigh, 1994a]. The reverse is found among lemuriforms in which frugivorous species grow more rapidly than folivorous species [Godfrey et al., 2004]. One possible explanation for these contrasting results is that the RAH is generally applicable to primates, but that the harshness and unpredictability of Madagascar's environment has led to unique adaptations among lemurs. Results of this study do not provide support for the RAH as the frugivorous *O. garnettii* females grow at relatively higher rate than gummivorous *Go. senegalensis* females, a case similar to that found among lemuriforms and contrary to that found among haplorrhines. However, no significant difference was found for males.

Both *O. garnettii* males and females grow at a significantly higher rate compared to gummivorous *Go. moholi* males and females respectively [O'Mara et al., in review]. However, O'Mara et al.'s study, focusing on intraspecific growth rates, estimated absolute growth rates rather than relative growth rates and, as noted above, growth rates increase with increasing body mass so these results are not surprising. Direct comparisons between similarly sized frugivorous *O. garnettii* and gummivorous *O. crassicaudatus* would be a useful test of the RAH hypothesis.

Leigh [1994a]notes that folivorous haplorrhines exhibit a more linear growth curve and that folivores cease growing relatively early and abruptly compared to frugivores. It appears that linearity of the growth curve and abruptness of growth cessation were visually determined and, without clearer definition of linearity and abruptness, similar patterns are difficult to assess with the loess curves for the species studied here. Godfrey et al. [2004]finds the opposite pattern with frugivorous lemurids reaching adult size relatively earlier than folivorous indriids. In agreement with Leigh's findings for folivorous haplorrhines, gummivorous *Go. senegalensis* ceases growth early (has an earlier age at growth cessation) compared to frugivorous *O. garnettii* (see Chapter 2). The same result is found in examination of growth durations of gummivorous *Go. moholi* which ceases growth earlier compared to *O. garnettii* [O'Mara et al., in review]. However, interspecifically, growth duration increases with increasing body mass [Leigh, 1994a]. In neither galagid comparison was interspecific differences in body mass accounted for. Whether gummivorous or frugivorous species cease growing earlier relative to body mass will require comparisons among a larger sampling of galagid species.

Reliability of gums

An assumption of this study is that gum is similar to foliage, both being reliable in space and time, and thus provide a novel test of the RAH. Gum, like leaves, may be more reliably available throughout the year compared to fruit [Bearder & Martin, 1980a; Charles-Dominique, 1974; Garber & Porter, 2010; Génin, 2008; Génin et al., 2010; Nash, 1986a; Nash, 1986b; Nash, 1989; Nash &

Harcourt, 1986]. Additionally, gums can be rapidly renewed and evenly distributed through space [Garber & Porter, 2010; Génin, 2008; Génin et al., 2010; Joly-Radko & Zimmermann, 2010]. However, variation in availability still exists [Garber & Porter, 2010; Génin et al., 2010]. Both the quantity and quality of gum may decrease seasonally being less available, and of lower quality, during the dry season [Anderson & Pinto, 1980; Bearder & Martin, 1980a; Charles-Dominique, 1974]. Composition of gums also varies during flowering season in some species [Corbeisier et al., 2001]. Insects, a supplemental food resource for both *O. garnettii* and *Go. senegalensis*, may also be seasonal, affecting both the availability of insects as food and the availability of gum sites since galagids feed on gums which are extruded in response to damage caused by insects [Nash, 1986b; Nash, 1989]. Fewer insects may mean fewer gum sites.

Primate species relying on gums or other exudates don't always change food resources during the dry season and primates which rely on other foods during the wet season switch to gums during the dry season [Bearder & Martin, 1980a; Garber, 1993; Génin, 2008; Isbell, 1998; Joly-Radko & Zimmermann, 2010; Nash, 1986a; Nash & Burrows, 2010; Porter & Garber, 2006; Radespiel et al., 2006; Smith, 2010; Swapna et al., 2010]. This suggests that gums are a more reliable food resource than fruit.

Alternate hypotheses to ecological risk aversion

While Leigh's study [1994a] of haplorrhine primates, the impetus for this study, provided support for RAH, it also provided support for alternate hypotheses. One explanation involved a proximate rather than an ultimate cause of increased growth rate. Compared to fruit, the relatively high protein content of foliage could allow a high growth rate. Support for this included the relatively high growth rate of *Erythrocebus patas* compared to similarly sized folivorous species. It is noted that insects and other invertebrates account for a large portion of patas monkey diets thus their diet, like that of folivorous primates, may be high in protein. Leigh also notes that milk of folivores is higher in protein compared to milk of frugivores. This would allow high growth rate prior to weaning which could then be continued after weaning as the young begin to consume high-protein foliage.

Unlike foliage, gum tends to be low in protein ranging from trace amounts to 10% on a dry matter basis [Bearder & Martin, 1980a; Nash, 1986a; Nash, 1986b; Nash, 1989; Power, 2010] (but see [Garber & Porter, 2010; Génin et al., 2010]). Additionally, the proteins found in gums are generally indigestible without fermentation [Power, 2010]. Galagids, both gummivorous and frugivorous species, acquire protein primarily from insects, which make up a considerable part of their diet [Bearder & Martin, 1980a; Nash, 1986a; Nash, 1986b; Nash, 1989; Nash et al., 1989]. Thus it is likely that protein content of both galagid species' diet would be similar. It is noted that content of galagid milk is high in both fat and protein compared to the milk of anthropoids, lemuriforms, and lorisids [Power et al., 2006; Power, 2006; Tilden & Oftedal, 1997]. Little is known of the variability among galagid species, though it is clear that body mass is not correlated with milk content as the protein content of the smaller *Go. moholi* is higher than that of *Otolemur* species [Tilden & Oftedal, 1997]. If protein intake is a proximate causal mechanism for the high growth rate of folivorous haplorrhines, then both galagid species should have similar growth rates. This is true of male galagids, but not females.

A second hypothesis supported by Leigh's haplorrhine data involves energy allotment. This hypothesis suggests that the higher growth rates of folivores is related to differences in resting metabolic rate [Leigh, 1994a]. While, at first glance, this seems counterintuitive as a high metabolic rate might be expected to correlate with high growth rate, an opposite conclusion could be drawn. Leigh suggests the possibility that the relatively low basal metabolic rate of folivores (compared to frugivores) translates to less energy needed for daily maintenance, thus freeing more energy for growth. This hypothesis is not supported by lorisoids. Compared to similarly sized lorisids, galagids have *both* a relatively higher metabolic rate and a relatively higher growth rate [Rasmussen & Izard, 1988]. However, when examining sexes separately, the same pattern is not found. Instead, lorisids grow at either similar or at absolutely higher rates than similarly-sized galagids [O'Mara et al., in review]. BMR was not correlated with body mass as the smaller *Go. moholi* has a higher relative metabolic rate than *O. crassicaudatus* [Genoud, 2002; Rasmussen & Izard, 1988]. Thus, metabolic rate is unlikely to explain the growth rate variability seen here.

Other hypotheses which are supported by the haplorrhine study include careless alloparenting and infanticide. Both of these behaviors may make rapid attainment of mass (i.e. a higher growth rate) a favorable risk aversion characteristic and may be the selective force for rapid growth [Leigh, 1994a].

Generally, species with allocare have higher growth rates compared to species in which the mother alone provides care [Bales et al., 2000; Gursky, 2000; Kappeler et al., 2003; Lee, 1996; Mitani & Watts, 1997; Ross, 2003; Ross & MacLarnon, 1995, 2000]. Sampling may have influenced Leigh's reported results. Colobines, among which both careless alloparenting and infanticide are common [Chism, 2000], accounted for half of the folivorous species included in the study. Consequently, the effects of phylogeny cannot be ruled out as an explanation for the observed pattern. Careless alloparenting and infanticide are commonly associated with folivory and may thus explain Leigh's results, but would not explain the results here as careless alloparenting and infanticide have not been observed in the wild among galagids [Nekaris & Bearder, 2007].

While the current results do not provide support for the ecological risk aversion hypothesis, they do accord with those reported for Malagasy lemuroids. In this group, frugivores had a significantly higher growth rate compared to folivores. Godfrey et al. [2004] linked life history variation between lemurids and indriids to population maintenance and recovery following ecological disturbances such as cyclones and droughts. Indriids adopted a "slow and steady" demographic strategy whereby few offspring are produced which then grow slowly and are at low risk of starvation due to rapid dental development and a folivorous diet. Lemurids, on the other hand, have a catch-up strategy whereby many offspring are produced, which grow rapidly, but suffer higher mortality during food shortages. Lemurids have earlier ages at maturity, twin more often, and have higher growth rates compared to indriids. These demographic patterns of slow or fast population recovery are the result of the life histories of each taxon, many traits of which are linked to growth as the process which regulates or drives life history.

While galagids do not face as extreme environmental instability as lemuriforms, it is possible that galagid growth rates may be linked to life history variation and population maintenance in a similar pattern. Both species studied here, *Go. senegalensis* and *O. garnettii*, are sometimes sympatric and thus exposed to similar overall environmental conditions [Nash et al., 1989]. The species which grows the fastest, *O. garnettii*, also produces larger litters (twins) at higher frequency (a “lemur” trait) while *Go. senegalensis* (like indriids) produce fewer offspring per parturition which then grow slowly [Nash et al., 1989]. However, *Go. senegalensis* increases its reproductive output by exhibiting post-partum estrus and producing two litters each year in some instances [Izard & Nash, 1988; Nash et al., 1989]. Thus, in a single year, both species may produce two offspring regardless of differences in growth rate. It does not appear that differing mechanisms for population maintenance explains differences in growth rate.

While data from lemuroids do not provided support for the RAH, which links growth rate to availability of food resources, results are suggestive of a different mechanism for offsetting possible starvation risk faced by juveniles. Leaves are more difficult to process and digest compared to ripe fruit [Eaglen, 1985; Knott, 2010]. Additionally, during the first post-weaning dry season, folivorous lemuroids consume unripe fruits, seeds, and mature leaves which are more difficult to process than young leaves [Eaglen, 1985]. While leaves may be more readily available, folivores may still face difficulty during the dry season if leaves are more difficult for juveniles to process and digest. In this sense, folivorous juveniles may face greater feeding risk compared to frugivores. Folivorous indriids exhibit rapid dental development compared to frugivorous lemurids, thus indriids have the dental equipment needed to process post-weaning foods and are therefore able to successfully obtain food resources [Eaglen, 1985; Godfrey et al., 2004]. *Hapalemur*, a folivorous lemurid, weans after the eruption of anterior permanent teeth and, like indriids, has the dental equipment necessary to process tough bamboo [Godfrey et al., 2004]. Having the dentition able to process the same foods as adults would be an advantageous, if different, way of dealing with starvation risk [Eaglen, 1985; Godfrey et al., 2004]. While little is known regarding the dental development of galagids, these studies of lemuroids suggest that there are multiple ways to offset feeding risk for juveniles. The RAH suggests a low growth rate of frugivorous haplorrhines offsets starvation risk while Godfrey et al. [2004] and Eaglen, [1985] suggest rapid dental development of indriids offsets starvation risk. For galagids, larger juvenile body size, if it gives an advantage in feeding competition, may offset starvation risk.

Weaning foods hypothesis

Perhaps, not food availability generally (i.e. folivory versus frugivory), but specific food availability during weaning influences growth in a pattern similar to that suggested by the RAH as it pertains to competition for food resources. Species consuming less readily available foods following weaning might grow faster to yield larger offspring who are better able to compete for the scarce food resources rather than grow slower to lower metabolic requirements.

Many galagid species wean their infants when foods, especially insects, are most abundant [Charles-Dominique, 1977; Nash, 1983; Nash & Whitten, 1989] thus juveniles would face relatively less competition compared to juveniles of species weaning during the lean season. *Galagoides demidovii, Gs. zanzibaricus, Go. moholi, Go. senegalensis*, and *O. crassicaudatus* all wean during the wet season and/or when insects are most abundant [Charles-Dominique, 1977; Nash, 1983; Nash & Whitten, 1989]. Conversely, *O. garnettii* are weaned during the dry season [Nash, 1983] when food resources are more scarce and competition presumably higher. Growing rapidly would yield relatively larger offspring which might provide them an advantage in resource competition [Nash, 1983]. *O. garnettii* are over 60% of adult mass at weaning while *Go. senegalensis* are closer to 50% of adult mass at weaning. Males and females of both species are similarly sized at weaning with sexual dimorphism appearing later in growth. As *Go. senegalensis* is weaned during a time of relative food abundance, juveniles would not face the same degree of competition as would *O. garnettii* juveniles, so *Go. senegalensis* juveniles can afford to be smaller, relative to adult mass, at weaning. That significant rate differences are found in the early growth phase lends support to this hypothesis.

Patas monkeys (*Erythrocebus patas*) are frugivorous with a seasonal reproduction pattern. The weaning process may begin during the end of the wet season, but is usually completed during the dry season when food is less available

[Chism et al., 1984]. Like frugivorous *O. garnettii*, which also weans during the dry season, patas monkeys exhibit a significantly higher growth rate than similarly sized folivores [Leigh, 1994a] and are close to 50% of adult mass when weaned [Lee & Bowman, 1991]. Generally, primate infants are weaned when they are approximately one third of adult mass [Charnov, 1991; Charnov & Berrigan, 1993; Kappeler, 1993; Kappeler et al., 2003; Lee, 1987; Martin, 2003]. Interestingly, juvenile *E. patas* are also involved in resource defense [Chism et al., 1984], something for which rapid growth and larger mass would be beneficial.

Many lemuriform species wean their infants when food is highly available [Wright, 1999]. However, birth seasons are highly variable such that both species that grow fast and those that grow slow wean at the same time [Godfrey et al., 2004; Wright, 1999]. Mass at weaning ranges from 20% of adult mass for *Propithecus diadema* to 70% of adult mass for *Varecia variegata* [Godfrey et al., 2004]. It is noteworthy that frugivorous species, with their higher growth rate, are closer to adult mass at weaning than are folivorous species. As many lemuriforms are born in tightly synchronous cohorts, being larger at weaning would be advantageous in competing with other juveniles for the more patchily distributed fruit. As discussed previously, the lack of clear correspondence between growth rate and diet may be, in part, due to the extreme seasonality of Madagascar. Nonetheless, that frugivorous species are relatively larger at weaning than are folivorous species suggests that mass at weaning may be an important factor in successful competition for resources. This same pattern is found in galagids with frugivorous *Otolemur* being closer to adult mass at weaning compared to gummivorous *Galago*.

Many neotropical primates reproduce seasonally or bimodally and frugivorous species are more likely to reproduce seasonally than folivorous species [DiBitetti & Janson, 2000]. Growth rate tends to increase with increasing body mass [Garber & Leigh, 1997]. *Aotus* and *Callicebus*, which grow relatively slowly for their body mass, wean infants during a time of more abundant food while cebids lactate during periods of high food availability and wean when food resource availability is declining. *Saimiri* also weans when food availability is decreasing, but they exhibit a lower than expected growth for their mass. This is contrary to the current hypothesis. However, *Saimiri* infants are quite large when weaned, being nearly 80% of adult mass [Lee & Bowman, 1991] indicating that larger mass at weaning can be attained by either rapid or slow, but prolonged, growth as was the case with lemuriforms.

H. lar are unusual among hominoids in having seasonal reproduction. Primarily frugivorous, their forests have two seasons of high food availability and gibbons appear to conceive during the first peak and wean during the second peak [Savini et al., 2008]. As *H. lar* should presumably face lower competition following weaning, a lower growth rate would be expected. However, *H. lar* grow as fast as similarly sized folivorous haplorrhines (*Alouatta caraya*) [Leigh, 1994a]. This may not be an adequate comparison as generally, New World monkeys grow faster than Old World monkeys which grow faster than hominoids [Kirkwood, 1985; Kirkwood & Mace, 1996]. Comparing the growth rate of *H.*

lar to asynchronously reproducing hominoids might be a more appropriate test for a link between food availability during weaning and growth rate as it leads to mass at weaning.

While an intriguing hypothesis, the idea that species weaning during the dry season should be comparatively larger at weaning compared to species weaning during the wet season requires more data to investigate. Targeted comparison of growth patterns and weaning mass with weaning seasonality are warranted. Additionally, the types and amount of competition faced by juveniles in differing dietary categories need to be better understood. While the current study provides support for the hypothesis for females, the question remains as to why the same pattern isn't found for male galagids.

What about males?

Like females, *Go. senegalensis* males wouldn't need to grow large to successfully compete for food. However, they would need to be large to successfully compete for females. Generally, female ontogeny is more subject to natural selection by competition for food while male ontogeny is more subject to sexual selection by competition for mates [Leigh, 1992a, b; Leigh, 1995; Wrangham, 1979]. As galagids reach sexual maturity within the first 1- 1½ years and are seasonal breeders [Nash et al., 1989], they may face strong selection pressures to reach adult mass quickly or risk losing a breeding season. Coupling both natural and sexual selection theories it is hypothesized that *Go. senegalensis* females, which experience low feeding competition both at weaning and, presumably during adulthood, grow slowly and cease growing at a relatively smaller size compared to *Go. senegalensis* males (*Go. senegalensis* females are 74% of males mass while *O. garnettii* females are 87% of male mass) and to *O. garnettii* females. As *O. garnettii* females face greater competition for food both during weaning during the dry season and also as adults relying on a more seasonal food resource, selection for rapid growth to attain larger mass at weaning could be advantageous. Males of both species have the need for large size to successfully compete for females. A similar pattern is found in African hominoids with folivorous *Gorilla* females ceasing growth earlier and at a smaller size compared to frugivorous *Pan* and SSD being attained primarily through bimaturism [Leigh & Shea, 1996]. This pattern of integrating both natural and sexual selection explanations may provide an adequate explanation for the growth patterns reported both here and in the previous chapter. Again, conclusions would be strengthened with the study of additional galagid species.

TABLE VIII. Summary of growth parameters (See Chapter 2).

	Neonatal Mass (SEM) (grams)	Adult Mass (SEM) (grams)	AGC (SEM) (days)	95% CI
O. garnettii males	54.0 (3.70) (n = 5)	1221.4 (36.4) (n = 14)	783.2 (11.73) (n = 38)	759.74 – 806.66
O. garnettii females	48.9 (2.53) (n = 4)	1064.2 (40.74) (n = 11)	557.0 (3.78) (n = 43)	549.44 – 564.56
O. garnettii pooled	51.7 (2.38) (n = 9)	1152.3 (30.98) (n = 35)	714.0 (8.29) (n = 81)	697.42 – 730.58
Go. senegalensis males	19.6 (0.95) (n = 19)	338.3 (20.19) (n = 12)	717.4 (4.99) (n = 19)	707.42 – 727.38
Go. senegalensis females	19.6 (0.55) (n = 17)	253.1 (11.23) (n = 15)	484.0 (2.94) (n = 18)	478.12 – 489.88
Go. senegalensis pooled	19.6 (0.37) (n =36)	287.4 (13.55) (n = 27)	710.1 3.70) (n = 37)	702.7 – 717.5

TABLE IX. Ordinary least squares regression comparing the slope of *O. garnettii* and *Go. senegalensis*; males and females compared separately. Slope = regression of ln (proportion of adult mass) on ln (age in days).

	Slope (SEM)	**95% CI**	**Adj. R^2**	**Significance**
O. garnettii males	0.504 (0.008)	0.488 - 0.519	0.905	NS
Go. senegalensis males	0.515 (0.009)	0.498 - 0.533	0.954	
O. garnettii females	0.499 (0.008)	0.482 - 0.515	0.934	P>.001
Go. senegalensis females	0.473 (0.009)	0.455 - 0.491	0.935	

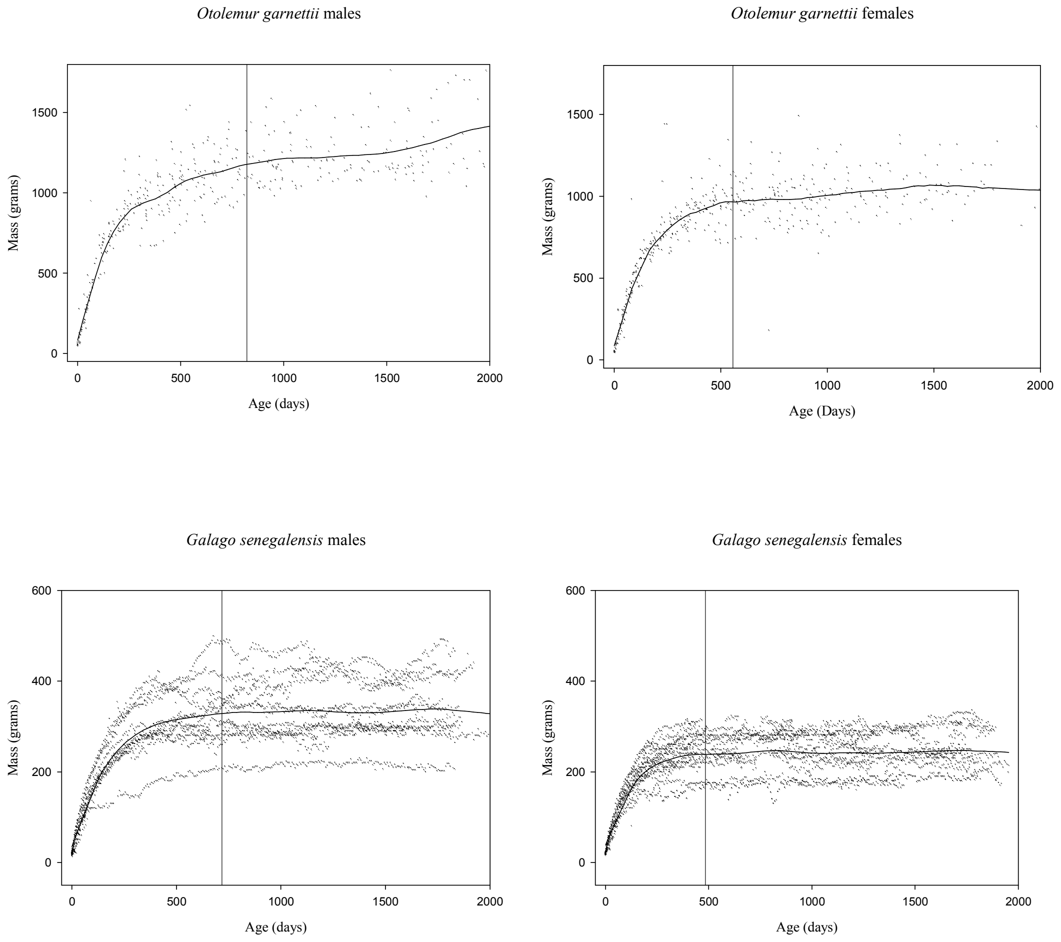
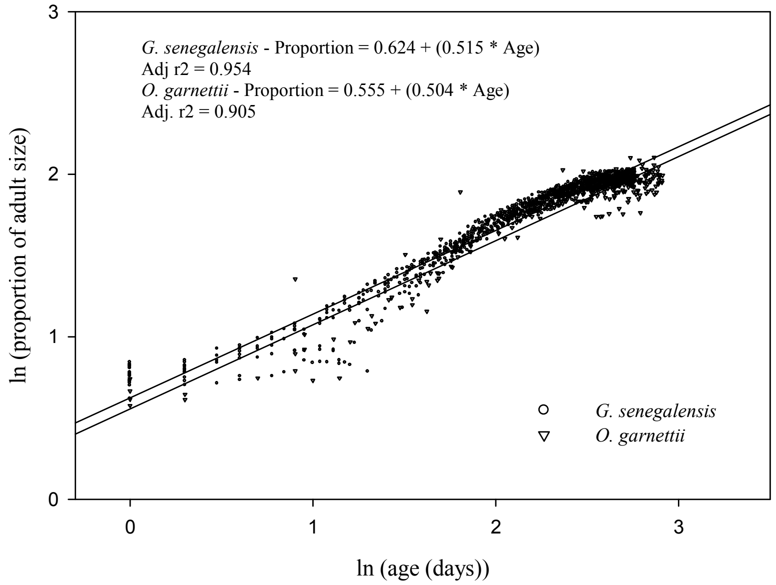


Fig. 12. Loess estimated growth curves fit for male and female galagids. Vertical line is placed at the bootstrapped estimated age at growth cessation (AGC).

Males



Females

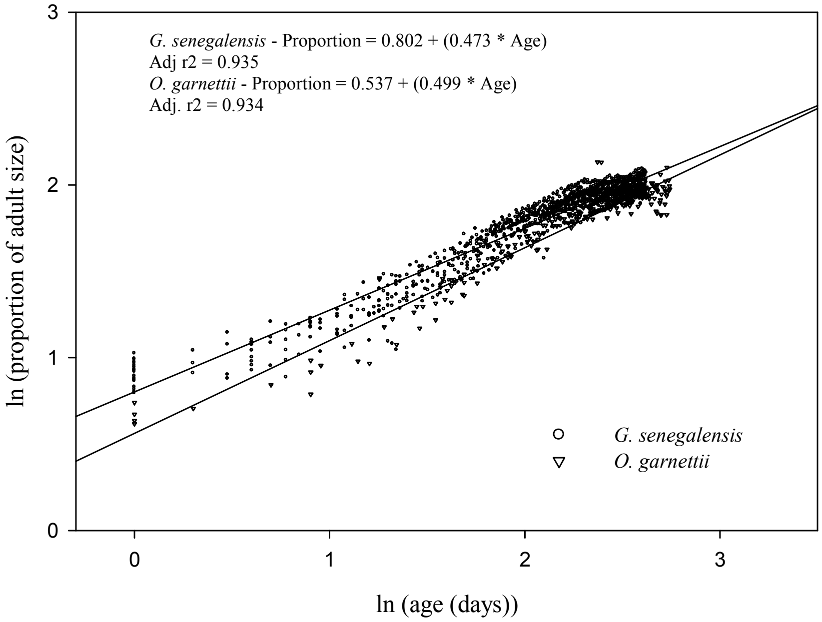


Figure 13. Ordinary least squares regression comparing slopes for *O. garnettii* and *Go. senegalensis*; males and females compared separately.

Chapter 5 - Summary and Conclusion

This study investigated the ontogeny of body mass (i.e. “growth”) of Galagidae. The processes of ontogeny include growth (increase in size), development (differentiation), and maturation (biological aging) [Godfrey & Sutherland, 1996; Gould, 1977]. Growth, specifically an increase in body mass, was the focus here. Ontogeny is associated with individual survival [Small & Smith, 1986] and is a variable with a time component linking it with a suite of life history traits within a species (e. g. birth mass, age and size at weaning, age and size at maturity) [Harvey et al., 1987; Lee, 1996]. Ontogeny can be the target of natural selection as differing growth patterns can be adapted to specific socioecological conditions [Pereira & Leigh, 2003] and through heterochrony, ontogeny is connected to phylogeny [Alba, 2002; Alberch et al., 1979; Gould, 1977; Gould, 1988, 2000; King, 2004; Rice, 1997]. “Clearly, organisms look and behave differently because at some level they develop differently.” [Parichy et al., 1992, p. 1252]. In short, ontogeny is an essential force in evolutionary biology.

This study is one of the first to examine the growth of galagids and to seek associations between socioecology and growth patterns of two galagid species, *Otolemur garnettii* and *Galago senegalensis*. Hypotheses that have been generated and tested using haplorrhine data were tested with this rarely studied clade. Previous testing of these hypotheses outside of haplorrhine taxa have yielded mixed results and had contrary findings. Often the previously studied strepsirrhines have been limited to Malagasy lemurs, many of which are more similar in body size, activity patterns, and social organization to haplorrhines than the less-studied small-bodied nocturnal solitary foraging lorisoids. The Galagidae thus offered an alternative way to test the generality of these hypotheses.

The main objectives of this study were to assess how galagids come to be differently sized and to test for associations between socioecological factors and growth patterns. Specifically, this study sought to examine (1) whether interspecific adult mass variability resulted from differences in growth rate and/or growth duration, (2) whether dispersed single-male/multi-female social groups were associated with growth rate differences between male and female galagids, and (3) whether gummivorous *Go. senegalensis* grows at a higher rate compared to the frugivorous *O. garnettii*. This study used previously collected growth data from captive subjects. Neither of the hypotheses linking growth patterns and social systems or growth patterns and diet was supported and the results led to more questions regarding the links between socioecology and growth.

Review of previous studies

Chapter 1 provided a review of the literature of primate growth. Studies of associations between growth in size, especially mass, and social and ecological factors are on the rise. Many of these studies have concentrated on large-bodied diurnal haplorrhine primates. Growth of lemuriforms has also been examined. Many lemuriforms, like many haplorrhines, are larger-bodied, diurnal, and live in relatively large social groups. These characteristics make them easier to study than the smaller nocturnal strepsirrhines. These similarities to haplorrhines make tests for convergence in adaptations and the generalities of adaptive hypotheses possible. Hypotheses developed from and supported by data from haplorrhine species are not always supported by data from lemuriform species. This calls into question the applicability of these hypotheses for primates in general.

Lemuriforms are not necessarily typical strepsirrhine primates. Malagasy primates exhibit several unique features which set them apart from other primates, both strepsirrhine and haplorrhine [Kappeler, 2010]. These features include female dominance, even sex ratios, cathemerality, high folivory relative to body mass, lack of sexual size dimorphism regardless of social system, and strict seasonal breeding [Kappeler, 2010; Wright, 1999]. Hypotheses regarding this uniqueness include the energetic costs associated with the harsh and unpredictable environment of Madagascar [Dewar & Richard, 2007; Jolly, 1984; Pereira, 1993; Richards & Nicoll, 1987; Wright, 1999] and evolutionary disequilibrium caused by recent human invasion and subsequent large fauna extinction [van Schaik & Kappeler, 1996; Wright, 1999]. Contrary results may reflect these unique socioecological features or the extreme seasonality and unpredictability of Madagascar.

Several hypotheses for the lack of similarities between haplorrhines and lemuriforms exist. These include a cladistic dichotomy between strepsirrhines and haplorrhines, the unique socioecology of Madagascar, and alternative solutions to similar problems. Whether differences result from these or a combination of these or other factors requires investigation. Further tests of the generality of hypotheses developed from and supported by haplorrhine data are also warranted.

Galagids provide such a test as they do not face the extreme seasonality of Madagascar and do not exhibit the same unique features which set lemurs apart from other primates. For instance, lemurids do not exhibit sexual size dimorphism (SSD) despite forming large multi-male/multi-female social groups; these groups are associated with SSD among haplorrhines [Kappeler, 1993; Leigh, 1995; Leigh & Terranova, 1998]. Hypotheses regarding the lack of SSD in promiscuous lemurids include constraints of body size, constraints on growth rate due to extreme food seasonality, and female dominance making post-copulatory competition an alternate solution [Kappeler, 1993; Leigh & Terranova, 1998]. As galagids exhibit SSD, a hypothesis of small body size constraint as an explanation for lack of SSD is not supported. Furthermore, haplorrhine data have suggested not only that the presence or absence of SSD is associated with social organization, but that social organization leads to different growth patterns leading to SSD. While this hypothesis could not be tested with monomorphic lemurids, it could be tested with sexually dimorphic galagids.

Growth variability in galagids

Chapter 2 sought to determine whether post-natal interspecific mass variability resulted from differences in growth rate, differences in growth duration, a combination of the two, or neither. Shea [2002] posits that, interspecifically, growth durations are more constrained and that closely related species are more likely to differ in growth rates. Conversely, comparisons of post-natal growth rates and genes underlying growth finds that growth rates may be constrained [Adkins et al., 2001; Kappeler, 1995; Kirkwood, 1985; Kirkwood

& Mace, 1996; Li et al., 2005; Liu et al., 2001; Wallis et al., 2001; Ye et al., 2005] which suggests adult mass variation may result from duration differences. *O. garnettii* grows both at a higher rate and for a longer duration than *Go. senegalensis*. Despite limited variability in growth hormones and their underlying genes, galagids exhibit considerable variability in growth patterns.

Variability in the growth patterns of *Go. senegalensis* and *O. garnettii* is in accordance with multiple studies of the adaptive nature of growth. Growth patterns seem to be highly responsive to differing socioecological pressures and adaptations to unique socioecological conditions may override phylogeny. Galagids fill a wide variety of ecological niches throughout Africa. They are found in a wide variety of habitats including primary and secondary rain forests, riverine and montane forests, thorn scrub and acacia woodlands, forest edges, and savannah. Galagids range at different elevations, latitudes and use varying levels in the canopy. Different species feed on varying combinations of gums, insects and small animals, seeds, and fruit. Life histories vary in the number of offspring per litter and number of litters per year as well as in weaning ages, ages at maturity, interbirth intervals, etc. While most galagid species are solitary foragers, there are varying amounts of association between individuals both during active time and during sleeping time [Nash et al., 1989; Nekaris & Bearder, 2007]. Each of these sociological and life history factors has potential implications for growth patterns so it is not surprising that growth patterns differ between these two species as they may have responded to each species' unique socioecology and life history. Associations between growth patterns and socioecological features are only the first step in assessing whether the growth pattern is an adaptation to the socioecological feature. Further study including additional galagids is needed. As interspecific growth rate differences were found to be present in galagids, subsequent tests sought potential associations between social organization and the ontogeny of sexual size dimorphism and between diet and growth rates.

Sexual Size Dimorphism

Chapter 3 examined the ontogeny of sexual size dimorphism (SSD) in both species. Previous research from haplorrhines has found that species forming multi-male/multi-female social groups generally attain SSD via differences in the duration of growth, with males growing longer than females. When living in multi-male/multi-female groups, it may be adaptive for a male to grow slowly thus delaying intrasexual competition for mates and increasing the time available for learning social skills needed to successfully compete and move up the dominance hierarchy. Conversely, species forming single-male/multi-female social groups generally attain SSD via differences in the rate of growth with a male adolescent growth spurt being common. In single-male/multi-female groups adolescent males may be expelled from the group relatively early and abruptly. This increases the need for males to rapidly attain large size to lower predation risk during solitary emigration and to successfully compete with other males for access to females and food.

Galagids are one of the few strepsirrhine taxa which exhibits SSD making them a useful taxon for testing the generality of the hypothesis linking growth patterns and social organization. This association is generally found among haplorrhine species, but not among lemurid species [Leigh, 1992a, b; Leigh, 1995; Leigh & Terranova, 1998]. Field research indicates that adult males of both species studied here rarely tolerate other adult males and social organization could be classified as dispersed single-male/multi-female groups. It was hypothesized that differences in growth rate between males and females would underlie the adult SSD present in both study species.

To test this, growth rate was converted into a proportion of adult mass gained per day because larger species tend to gain more grams per day than closely related smaller species [Godfrey et al., 2004; Leigh, 1994a]. There was no significant sex difference in the growth rate for *O. garnettii*, but male *Go. senegalensis* gain a significantly greater proportion of adult mass per day than females of that species. Alternatively stated, *Go. senegalensis* females grow significantly slower than males. Differences in the duration of growth were present in both species with males growing for a longer duration compared to females. Thus the hypothesis was supported for *Go. senegalensis*, but not for *O. garnettii*.

The ontogeny of SSD has been reported for third galagid. Like *O. garnettii*, *Galago moholi* attains SSD through bimaturism [O'Mara et al., in review]. This pattern is dissimilar to that found for *Go. senegalensis* in which males grow both at a higher rate and for a longer duration compared to females. As *Go. moholi* and *Go. senegalensis* are similarly sized, there is no clear body mass influence on the ontogeny of SSD. Even though *Go. moholi* and *Go.*

senegalensis are ecologically similar and closely related, it remains possible that they differ in mating systems with *Go. moholi* females mating promiscuously and *Go. senegalensis* females mating with a single male. In this scenario, the results of this study would support a sexual selection hypothesis linking mating system and ontogeny of SSD. Limited data suggests mating systems in which females mate with a single male (both single-male/multi-female and single-male/single female) are present in other species of the galagid clade (e.g. *Sciurocheirus*, *Gs. cocos*) [Charles-Dominique, 1977; Harcourt & Nash, 1986a]. Examination of additional sexually dimorphic galagid species is needed to uncover the reasons for this difference. Clarifying the social organization of differing species is also needed.

Social organizations are difficult to establish for galagids and many studies have relied on patterns of social and spacing systems. Mating systems of both species are not well-understood and are the aspect of social organization most likely to influence sexual selection. A dispersed single-male/multi-female social organization has been proposed for both species. This is based primarily on sleeping associations and ranging patterns. Recent detailed field observations on some galagid species have demonstrated that greater complexity in social organization exists.

Several species (e.g. *Galagoides demidovii*, *Gs. cocos*, *Go. moholi*, [Bearder & Doyle, 1974a, b; Charles-Dominique, 1977; Harcourt, 1986c; Harcourt & Nash, 1986a; Nash, 1984]) reportedly have two types of adult males: larger “A” males and younger, smaller “B” males which may be tolerated by A males. While

A and B males have not been documented for either species studied here, it is noteworthy that no long-term field studies examining social organization have been undertaken for *Go. senegalensis*. Research on *O. garnettii* have been short-term and have found that larger males tolerate younger, smaller males which is suggestive that a similar pattern of A males and B males exists in this species. The existence of A and B males was first described for *Go. moholi* [Bearder, 1987], a species closely related to and ecologically similar to *Go. senegalensis,* making it likely that A and B males would be present in *Go. senegalensis* as well.

Data on the mating systems and reproductive success of differently sized males are largely lacking though inferences on mating systems have been drawn from studies of relative testes size. Galagid species for which testes size is known (e.g. *Gs. demidovii*, *Go. moholi*, *Go. senegalensis*, *O. garnettii*, and *O. crassicaudatus* [Dixson & Anderson, 2004; Harcourt et al., 1995]) have large testes for their body size suggesting sperm competition which is generally associated with promiscuous mating systems. Categorizing species as multi-male/multi-female versus single-male/multi-female requires direct data on mating and paternity and in its absence, conclusions regarding the absence of a link between growth patterns and social organization for galagids are inconclusive. Clearly further study is warranted to gain a clear understanding of the diversity of social, spatial, and mating systems in this diverse clade.

Reasons postulated for the pattern linking growth and social organization found in haplorrhines are that males in single-male/multi-female groups face a rapid increase in intrasexual aggression and predation pressure once expelled from the group and that rapidly attaining large size may offset these risks. It is questionable whether galagids face a similar increase in intrasexual or predation risk. Adult males of several species seem to tolerate other younger adult males [Bearder, 1987; Charles-Dominique, 1977; Harcourt, 1986c; Harcourt & Nash, 1986a; Kappeler, 1997a; Nash, 1984] indicating intrasexual risk is not as high as in haplorrhine species. Additionally galagids spend a great deal of time solitary throughout the entire life cycle [Kappeler, 1996; Ross, 2001] and not just upon reaching maturity and being expelled from the group. That galagid males presumably do not face a similar increase in risks suggests they would not need to rapidly attain adult size so the results are thus expected. Data on predation risk and mortality schedules are needed to effectively test this.

Chapter 3 concluded with a suggestion that the intersexual growth patterns could possibly be explained by integrating both sexual and natural selection pressures. Dietary differences and thus starvation risk each species faces may be an interacting factor. *Go. senegalensis* is gummivorous while *O. garnettii* is frugivorous. Both species supplement their diets with insects. The next chapter investigated this hypothesis further.

Gummivory and the Ecological Risk Aversion Hypothesis

Chapter 4 sought to test a novel interpretation of the ecological risk aversion hypothesis (RAH). Proposed by Janson & van Schaik [1993] this hypothesis links growth rate, juvenile foraging competency, and food resource availability. Specifically, they suggest that the unusually slow growth rate of primates compared to other mammals is a starvation risk aversion strategy.

Juveniles of species consuming seasonally available food resources, such as fruit, can minimize energetic requirements by growing slowly. Extending this line of reasoning, juveniles of species consuming readily available food resources such as foliage don't face starvation risk and can consequently grow more rapidly.

This study suggests that, because gums, like foliage, are more reliably available year-round [Bearder, 1987; Nash, 1989], gummivorous galagids should grow more rapidly than frugivorous galagids. Both species studied consume insects, but *Go. senegalensis* also relies on gums while *O. garnettii* also relies on fruit [Nash et al., 1989]. Thus, the RAH proposes that *O. garnettii* should grow more slowly compared to *Go. senegalensis*. Methods mirrored those in Chapter 3, but with the comparison being between *O. garnettii* males and *Go. senegalensis* males and between *O. garnettii* females and *Go. senegalensis* females.

There were no significant differences in the proportional growth rate between male *O. garnettii* and *Go. senegalensis*, but *Go. senegalensis* females grow more slowly than *O. garnettii* females so the hypothesis was unsupported. Questions were raised regarding the underlying assumption that gums are similar to foliage in that they are more reliably available compared to fruits. However, that gums are a fallback food for many species suggests this assumption is valid [Bearder & Martin, 1980a; Garber, 1993; Génin, 2003; Génin et al., 2010; Isbell, 1998; Joly-Radko & Zimmermann, 2010; Nash, 1986a; Nash & Burrows, 2010; Porter & Garber, 2006; Power, 2010; Radespiel et al., 2006; Smith, 2010; Swapna et al., 2010].

It was also noted that *O. garnettii* wean their infants during the dry season while *Go. senegalensis* wean their infants during the wet season. *O. garnettii* would presumably face greater resource competition and would benefit from growing faster and being larger at weaning. *Go. senegalensis* females on the other hand would not face the same level of resource competition either following weaning or during adulthood as their food resources are more readily available. They can thus afford to grow slowly and cease growing at a smaller mass. This would allow them to begin reproducing earlier thus increasing their reproductive success. That a significant difference in growth rate was indicated for early growth but not late growth is suggestive that resource competition at weaning is an important factor influencing growth. Further study of the life history of each species would be helpful.

While the growth of females might be strongly influenced by natural selection and competition for resources following weaning, the growth of males may be more strongly influenced by sexual selection. Coupling both natural and sexual selection theories it is hypothesized that *Go. senegalensis* females, which experience low feeding competition both at weaning and, presumably during adulthood, grow slowly and cease growing at a relatively smaller mass. As *O. garnettii* females face greater competition for food both following weaning and as adults relying on a more seasonal food resource, selection for rapid growth to attain larger mass at weaning could be advantageous. Males of both species have the need for larger size to successfully compete for females. As galagid males would not face rapid increases in either intrasexual aggression or predation risk, rapid growth in the form of an adolescent growth spurt (as commonly characterizes male haplorrhines forming single-male/multi-female groups) is unnecessary and lengthening the duration of growth is sufficient. Thus, the growth patterns of these galagids might best be modeled by integrating both natural selection focusing on resource competition following weaning and sexual selection with life history schedules and the timing of weaning.

It is interesting that in both the comparisons made in Chapter 3 and Chapter 4, *Go. senegalensis* females grow significantly more slowly. Chapter 3 shows that *Go. senegalensis* females grow slowly compared to *Go. senegalensis* males while Chapter 4 shows that *Go. senegalensis* females grow slowly compared to *O. garnettii* females. Additionally, piecewise regression indicates that *Go. senegalensis* females begin growth deceleration earlier than *Go. senegalensis* males and both *O. garnettii* males and females. The inclusion of additional galagid species could lead to conclusions as to whether the growth pattern of *Go. senegalensis* females is unusual within the galagid clade.

Results of both comparisons in Chapter 3 and Chapter 4 correlate partially with Leigh's [1994a] finding linking growth patterns and diet. Leigh demonstrated that folivorous haplorrhine females cease growing at a smaller mass. The reasoning is that since foliage is a reliable food resource, intrasexual competition is reduced. As folivorous females face less feeding competition, there is little advantage to growing large so energy investment can be allocated from growth to reproduction at an earlier age. *Go. senegalensis* females do cease growing at a relatively smaller size compared to frugivorous *O. garnettii* females.

The same pattern would not be expected for males. While folivorous males may not need to be large to successfully compete for food, like frugivorous males, they would need to be large to successfully compete for females.

Future Research

This study leads to several questions regarding hypothesized links between body mass ontogeny and socioecology. Questions are raised not only regarding galagids, but for other primates as well. There is an unfortunate paucity of body mass growth data from non-Malagasy strepsirrhines. Strepsirrhines represent the link between higher primates and other mammals [Kappeler, 1996]. In fact, strepsirrhine growth hormones and their underlying genes are more similar to nonprimate mammals than they are to higher primates. Haplorrhine growth hormone genes appear to have undergone rapid evolution, and are characterized by high variability [Adkins et al., 2001; Li et al., 2005; Liu et al., 2001; Wallis et al., 2001; Ye et al., 2005]. Thus, analysis of additional strepsirrhines would broaden our understanding of growth and its flexibility among not only primates, but mammals in general. Also, studies of strepsirrhine growth can examine the influence of socioecological factors that are rare or absent among haplorrhines.

In the introduction it was noted that hypotheses developed from haplorrhine studies are not always supported by strepsirrhine data. The majority of growth studies of strepsirrhines have focused on lemurs. Explanations for contrasting results included a strepsirrhine/haplorrhine dichotomy and phylogenetic constraints, possibly relating to the amount of growth variability present within each clade [Adkins et al., 2001; Kirkwood, 1985; Lee & Kappeler, 2003; Roberts, 1994; Wallis et al., 2001], and the unpredictability of Madagascar's environment leading to unique adaptations within the lemuriforms [Dewar & Richard, 2007; Jolly, 1984; Pereira, 1993; Richards & Nicoll, 1987; van Schaik & Kappeler, 1996; Wright, 1999]. In the first case, galagids would be expected to share similarities with lemuriforms while in the latter case galagids might be expected to share similarities with haplorrhines. This study did not support either scenario unequivocally. Despite limited variability in growth hormone genes, strepsirrhines exhibit considerable variability in both growth rates and growth durations and do not appear to be constrained in either growth processes. In examination of associations between growth and diet, my results do not clearly accord with those reported for either lemuriforms or haplorrhines. Instead, a more complex interaction between diet, growth and weaning seasonality was proposed. In examination of the ontogeny of SSD, a complex interaction between social organization, mating system, and litter size may be at play.

Galagids have been kept in captivity at several institutions and it is likely that growth data exists for additional species. For instance, the Duke Lemur Center has housed *Otolemur crassicaudatus*, *Go. moholi* and *Gs. demidovii*. Growth data is known to exist for the first two species and possibly exists for *Gs. demidovii*. Additional growth data may exist for *Gs. zanzibaricus*, a portion of which is referenced in Chapter 2. Galagid skeletal specimens are held in numerous museums and other research institutions [Olson & Nash, 2002-2003].

It is likely that these collections include subadults. Data from these sources could be gathered and incorporated into a study of ontogenetic and/or allometric scaling. Problems with using these data in this fashion currently include a lack of foundation for assessing age of galagids without know dates of birth and a lack of information regarding the relationship between linear skeletal elements and body mass. Linear growth data are available for *Go. senegalensis* and would, therefore, be more directly comparable to museum specimens.

Chapter 3 identified the need for greater information regarding different aspects of galagid social organization. Specifically more data on mating systems, the presence of two types of males, and paternity are needed. These could be used for subsequent evaluation of the mechanism by which sexual size dimorphism is attained in various species. Pullen [2000; 2000] has demonstrated both paternity and longitudinal growth data can be collected in the field. *Go. moholi* were trapped and fitted with radio-collars. Radio-tracking allowed females, and thus their infants, to be repeatedly located during the non-active period and removed from the nest for further data collection. Radio-tracking has previously been used by several researchers studying galagids during their night-time activities and to examine day-time sleeping associations, but subjects are generally handled rarely once they are fitted with radio-collars. Pullen used radio-tracking to locate infants during the inactive period so longitudinal growth data could be collected. Tissue samples from infants were also collected for paternity testing which was then compared with data on copulatory behavior.

Such methods could be replicated for additional species of galagids. However, limitations for certain species exist. For instance, while other small primates (e.g. *Microcebus*, *Tarsius* [Gursky, 1998; Radespiel et al., 1998]) have been fitted with radio-collars, the influence of the collar's additional mass on the behavior of smallest species is unknown. No behavioral difference were reported for *Tarsius spectrum* [Gursky, 1998], but health was not examined and this tarsier species is approximately twice the mass of the smallest galagids. Studies of the effects of radio-collars on behavior, health, and survival of other small mammals and birds have produced conflicting reports [Gursky, 1998] and further study of the effects, if any, on the smallest of primates would be helpful. Additionally, galagids inhabiting difficult terrain or higher altitudes of the forest will be more difficult to observe, follow, trap, and remove from sleeping sites. Pullen [2000] notes that *Go. moholi* nesting in tree hollows were difficult to extract while other galagids (e.g. some *Galagoides*, *Euoticus*) are difficult to trap, and thus radio-collar, in the first place [Charles-Dominique, 1977; Honess, 1996].

Chapter 4 was an initial attempt to link a gummivorous diet with growth. Further studies of other gummivorous or exudativorous primates would be useful. Species consuming plant exudates, either regularly or as a fall-back during the dry season, are found not only within the Galagidae, but also within lorisids, lemuriforms, cebids and catarrhines [Nash, 1986a; Smith, 2010]. Comparisons of the growth of species regularly consuming gums and other exudates with their closely-related non-gummivorous counterparts could uncover whether the differences found here are generally applicable to gummivores in general. This comparative method could help uncover whether or not there are growth pattern correlates of gummivory.

Examination of the growth patterns of other species with reliable food resources could test the applicability of the RAH in general. *Erythrocebus patas* consume gums, social insects and swollen thorns all of which the authors suggest are reliable in both space in time [Isbell, 1998; Isbell & Young, 2007]. That this species grows more quickly than similarly sized frugivorous cercopithecids [Leigh, 1994a] supports the RAH suggesting that a wider variety of dietary categories can be useful for testing this hypothesis. *Hapalemur* species consume variable amounts (and different parts) of bamboo which has a stable distribution through time [Overdorff et al., 1997; Tan, 1999a; Wright & Randrimanantena, 1989]. *Daubentonia* relies on seeds and galls, both of which are readily available year-round [Iwano & Iwakawa, 1988; Pollock et al., 1985; Sterling, 1994]. The RAH would predict that these latter two species should grow more quickly compared to their fruit-eating counterparts.

Additionally, the availability of specific food resources within the larger dietary categories (e.g. folivory, frugivory) needs investigation. For instance, some fruit resources may be more reliable than some foliage resources. Certain tree species might produce gum more reliably than others [Génin, 2008; Génin et al., 2010]. Many insects may be seasonally available [Karr, 1976; Wolda, 1988], but the social ants upon which *E. patas* relies are said to be stable through time [Isbell, 1998]. While there may be general differences in availability between dietary categories, further investigation of availability within each dietary category, and indeed, within different habitats, is needed.

Chapter 4 proposed that resource reliability coupled with weaning seasonality explained growth differences. For further testing of this hypothesis, socioecological, ontogenetic and life history data are needed. Generally, birth seasonality (and presumably weaning seasonality) is more common among primates relying on seasonally available food resources and variability of weaning foods may be a primary driving force for reproductive seasonality [DiBitetti & Janson, 2000]. More research is needed on weaning schedules for individual primate species and their growth patterns along with weanling food availability. Comparisons of growth rates between species with high food availability following weaning and species with low food availability following weaning would provide tests of this hypothesis.

Examination of growth patterns of non-seasonally reproducing primates may also be fruitful. The current hypothesis links weaning food availability with growth rate. Species that wean when food availability is low face selection pressure to grow quickly to produce a larger, and presumably more competitive, weanlings while species that wean when food availability is high can afford grow slow (can afford to be small at weaning) as they face lower competition for resources. Following this line of reasoning, species that do not breed seasonally should be correlated with high food availability year-round and would not face selection pressure to grow quickly and produce larger weanlings.

While the majority of Malagasy primates are strict seasonal breeders [Wright, 1999], *Daubentonia* is not [Ancrenaz et al., 1994; Sterling, 1994]. This species is omnivorous and several of its food resources are reliable in space and time [Ancrenaz et al., 1994; Erickson, 1995; Iwano & Iwakawa, 1988; Pollock et al., 1985; Sefczek, 2009]. Glander [1994] reports a linear growth rate of 4 grams per day for captive subjects. Comparing this to Godfrey et al.'s [2004] Fig. 8 suggests that this lies much closer to the regression for folivorous indriids than for frugivorous lemurids. In other words, *Daubentonia* grows more slowly compared to similarly sized frugivorous lemuroid species and more like folivorous lemuroid species. Such would be expected if high growth rate is associated with low availability of food following weaning.

Comparisons of the growth rates of *Hapalemur* could be similarly informative. Like *Daubentonia*, *Hapalemur* may breed less seasonally than other Malagasy primates [Overdorff et al., 1997; Tan, 1999b; Wright, 1999]. Tan [1999b] reports that *Hapalemur griseus* has an extended birth season suggesting a lack of weaning seasonality. A linear growth rate of 3.2 grams per day is reported for *Hapalemur griseus* [Godfrey et al., 2004]. Comparison of this growth rate with Godfrey et al.'s Fig. 8 shows that this lies where the regressions for indriids and lemurids cross making it difficult to ascertain whether *Hapalemur* is more similar to folivorous or frugivorous lemuroids. Leigh's [1994a] Fig. 3 suggests that *Hapalemur* grows more slowly than similarly sized frugivorous *Eulemur* providing limited support for the hypothesis. Comparison of growth patterns between differing *Hapalemur* species would be useful.

Further research on juvenile foraging competency and weaning food availability would also be an area of research interest. Little is known of the actual foraging capabilities of juveniles for most species of primates. Foraging competency would vary not only with dietary type and ontogeny of morphology, but with social organization and life history, especially as they relate to the number of competitors. While studies of diurnal juveniles should be no more difficult that studies of diurnal adults, obtaining data on feeding behavior of nocturnal species may be near impossible. However, Nekaris [2009; 2003] shows that, for some species, it can be accomplished.

None of the hypotheses linking growth pattern and socioecology was clearly supported. Instead, the need for future research was highlighted. Gursky & Nekaris [2003] note that "… it is important to study the variation present in the nocturnal prosimian primates if we are ever able to make broad correlations concerting ecology and behavior." As the ancestral primate is described as similar in size, morphology, and behavior to galagids (e.g. small body mass, nocturnal, hind-limb dominated leaping, insect predation, and, possibly the consumption of gums [Charles-Dominique & Martin, 1970; Martin, 1972a, 1979; Martin, 1990; Nash, 1986a]), the primitive growth pattern of this clade could be inferred as the primitive growth pattern for primates in general. Study of how and why growth patterns have diverged through evolution is important in discerning the evolutionary history of species. This study examined a small piece of the puzzle, the association of social organization and of diet with growth patterns of galagids. Similar avenues of study should provide research opportunities for years to come.

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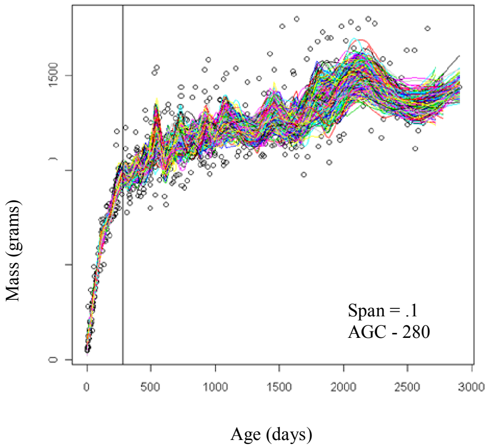
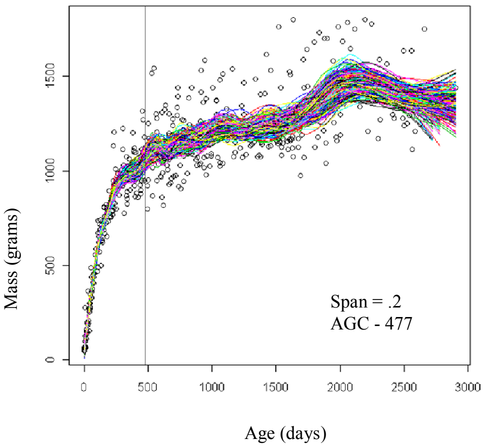
APPENDIX A

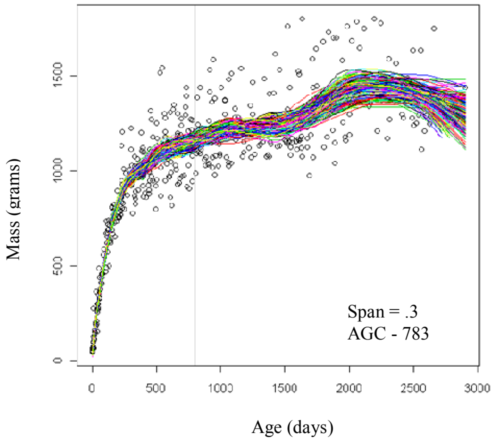
CHOOSING SMOOTHING PARAMETER

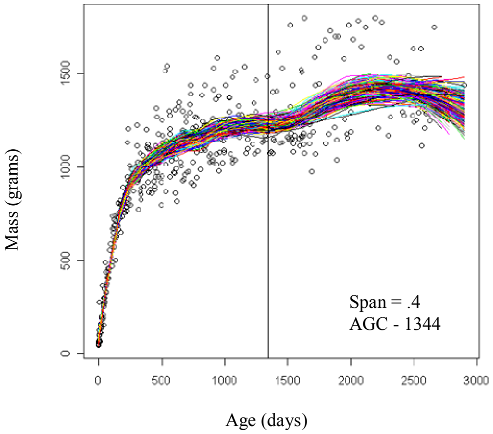
Using R2.10.0, resampling with replacement (bootstrapping) (Appendix B) was used to fit the ontogenetic data with LOESS. Graphics are depicted below showing the bootstrapped LOESS trajectories and estimated age at growth cessation AGC (vertical line) with spans of .1, .2, .3, and .4. The AGC should estimate the point where the ontogenetic trajectory is no longer increasing in size and levels off. Upon visual inspection of the graphics using spans of .1 and .2, the LOESS is jagged and appears to underestimate AGC (the estimated AGC precedes the point where the LOESS trajectory levels off). LOESS using spans of .3 and .4 are smoother, but the span of .4 appears to overestimate AGC (the LOESS trajectory appears to level off prior to this estimated AGC). A span of 0.3 was selected as the smoothing parameter that that accounted for all prominent features of the data without undue noise [Cleveland, 1979; Cleveland & Devlin, 1988]. For the other three groupings of data, a similar pattern was found at each span, respectively. Thus, the span of .3 provided the best fit (smoothing and AGC estimation) for all four groupings of the data.

Otolemur garnettii males

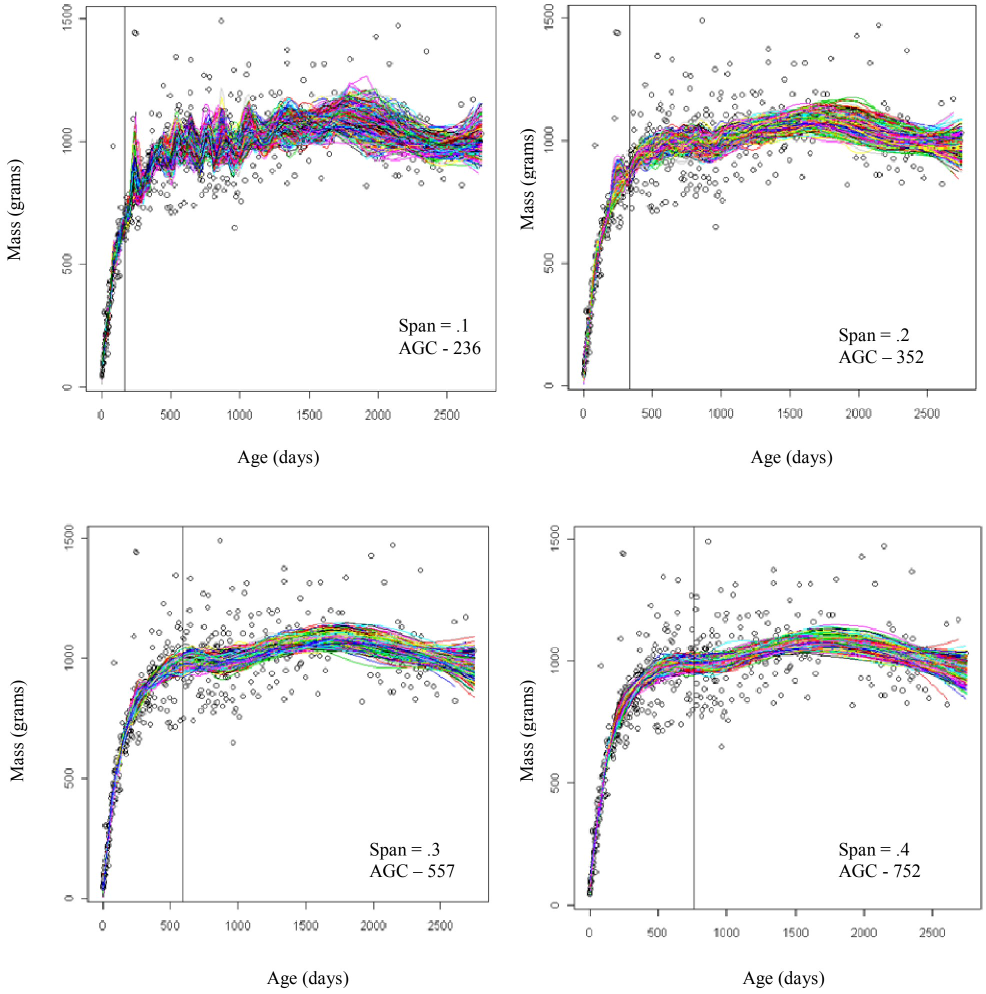




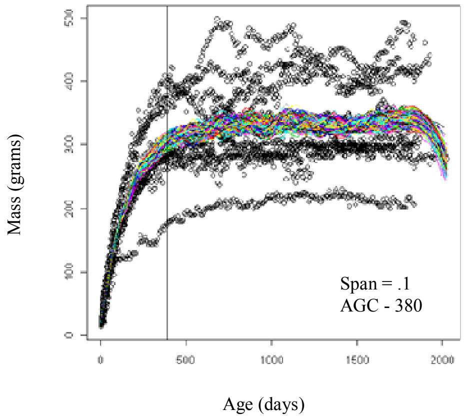


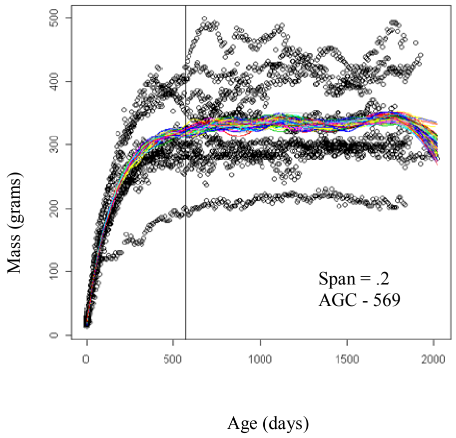


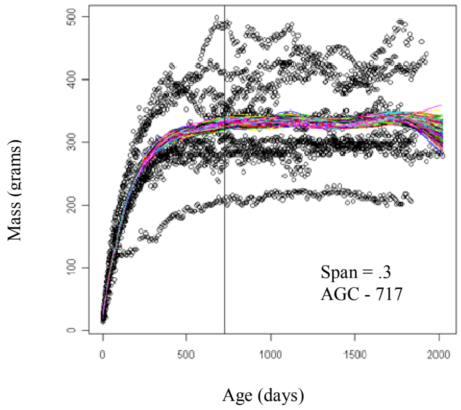
Otolemur garnettii females

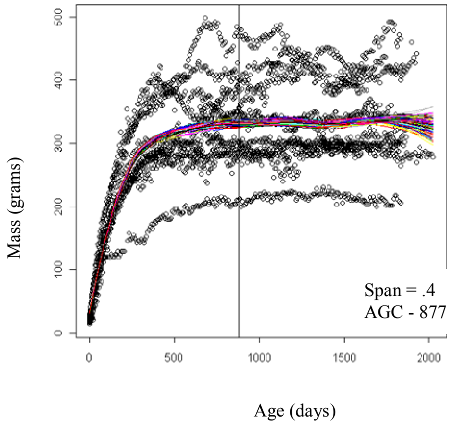


Galago senegalensis males

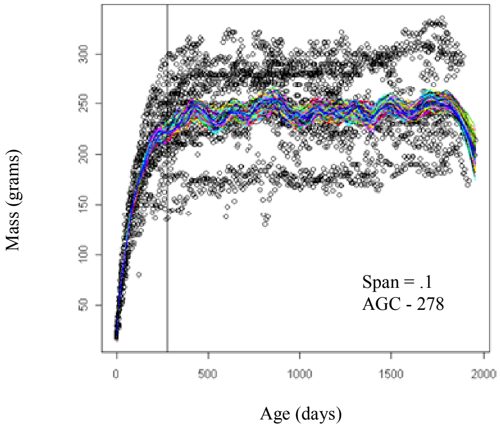


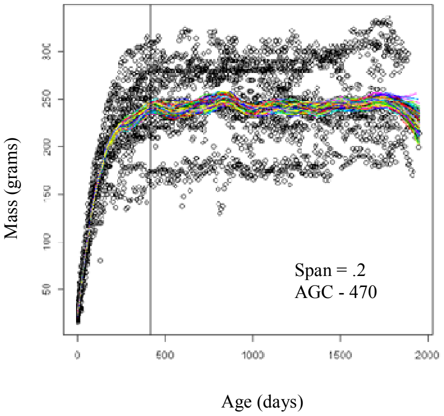


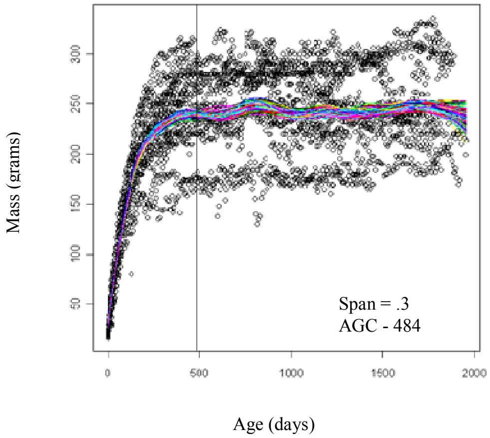


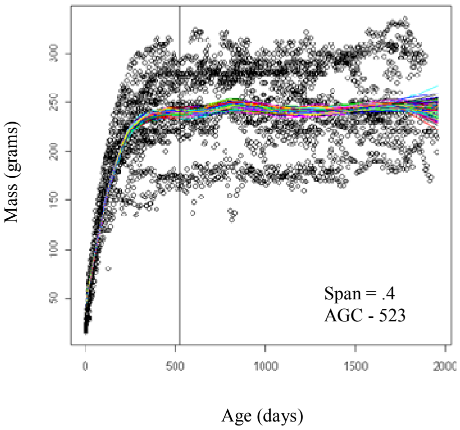


Galago senegalensis females









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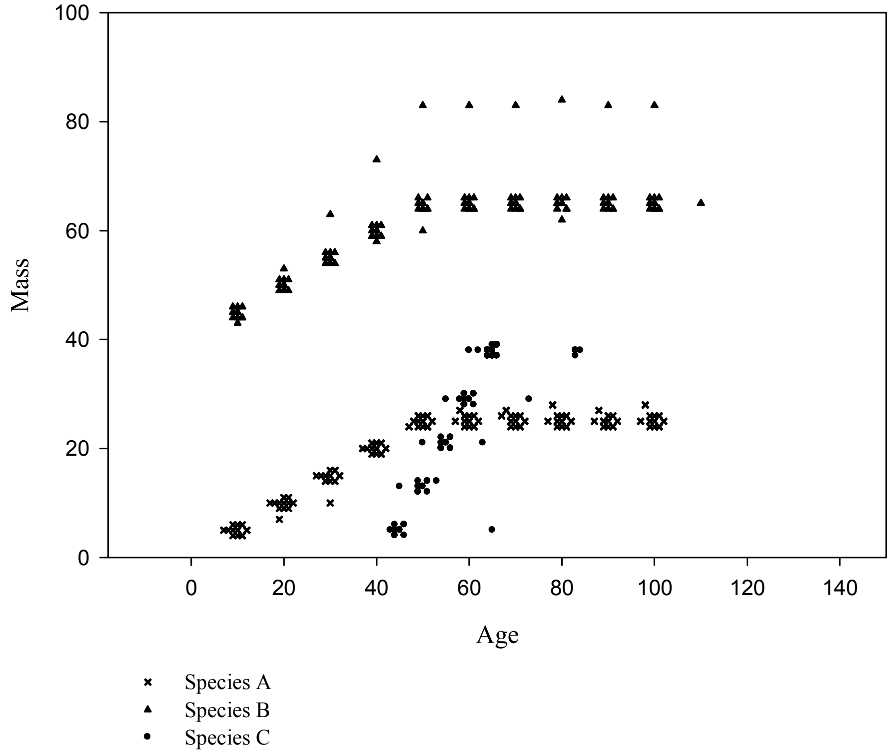
APPENDIX B

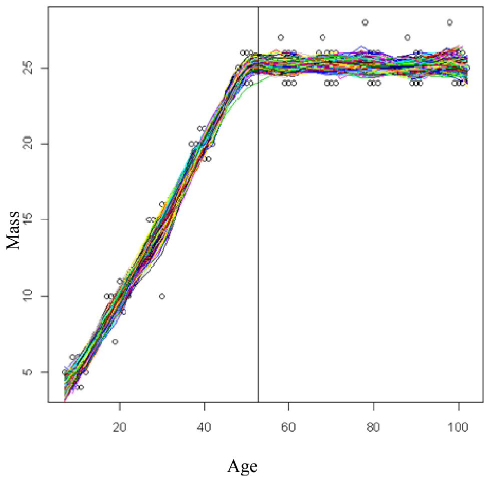
TESTING PROGRAMS WITH SIMULATED DATA

The program used to estimate the age at growth cessation (AGC) and the program used to compare slopes were first tested using simulated data. Three dataset, each including 130 data points (mass at age) with known AGC and slope were created. A program was written in R2.10.0 (Base Package) to collect the first local maximum of the growth curve from each bootstrapped sample. The first local maximum of the growth curve is equivalent to the first time the first derivative of the growth curve with respect to age (i.e. a pseudovelocity curve) is equal to zero. This first local maximum represents the first point of the trajectory where there is no size increase [R Development Core Team, 2009; Venables & Ripley, 2003] and estimates the age at growth cessation. In all runs of the program using the simulated datasets, AGC was correctly estimated to within 2 days of the actual AGC. Assistance in writing the source code was provided by S. Latimar, MSTAT, Senior Research Analyst, University of Utah.

Simulated Data



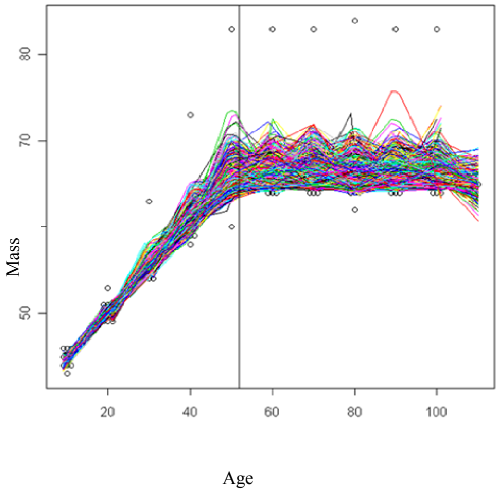
“Species A”



Actual AGC = 50 days
Estimated AGC = 51.2 days (SEM = 0.331, 1000 replications)

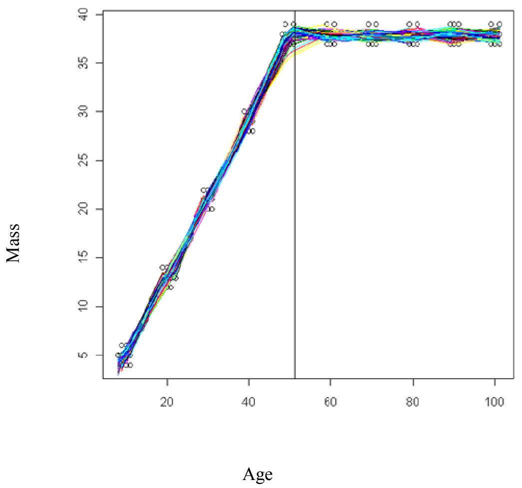
Actual Slope = 0.500
Estimated Slope = 0.498 (± 0.021)

“Species B”



Actual AGC = 50 days
Estimated AGC = 51.8 days (SEM = 0.411, 1000 replications)

Actual Slope = 0.500
Estimated Slope = 0.512 (± .029)



“Species C”

Actual AGC = 50 days
Estimated AGC = 51.4 days (SEM = 0.216, 1000 replications)

Actual Slope = 1.00
Estimated Slope = .986 (± .029)

The second program tested used an exact F-statistic to compare the sum of squares when a common slope is fitted to pooled data and when a separate regression line is fitted to each sex separately [Sokal & Rohlf, 1995; Warton et al., 2006]. This method is robust to non-normality and does not assume equal variance between groups [Warton, 2007; Warton et al., 2006]. The F-test program correctly identified which slopes were significantly different and which ones were not. The ANOVA function (Base Package, P.2.10.0) was used to compare the two models.

Comparison	F statistic	Significance
Species A versus Species B	0.772	P > 0.381
Species A versus Species C	87.65	P > 0.001***
Species B versus Species C	97.39	P > 0.001***

---

bootloess *Bootstrap estimation of age at growth cessation*

Description

This function takes data on age and mass and computes local regression curves using bootstrap resampling. It returns a vector containing the bootstrap estimates (the first local maximum) for age at growth cessation and mass at growth cessation.

Usage

`bootloess(X,N=1000,span=.1)`

Arguments

X	a data matrix with two columns age and mass
N	The number of bootstrap samples
span	The smoothing parameter for the local regression Span is the proportion of the data vector used in each local regression.

Details

This performs bootstrap resampling of the data, computes the local regression fitting, and identifies the first local maximum of the resulting fit.

Value

aagc A two by N matrix, the first column containing the age at growth cessation estimates, the second column containing the mass at growth cessation estimate.

Authors

S. Latimar, seth.latimar@nurs.utah.edu; M. Schaefer, asums@asu.edu
10-20-2010

Examples

```
bootloess=function(X,N=1000,span=.1)
{plot(X) n=length(X[,1]) aagc=matrix(0,ncol=2,nrow=N)
for( i in 1:N)
{XX=X[sample(1:n,n,replace=T),] out=loess(XX[,2]~XX[,1], span=span)
pred=predict(out)[order(XX[,1])] lines(sort(XX[,1]),pred,col=sample(1:8,1))
aagc[i,]=c(age=sort(XX[,1])[which(diff(pred)<0)[1]],mass=sort(XX[,2])[which(di
ff(pred)<0)[1]])}
aagc}
```

---

slope *Common slope test for two regression lines*

Description

This function tests if two Ordinary Least Squares regression lines share a common slope.

Usage

```
anova(lm1,lm2)
```

Arguments

lm1	linear model fit to pooled data
lm2	linear model fit to subsets of data

Details

This function tests if the line-of-best-fit has a common slope for pooled data as for separated data. The line-of-best-fit is estimated using the Ordinary Least Squares.

Value

F	The exact F-statistic
p	The p-value of the test
b1	the slope and standard error of OLS fit to pooled data
b2	slopes and standard error of OLS fit to separately to subset of data

Authors

Seth Latimar, seth.latimar@nurs.utah.edu; Melissa Schaefer, asums@asu.edu 10-20-2010

Examples

```
lm1=lm(mass~age+sex)
summary(lm1)
lm2=lm(mass~age+sex+age*sex)
summary(lm2)
anova(lm1,lm2)
```

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APPENDIX C

EVALUATION OF NUMBER OF ITERATIONS

The age at growth cessation (AGC) for each group was estimated using resampling methods, specifically, resampling with replacement or bootstrapping [Roff, 2006]. When resampling, the standard error of the mean (SEM) decreases with increasing number of replications. This pattern is seen below. The age at growth cessation (AGC), the standard error, and the standard error of the mean were estimated using 200, 1000, 2000, and 5000 replications. The number of replications had little directional effect on the mean AGC, but it did influence the SEM. Too many replicates can render the confidence intervals estimated from bootstrapped estimates too small to make comparisons between estimates entirely reliable [Potvin & Roff, 1993]. Roff [2006] recommends using 200 replications to estimate the standard error and 1000 replicates to estimate confidence intervals. This protocol for estimating confidence intervals from SEM estimated from 1000 replications was used for this study to provide larger confidence intervals and thus greater confidence in the results.

Span .3 was used for all groups

Number of replicates	*O. garnettii* male	SE	SEM	*O. garnettii* female	SE	SEM
200	795.8	347.0677	24.541390	555.2	118.60156	8.386397
1000*	783.2	370.8230	11.726452	557.0	119.67305	3.784394
1000	772.4	364.5148	11.526971	556.1	121.04078	3.827646
2000	774.0	375.7473	8.401964	558.1	127.99053	2.8619551
2000	785.1	364.9289	8.160057	555.7	120.06046	2.684633
5000	772.8	373.4170	5.280913	556.0	132.16308	1.8690681
5000	782.6	367.0360	5.190673	557.6	129.01018	1.8244795
	Go. senegalensis male			*Go. senegalensis* female		
200	719.7	150.64631	10.6523032	487.1	96.18869	6.8015676
1000*	717.4	157.84227	4.991411	484.0	93.07583	2.9433163
1000	728	151.95950	4.8053816	482.1	83.134003	2.6289280
2000	722.5	156.4469	3.2469849	481.7	87.516976	1.956939
2000	716.7	152.52641	3.4105942	483.4	89.398851	1.9990191
5000	714.4	153.27816	1.9857689	483.6	91.332688	1.2916393

*Results used in this study.

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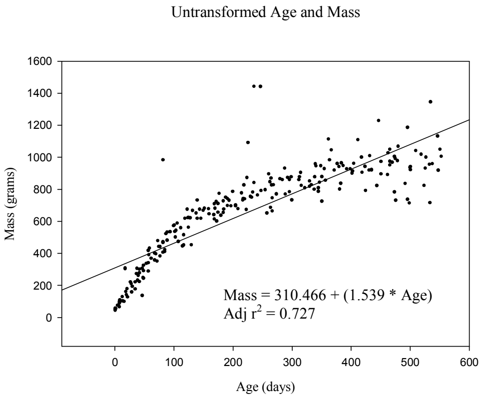
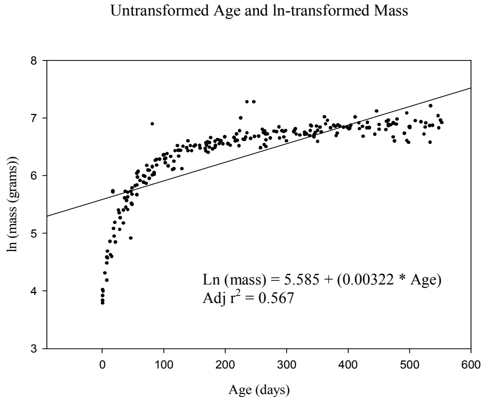
APPENDIX D

NATURAL LOG TRANSFORMATION

APPENDIX D

Log-transformation of data is statistically useful because linear regression lines are easier to visually inspect, outliers are more easily recognized, and the variables under examination are more likely to be normally distributed, homoscedastic, and linear when log-transformed compared with raw data [Smith, 1993; Sokal & Rohlf, 1995]. Below are graphics of ordinary least-squares regression (OLS) fit to untransformed data, untransformed age and natural log-transformed mass, and natural log-transformed age and natural log-transformed mass. *Otolemur garnettii* female data were used for visual depiction of this process though all four groups (*O. garnettii* males, *O. garnettii* females, *Galago senegalensis* males, and *G. senegalensis* females) were examined (Table 1). The r^2 gives an indication of goodness of fit of the regression to the data; the higher the r^2, the better fit. Natural log-transforming both age and mass provided the best fit of OLS regression. Visual inspection of the graphics also indicates that OLS fits the natural log-transformed data best.





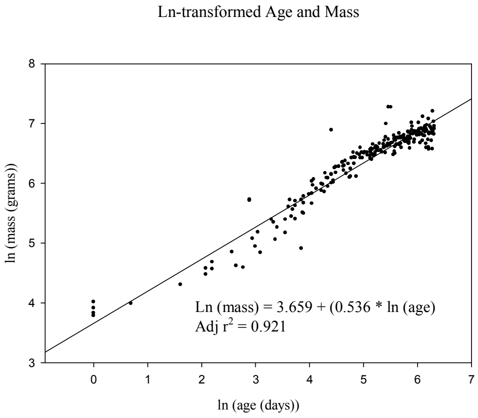


Table 1. Results of OLS regression on raw and natural log-transformed data.

Group	Regression	Adjusted r^2
O. garnettii males		
raw data	mass = 398.672 + (1.245 * age)	0.687
(ln) mass x age	(ln) mass = 5.736 + (0.00233 * age)	0.518
(ln) mass x (ln) age	(ln) mass = 3.755 + (0.522 * (ln) age)	0.906
Go. senegalensis males		
raw data	mass = 118.322 + (0.384 * age)	0.614
(ln) mass x age	(ln) mass = 4.565 + (0.00233 * age)	0.517
(ln) mass x (ln) age	(ln) mass = 2.747 + (0.488 * (ln) age)	0.883
Go. senegalensis females		
raw data	mass = 90.633 + (0.413 * age)	0.640
(ln) mass x age	(ln) mass = 4.351 + (0.00322 * age)	0.550
(ln) mass x (ln) age	(ln) mass = 2.817 + (0.455 * (ln) age	0.895

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