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ONTOGENY AND THE EVOLUTION OF BODY SIZE DIMORPHISM IN PRIMATES

ABSTRACT: Recent research shows that anthropoid primates exhibit considerable variation in the ontogeny of body size sexual dimorphism. In general, there are two basic patterns by which primates become sexually dimorphic. Dimorphism can develop through differences in the rate of body weight growth. In such species, males tend to exhibit very obvious pubertal or "adolescent" growth spurts. Although males of these species typically grow for longer periods of time than females, the duration difference in growth often contributes little to the total resultant dimorphism. A second ontogenetic pathway to sexual dimorphism mainly involves sex differences in the duration of the growth period (bimaturism). In these taxa, males typically grow for longer periods of time than females, but there are often only slight sex differences in growth rates. In species that are not sexually dimorphic as adults, there is usually little variation between sexes in growth rate and duration.

Investigation of these alternative ontogenetic pathways indicates that multiple factors influence the ontogeny of sexual dimorphism in primates. Interspecific variation in female ontogeny, which can be quite substantial, corresponds to life history variation. Specifically, dietary and reproductive correlates of female ontogeny are apparent. In addition, differences among species in the degree and kind of interfemale competition relate to ontogenetic diversity. Variation in male ontogeny covaries most closely with intermale mating competition. Ontogenetic variation among species in male growth is structured according to the kinds of risks that males encounter. Specifically, prolonged growth with bimaturism is related to risks of intermale competition that increase steadily with age. On the other hand, risks encountered by males seem to change rapidly in those species that exhibit large male growth spurts, limited bimaturism, and high dimorphism. These analyses demonstrate the importance of ontogenetic and life history information in explaining the complex phenomenon of primate sexual dimorphism.

KEY WORDS: Monkeys and apes – Growth – Development – Sexual selection

INTRODUCTION

The popularity of ontogenetic approaches to evolutionary problems has increased considerably in the last twenty years. One area in which ontogenetic research holds compelling promise is in the study of primate sexual dimorphisms. Evaluations of primate dimorphism can take advantage of an ontogenetic perspective mainly because information about ontogeny reveals the actual proximate causes of adult morphologies. In other words, study of ontogeny provides information about the developmental processes that actually lead to adult results (Shea, 1986). It is thus imperative that ontogenetic analyses find application to investigations of sexual dimorphisms in primates. With this basic principle as a foundation, the present paper focuses on the role of ontogeny in producing primate sexual dimorphisms. Specifically, this paper examines historical ideas about sexual dimorphism and explores the links between these concepts and ontogenetic theory. Current studies of the relations between ontogeny and dimorphisms are reviewed. Finally, directions for future research are identified and considered.

HISTORICAL ASPECTS OF SEXUAL SELECTION THEORY

As recognized by Darwin (1859; 1871), the vast majority of sexual dimorphisms in morphologies cannot be explained in terms of natural selection (*contra* Wallace, 1895). This fact forced Darwin to recognize sexual dimorphisms as important exceptions to the theory of evolution by natural selection. The challenge posed by sexual dimorphisms to the concept of natural selection was so serious that, in *On the Origin of Species*, Darwin cautiously explained the basic idea behind sexual selection, then deferred extensive discussion of the issue until publication of *Sexual Selection and the Descent of Man* (1871). Darwin's caution was justified: according to Huxley, "None of Darwin's theories have [*sic*] been so heavily attacked as that of sexual selection" (1938:11).

In *Sexual Selection*, Darwin argued that sexual dimorphisms could evolve in the presence of selection only in relation to reproduction. In other words, sex differences in secondary sexual characteristics could evolve if those individuals possessing certain traits left more offspring than individuals without such traits. Sexual selection was "less rigorous" than natural selection. It did not necessarily result in morbidity or mortality (1871:278) but was instead a "struggle for reproduction" (Huxley, 1938:12). Moreover, Darwin recognized that this process applied almost exclusively to males, and perceptively identified two basic ways in which sexual selection could operate. These mechanisms have been fully verified by subsequent researchers, although considerable debate about their relative importance remains (Moore, 1990; 1994). First, females could choose mates based on certain attributes (such as plumage in some highly ornamented birds). These traits are of no apparent advantage in terms of natural selection. On the contrary, such traits could elevate risks of predation on males. Second, sexual selection could be manifested by intermale competition, so that males with the most effective weaponry could outcompete other males for access to mates. Together, these mechanisms seem to explain the evolution of certain male characteristics. Darwin emphasized each mechanism equally, although there has been persistent debate on whether or not he emphasized one mechanism at the expense of the other.

Throughout the early part of the 20th century, comparatively few theoretical or empirical analyses of sexual dimorphism were undertaken. However, R.A. Fisher greatly expanded the applicability of sexual selection theory by providing a detailed assessment of the process (1930). At the most basic level, his study provided a mathematical and theoretical foundation for sexual selection theory that demonstrated the power of this process. Most importantly, Fisher clearly specified a process by which "maladaptive" traits can evolve, thus explaining the evolution of male ornamentation. Fisher's model relies on two foundations. First, one sex (usually the female) must express a mating preference based on the trait. Second, ecological conditions must allow the existence of this mating preference, conferring a reproductive advantage to individuals with this preference. Under these conditions, a trait under sexual selection can evolve rapidly even when the advantage of that trait is minimized under natural selection (1930:152). If female preference is of sufficient intensity, the trait will continue to evolve towards a more extreme male character state until sexual selection is checked by "severe counterselection in favor of less ornamented males" (Fisher, 1930:152). Fisher termed this model "runaway selection," marking the beginning of sophisticated theoretical treatments of sexual selection.

A major component of Fisher's model involves the arbitrariness of female mate choice, suggesting that female mate choice need not be based on characters that signal male viability (although selection on this basis could occur). In essence, runaway selection requires only that some characteristic be chosen by females, whether or not such traits are correlated with increased male survivability. In contrast to this idea, several researchers have suggested that "maladaptive" or "arbitrary" male characters actually signal male viability (or "good genes"). This idea has historical roots in Wallace's argument that females choose mates based on "vigour and liveliness" (1895:369; see also Maynard Smith, 1956:278). In general terms, arbitrary mate choice models and viability models are posed as alternative possibilities (see Arnold, 1983; Borgia et al., 1985), but they need not be mutually exclusive alternatives (Moore, 1994). Historically, these models have proven exceptionally difficult to evaluate, and the relative importance of these processes remains a source of controversy among sexual selection theorists.

CONTEMPORARY SEXUAL SELECTION THEORY

Interest in sexual selection theory increased tremendously in the 1970's and early 1980's, primarily because analyses that could integrate theoretical and empirical data from the laboratory and the field became possible. For example, Emlen and Oring's study of birds (1977) showed that sufficient field data had become available for coherent integration of data with theoretical models. Goss-Custard et al. (1972) evaluated correlates between sexual selection and primate social organization. Similarly, Trivers (1974) made a major advance by defining the potential differences in female and male reproductive strategies. Trivers' idea builds on Bateman's (1948) finding that female reproductive output in *Drosophila* is limited by the number of eggs that can be produced, whereas male output is limited by the number of mates. Bateman and, later, Trivers realized that this favored two very distinctive strategies between the sexes. Trivers further reasoned that this basic difference meant that females should invest in quality of offspring, while males should seek to maximize mating opportunities. The fundamental distinction that Trivers identified can be seen as a cornerstone of the evolution of sexual dimorphisms in mammals, as well as any other taxa in which investment in offspring differs according to sex.

Empirical and theoretical lines of inquiry were further advanced by Ralls' evaluations of sexual dimorphism in mammals (1976; 1977). This research significantly extended the research of Emlen and Oring as well as Trivers. Ralls argued that models formulated to explain sexual dimorphism in birds did not apply well to mammals. Specifically, Ralls noted that body size dimorphism, rather than dimorphism in ornamentation, was quite common among mammals. She also recognized complications in explaining body size dimorphism in terms of models that addressed the evolution of arbitrary characters. Although body size could be an arbitrary characteristic, it is generally tightly integrated with all aspects of anatomy, physiology, and behavior (Schmidt-Nielson, 1984). Therefore, Ralls affirmed the need for new theoretical advances in studies of mammalian sexual dimorphism. In so doing, she explicitly discussed the potential held by ontogenetic studies, and called for such approaches. For example, Ralls emphasized research by Wiley (1974) which showed that age at maturation among male grouse was positively correlated with probability of mating success.

Advances in sexual selection theory during the late 1970s and 1980s focused mainly on the quantitative genetics of mate choice. In an important series of articles, Lande (1980; 1981; 1987) made significant advances towards understanding the evolution of female mate choice. Specifically, Lande demonstrated the importance of genetic correlations for the evolution of sexual dimorphisms. According to Lande, correlations between female preferences and male traits may have a powerful impact on rates of evolution (1980). Rates of evolution by sexual selection were later shown to vary depending on the level of the additive genetic correlation between a male trait and female preference for that trait (Lande, 1987). Lande also found that sexual selection can play an important role in reproductive isolation and speciation among taxa (1981). In addition, Arnold (1983) linked laboratory and field results with quantitative genetic theory. These authors convincingly argued that arbitrary characters need not signal male viability, an assertion that directly contrasts with cogent suggestions by other authors (e.g. Borgia et al., 1985). In addition, Lande and Arnold's research implied a secondary role for intermale competition in the operation of sexual selection, at least in cases where ornamentation is particularly obvious. Much subsequent research has explored these issues, but review of these studies is beyond the scope of the current contribution (see Andersson, 1994). It can be noted that the best-designed studies (e.g. Moore's analysis of sexual selection in dragonflies (*Libuella loctuosa*) [1990] and cockroaches (*Nauphoeta cinerea*) [Moore et al., 1995]) show significant contributions to the evolution of dimorphisms from intermale competition, male experience, and female mate choice. It can also be noted that the experimental protocols employed by studies such as Moore's would be extremely valuable if they could be applied to primates. However, such studies are probably impossible for primates.

PRIMATE SEXUAL DIMORPHISM

The inherent problems of studying primates, including long developmental periods, inaccessiblity, rarity of many taxa, destruction of habitats, and lack of habituation, have resulted in analyses that typically utilize comparative and correlational approaches to analyses of sexual dimorphism. Despite these limitations, a great deal has been learned from comparative analyses. For example, Clutton-Brock and Harvey's (1977) contribution was especially influential in showing that much information could be gained from this kind of approach. In addition, these authors demonstrated the importance of phylogenetic information in comparative studies, providing a framework for subsequent research. Clutton-Brock and Harvey's findings showed that dimorphism covaried with a number of social and ecological variables. This basic result convincingly illustrated the multifactorial nature of adult body size dimorphism in primates. But, at the same time, the study illustrated the difficulties in approaching the problem of primate dimorphism. Unfortunately, it became obvious that the proportional contribution of each separate factor to dimorphism in each species would be extremely difficult to estimate.

The difficulties implied by initial studies of primate sexual dimorphism were realized and fully exposed in subsequent studies of this problem. For example, Leutenegger and Cheverud's (1982) statistical analyses implied a strong scaling component to primate sexual dimorphism. They also found that size and degree of intermale competition were important factors in the evolution of sexual dimorphism. Lesser influences included activity pattern and diet. Later research by Cheverud and colleagues (Cheverud et al., 1985) seemed to confirm this basic point, but also recorded a large phylogenetic component to primate sexual dimorphism. This result, and the earlier finding of a major size component to primate sexual dimorphism, were severely challenged (Ely and Kurland, 1989; Gaulin and Sailer, 1984). This controversy is still largely unresolved, and may not be settled using currently available data on adult size. For example, Martin et al. note that, despite numerous analyses of adult size dimorphism, there has as yet "been no convincing demonstration of a link between sexual dimorphism in body weight and the level of competition among males for access to females" (1994:174). This extremely important point implies that variation in body size sexual dimorphism has not yet been explained by studies of adult dimorphism, at least not beyond the general observation of low dimorphism in "monogamous" species and high dimorphism in some "non-monogamous" species. It can be noted that a more recent investigation tends to support the position of a major influence of intermale competition on primate body size dimorphism (Plavcan and van Schaik, ms). However, this applies, somewhat paradoxically, only to non-colobine anthropoids. It is apparent that there remain subtle but complex problems in analyzing adult body size dimorphism in primates. These problems are a result of the multifactorial nature of the causes of size dimorphism, inaccurate size data, and difficulties in measuring sexual selection. Primate studies are further constrained because these variables cannot be measured in laboratory settings. These difficulties suggest that future studies of adult dimorphism may lack sufficient power to resolve outstanding controversies. Thus, evaluations of sex differences in size among primates must seek other ways to address this important and interesting problem. One way that holds considerable potential involves conducting ontogenetic analyses of this problem.

ONTOGENETIC APPROACHES TO DIMORPHISM

In *Sexual Selection,* Darwin (1871) mentioned, but did not assess, the potential relevance of ontogeny to the evolution of sexual dimorphism. Specifically, he noted that maturational differences between the sexes bore a relation to adult sexual dimorphism in some animals (e.g., *Cebus*). He also noted that humans follow what he felt was a general primate pattern of bimaturism (female maturation prior to male maturation). Formal considerations of the relations between bimaturism and sexual dimorphism were, however, provided by Wiley (1974). His research serves as the theoretical basis for many subsequent investigations into the ontogeny of sexual dimorphisms. Wiley explored the relations between developmental or life history strategies and sexual dimorphism in vertebrates. Specifically, he showed that a male grouse's chances for successful mating are tied to size and experience. Males gain these attributes mainly though prolonged development. In other words, male grouse that survive for several years compete against younger, less experienced males for preferred lekking sites. Males can realize reproductive benefits if they defer reproduction. This research added a new dimension to models of optimal age at maturation because it showed that males and females could be expected to follow differing strategies in dimorphic species. Moreover, Wiley's research tied the evolution of sexual dimorphism to sexual differences in life history strategies.

Several researchers have applied and extended Wiley's research (Jarman, 1983; Ralls, 1977; Shea, 1986). In particular, Jarman's research on sexual dimorphism in large terrestrial herbivores has provided a major focal point for subsequent ontogenetic studies (see also Georgiadis, 1985). Jarman linked sexual dimorphism to bimaturism through sexual selection for competitive abilities among males. Delays in maturation can benefit males in two ways. First, young males can minimize the chances for injury or death through competition by retaining a juvenile appearance. Second, delayed maturation allows males to grow to sizes that would enable competition. In many species of terrestrial herbivores, this additional time permits the development of elaborate and effective weaponry.

Shea (1985; 1986; 1990) investigated the ontogeny of sexual dimorphism in primates. Shea's research followed general theoretical calls (Fedigan, 1982; Leibowitz, 1975) for increased attention to the developmental bases of sexual dimorphism in primates. Shea formalized these ideas by linking the ontogeny of sexual dimorphism directly to heterochronic and life history theories. Moreover, he provided evidence that sexual dimorphism in primates was underlain by differing ontogenetic mechanisms. This research, as well as later contributions, are evaluated in subsequent sections.

THE THEORETICAL IMPORTANCE OF ONTOGENY TO PRIMATE SIZE DIMORPHISM

Several theoretical justifications exist for analyzing ontogeny in relation to dimorphism. First, ontogenetic approaches recognize that variable ontogenies can lead to comparable levels of dimorphism. For example, the level of adult dimorphism is not solely a product of bimaturism, with the level of bimaturism directly proportional to the degree of adult dimorphism. Second, ontogenetic protocols permit evaluation of life history correlates of dimorphism. Life history theory has grown tremendously in recent years, and has significant applications in primate biology. At a more practical level, the preadult period represents a major portion of an individual's total lifespan. Third, ontogenetic analyses allow examination of female components to dimorphism. Adult dimorphism can potentially be separated into component parts, one broadly representing a "female component," the other representing a "male component." Finally, an ontogenetic perspective facilitates investigations of several correlates of dimorphism. Researchers are not limited to the evaluation of how a single "dependent" variable (i.e., adult dimorphism) covaries with a set of "independent" variables (i.e., intermale competition, female mate choice, and ecological factors). Together, these points provide a firm rationale for pursuing ontogenetic approaches to the study of sexual dimorphism.

ONTOGENETIC VARIATION

Shea's analysis (1986) showed that differing developmental pathways can result in similar or identical levels of adult dimorphism. He further noted that these contrasting "modes" of dimorphic ontogeny could signal important life history contrasts between females and males of a species. In theory, any aspect of ontogeny can vary between the sexes and lead to some level of sexual dimorphism. The presence of this potential variation strongly suggests that studies of adult dimorphism (including attempts to measure the strength of association between intermale competition and adult dimorphism) are incomplete. Such studies unavoidably ignore the developmental processes that actually produce adult body size. The presence of variation in the ontogeny of dimorphism strongly suggests that the ontogenetic responses to selection require investigation. The range of variation in the ontogeny of primate body size dimorphism is discussed in detail by Leigh (1992a). This study examined 45 anthropoid primate species, and attempted to quantitatively explore the contribution of rate and duration differences to adult body size dimorphism. The analysis confirmed Shea's earlier results (1986) by indicating that primate dimorphism can be produced by either rate or duration differences in growth. In some cases, dimorphism is almost exclusively a product of sex differences in the rate of growth (e.g., blue monkeys, *Cercopithecus mitis*). In other cases, bimaturism is mainly responsible for the production of dimorphism (e.g., talapoins, *Miopithecus talapoin*). The level of adult dimorphism appears to vary independently of these different process, so that equal levels of dimorphism can be produced through very distinct growth mechanisms. Moreover, the large number of species represented by this study demonstrated the degree of variation represented within clades, and pointed to socioecological variables that might be associated with this variation.

The degree of diversity in the ontogeny of primate dimorphism may help explain why previous studies have been unable to provide a satisfactory understanding of the socioecological correlates of adult dimorphism. For example, Martin et al. (1994) recognized that links between competition and body size dimorphism are obscure, strongly implying a need for an ontogenetic approach to this problem. Although competition-based explanations of sexual dimorphism seem to be sufficient for defining a contrast between "monogamous" or "polyandrous" and "nonmonogamous" taxa, this explanation does not in itself seem sufficient to account for variation within the latter group (Martin et al., 1994). This finding implies that intermale competition seems to provide a foundation or "baseline" or "template" for dimorphism, but other variables result in variation around this baseline. The degree of variation around this baseline is very high, so that it cannot be considered ancillary to the variation around competitive baselines. However, previous comparative analyses of adult sexual dimorphism seem to have failed in explaining this variation. The reason that such analyses have fallen short of their objectives is a consequence of the multifactorial causes of variation around these baselines or templates. One major objective of ontogenetic research should be to link the multifactorial causes of this "supra-baseline" level of variation to factors that influence ontogeny. This means that the components of ontogeny, and variable patterns of dimorphic growth that lead to adult size, must be understood. These components include variables such as prenatal growth rates, birth weights, postnatal growth rates and durations for each sex. It is in this context that life history theory, with its emphasis on both growth rates (Janson and van Schaik, 1993) and maturational timing (Pagel and Harvey, 1993; Ross, 1989; Rubenstein, 1993), is particularly important.

LIFE HISTORY CORRELATES

The correlations between differing modes of dimorphic ontogeny, adult body size dimorphism, and life history variables offer a second major advantage to ontogenetic analyses of body size dimorphism, but these are only now being explored. Life history approaches to primate dimorphism should focus on issues regarding growth rate variation and growth duration variation. Currently, theories about age at maturation are relatively well-developed by life history theorists. For example, demographic data, including the intrinsic rate of increase (r) and other demographic information, can be used to model optimal age at maturation (Stearns, 1992; Stearns and Koella, 1986). Although rarely applied to primates other than humans, this theoretical framework should have considerable predictive power for explaining age at maturation in both females and males. It can be noted that, for males, life history models of age at maturation are less well-developed. Nevertheless, these models should have predictive power in analyses of sexual dimorphism in primates.

The theoretical foundations for analyses of growth rate variation are less complete, but are likely to be important given the high degree of growth rate variation in primates (Leigh, 1995). Janson and van Schaik (1993) have helped to fill this theoretical gap by suggesting that primate growth rates are primarily influenced by a balance of factors related to both the risks of predation and the metabolic risks of starvation. When risks of predation are high, selection favors individuals that tend to live in groups. However, group formation increases feeding competition among individuals, thus elevating the metabolic risks of starvation. Janson and van Schaik suggest that a balance between these factors explain the relatively low primate growth rates and long prematurational periods. They suggest that slow growth rates reflect a risk aversion strategy that is ultimately a response to predation pressure. It can be noted that some elements of Janson and van Schaik's model, particularly their attempt to demonstrate that juveniles must contend with reduced foraging efficiency, are tentative (Garber, personal communication). This is an important point because Janson and van Schaik try to suggest that inefficient foraging results in increased metabolic costs. However, currently available data on juvenile foraging efficiency are probably not adequate for evaluating this argument. It is likely that metabolic costs, whatever their sources, are very important in controlling growth rates. Further analysis of this problem will be crucial to explaining many aspects of primate evolutionary biology.

Janson and van Schaik invoke this model as an alternative to social complexity models, which have been proposed to explain the relatively long developmental periods of primates. However, Janson and van Schaik's model also seems to have predictive power for understanding the ontogeny of primate sexual dimorphism. First, this model may be especially productive for understanding female ontogeny and, thus, the influence of female ontogeny on dimorphism. Females may be more likely than males to adopt risk averse ontogenetic strategies, in part because of the metabolic costs of pregnancy and lactation (Leigh, 1996). Second, differing modes of dimorphic growth among primate species are related to alternative risk aversion strategies during late ontogeny. Jarman (1983) made a similar proposition to explain bimaturism in large terrestrial herbivores. Jarman argued that young males may retain a juvenilized morphology in order to avoid competition with fully adult or prime age males. Moreover, Jarman indicated that additional learning time may result in the evolution of bimaturism, provided that males encounter socially complicated environments. For primates, these generalizations, particularly the former, seem to have predictive power in explaining ontogenetic diveristy. Therefore, the lack of dimorphic ontogenies in monomorphic species may be related to very similar distributions of risks between the sexes. On the other hand, among species with dimorphic ontogenies, the lifetime distribution of risks very likely differs by sex. In such species, the two modes of dimorphic ontogeny previously described may correspond to distinctive differences in patterns of risk distribution. An ontogenetic perspective permits a focus on factors that influence growth rates at all periods during ontogeny for each sex. This information can then be evaluated in relation to adult body size dimorphism.

A recent study of the ontogeny of sexual dimorphism in primates suggests that there are potentially close relations between the distribution of risks and ontogenetic patterns, at least for males (Leigh, 1995). For example, species that can be classified as multimale/multifemale tend to become dimorphic through sex differences in the duration of growth. This may relate to a temporal distribution of risks for males that is either predictable, relatively uniform, or increases regularly through time *(Figure 1)*. These kinds of risks may favor growth at a constant rate, ultimately resulting in bimaturism. In essence, either multimale/multifemale species (or species in which the level of intermale competition changes uniformly with age) may gain some future reproductive advantages by retaining a juvenile morphology. This could be seen as a form of crypticism, and parallels Jarman's (1983) explanation for delayed maturation in large terrestrial herbivores.

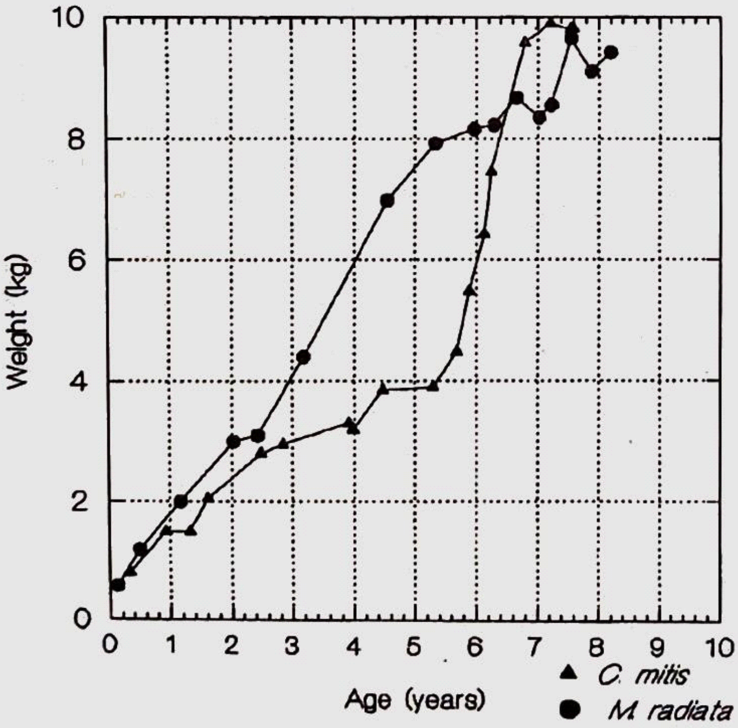

FIGURE 1. Longitudinal growth data for individual male monkeys. These longitudinal plots represent individual male *Cercopithecus mitis* (blue monkey) and *Macaca radiata* (bonnet macaque). These growth trajectories summarize the differences in ontogenetic patterns among species. The blue monkey can be classified as a "rate dimorphic" species, partly because of the rapid male growth spurt. The bonnet macaque can be classified as a "time dimorphic" species, lacking a clearly-defined growth spurt, and growing at a steady rate throughout the developmental period.

Other forms of social and mating systems may result in differing distributions of risks to males. For example, prominent growth spurts are observed in species that can be classified as single male/multifemale. These may be species in which the level of intermale competition changes dramatically or unpredictably. In these cases, the risks of intermale competition probably increase with age, but they may do so in an unpredictable or irregular fashion. Growth spurts are largely responsible for a dimorphism in these species which, on average, equals dimorphism in "multimale/multi-female" species. In species that are "rate-dimorphic," male crypticism through retention of a juvenilized morphology may not confer risk aversion advantages, ultimately allowing later reproductive opportunities. It can be noted that body weight may be an especially important signal of reproductive maturity in primates, because these taxa lack prominent external weaponry (e.g., antlers, horns) that might signal reproductive maturity. Finally, the relations between additional learning time and prolonged development are difficult to define. Leigh (1995) found that male growth duration did not vary by social or competitive category. This may suggest that additional learning time is not important in the evolution of dimorphic ontogenies (assuming that growth time and learning time are associated).

It should be emphasized that analyses of adult dimorphism are not informative in this example (as well as in others). These groups of species (multimale/multifemale and single-male/multifemale) do not differ in average adult dimorphism (Leigh, 1992b), suggesting independence between adult dimorphism and social differences in these categories. This independence obscures the sex differences in the ontogeny that characterize these groups. Clearly, ontogenetic differences would seem to have important social and ecological correlates, and this may be reflected by the fact that ontogeny differs perceptibly between these categories (Leigh, 1995). Finally, this ontogenetic diversity, coupled with the absence of differences in mean dimorphism, reveal yet another deficiency of analyses of adult dimorphism: such analyses do not account for the ways in which competition develops. Consideration of life histories, particularly for males, should be one way to help explain variation in dimorphism that cannot be resolved through traditional analyses.

FEMALE CONTRIBUTIONS TO DIMORPHISM

A third major advantage of an ontogenetic approach to the problem of primate sexual dimorphism is that ontogeny provides insight into factors that may influence dimorphism through female ontogeny. In general terms, the female component to dimorphism is significant because, as explicitly recognized by Martin et al. (1994), the evolution of sexual dimorphism can involve either a decrease in female size or an increase in male size. These authors reasonably suggest that those possibilities should be considered "equally likely" (Martin et al., 1994:199). More specifically, female ontogeny responds both to the adaptive demands of metabolic selection (Janson and van Schaik, 1993) and to reproductive selection on age at maturation (Stearns, 1992). Age at maturation may be especially important for understanding the female component of dimorphism because successful reproduction requires minimal adult size (Sade, 1990) and experience.

The potential importance of female ontogeny to the production of adult body size dimorphism has been mentioned by Liebowitz (1975) and considered by Rowell (1977). Rowell noted that female patas monkeys mature early relative to talapoins, and suggested that ecological conditions ("r-selection") could favor this pattern. Early female maturation strongly implies that the high dimorphism in patas monkeys is partly a consequence of ecological factors acting on females. Shea (1985; 1986) argued for a comparable phenomenon in gorillas. Together these sources imply that much of the variation in adult body size dimorphism can be attributed to factors that influence female ontogeny.

The contribution of female ontogeny to variation in sexual dimorphism was evaluated in a study of apes (Leigh and Shea, 1995). This analysis examined ontogeny in all six extant hominoid species. Variation in female ontogeny is particularly significant in producing species differences in dimorphism among African apes (*Pan* and *Gorilla*), with female growth patterns impacting markedly on variation in dimorphism among species *(Figure 2)*. For gorillas, adult dimorphism is very high, and probably exceeds what would be expected solely based on the level of intermale competition. Thus gorillas may be "overdimorphic" relative to the level of intermale competition they exhibit. This condition is partly a consequence of relatively and absolutely early cessation of growth in female gorillas. Cessation of female growth in gorillas occurs during a comparatively short time interval, and is thus abrupt. In contrast, female common chimpanzees *(Pan troglodytes)* grow for a longer time period than female gorillas, and growth cessation is a gradual process. Growth patterns that lead to dimorphism in pygmy chimpanzees *(Pan paniscus)* are generally comparable to growth patterns in *Gorilla*, but the level of adult dimorphism is far less than in *Gorilla*. It can be noted that a subsequent analysis of growth in pygmy chimpanzees may suggest further distinctions between the *Pan* species (Parish, personal communication).

Intermale competition, in and of itself, serves poorly as a predictor of adult dimorphism for African apes. Although intermale competition among gorillas is certainly substantial (Harcourt et al., 1981), silverback males will tolerate males of near-reproductive age (presumably their sons). This age-graded social organization of gorillas has proven difficult to characterize in term of the degree of sexual selection associated with it. Intermale competition in gorillas may be low relative to equally dimorphic primate species. Ontogenetic information reveals how gorillas can attain such high adult dimorphism without extreme levels of intermale competition. This interpretation requires information about female somatic and behavioral ontogeny. In general, the pattern of female gorilla ontogeny can be seen as an adaptive process that has, when compared to other anthropoids, resulted in an absolutely and relatively early age of maturation (9-10 years of age). This obviously enables the female reproductive lifespan to begin at a relatively early chronological age, but secondarily increases the level of adult dimorphism. Furthermore, a recent study of behavioral ontogeny in captivity shows that females base their mate choice partly on male size and age (Lambert, 1996). Younger, smaller males may be dominated by females, and appear to be subjected to physical tests via aggressive behavior. For gorillas, Lambert's results imply the existence of sexual selection through a female mate choice component that is at least partly independent of intermale competition. Thus, ecological factors, coupled with female choice selection, contribute to the high level of adult dimorphism in this species. The possibility that gorilla dimorphism is partly a consequence of large size is also plausible (Leutenegger and Cheverud, 1982). However, this idea has proven very difficult to evaluate, and remains uncertain. Finally, analyses by Martin and colleagues may suggest evolutionary size reduction of gorilla females. Specifically, they find that female gorilla brains are "overscaled," which, according to their theoretical model, implies ontogenetic shifts in body development (Martin et al., 1994; Willner and Martin, 1985). In sum, detailed ontogenetic studies of behavior and morphology strongly indicate that gorillas are more dimorphic than could be expected based solely on intermale competition. Instead, female ecology and behavior have profound effects for the evolution of gorilla dimorphism.

Analysis of the ontogeny of dimorphism in the genus *Pan* provides additional evidence about the importance of female ecology on size differences and dimorphism in African apes. Although statistically significant differences in adult dimorphism are not readily apparent in these species, the differences in ontogeny are marked (Leigh and Shea, 1995). In particular, differences in the general attributes of growth between females of these species are apparent. Thus, females appear to vary more with respect to the presence of growth spurts and in age at growth cessation than males. The variation in ontogeny between females of the *Pan* species can be related to ecological factors. For example, resources and foraging strategies differ between these two species (Malenky and Wrangham, 1994), resulting in high levels of interfemale competition in common chimpanzees, but not in pygmy chimpanzees. The ontogenetic response to these selective factors involves prolongation of the growth period in female *Pan troglodytes*. Thus, female *Pan troglodytes* experience prolonged growth, resulting in comparatively large size. This large size enables them to better compete with one another for resources, much as large size enables males to better com-

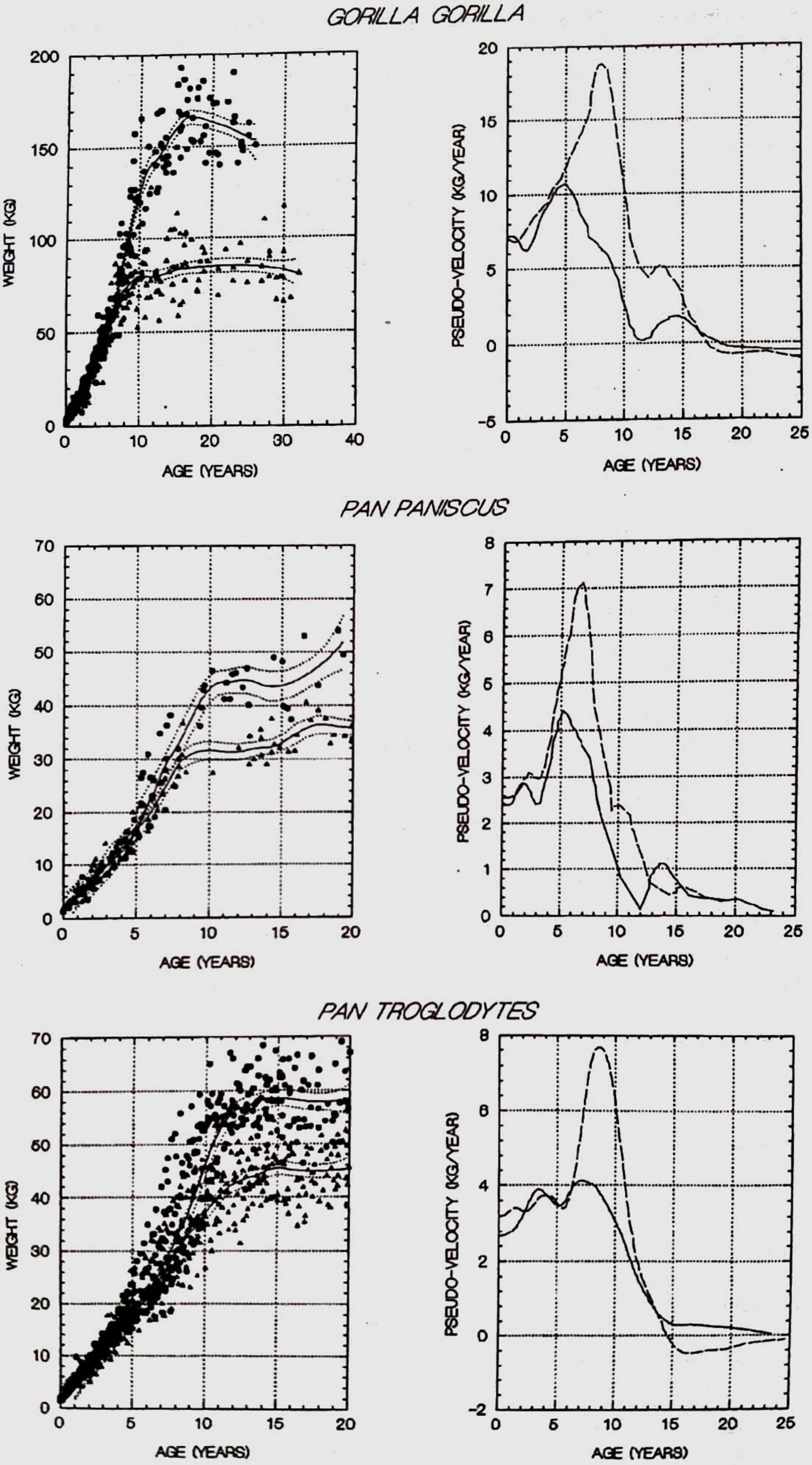

FIGURE 2. Ontogenetic variation in African ape species. These plots show nonparametric loess regressions for all three species of African ape. The plots in the left-hand column show weight-for-age (or distance). Confidence intervals on the loess line (95%) are shown as dotted lines. The right-hand column shows an estimate of growth rate in each sex and species (dashed lines are males, solid lines are females). Note the absence of a single, clearly defined growth spurt in female *Pan troglodytes*.

pete for mates. In any case, the level of intermale competition does not seem to vary between these species to the degree that differences in female ecology differ. Thus, ontogenetic differences between these species accounts almost entirely for the nominal (but not statistically significant) difference in degree of adult dimorphism.

Although female ontogeny plays an important role in *Pan,* it is worth discussing instances in which dimorphism appears to be largely independent of female ontogeny. Orangutans *(Pongo pygmaeus)* provide such an example. Dimorphism in this species is most clearly related to high levels of intermale competition. Males exhibit indeterminate growth, and appear to be unique among primates in this respect. Moreover, males are known to pursue two distinctive mating strategies that may be tied to indeterminate growth. First, crypticism in external morphology is a strategy adopted by males who are either too young or too small to compete directly for mates. These individuals are fully capable of reproducing, but lack secondary sexual characteristics (Maggioncalda, 1995) and may retain this juvenilized morphology for many years. Orangutans also appear to complete cranial suture closure at developmental ages (estimated by tooth wear) that are late relative to African apes (Uchida, 1992). Males who are able to compete develop prominent laryngeal pounchs, cheek phlanges, and large body size through indeterminate growth. The effects of indeterminate male growth are so profound that female ontogeny does not have the major effects seen in African apes. It can be noted that the presence of indeterminate growth in orangutans strongly implies that analyses of adult sexual dimorphism in this taxon have little explanatory power.

In sum, a consideration of ape dimorphism indicates that female ontogeny can play a significant role in producing variation in sexual dimorphism. It is very likely that similar processes probably relate to sexual dimorphism in other taxa. However, the paucity of reliable socioecological data for other taxa often precludes more highly detailed analyses.

CORRELATES OF ONTOGENY

A fourth and very practical reason for evaluating the ontogeny of sexual dimorphisms is that an ontogentic perspective enables analysis of numerous variables that may play small but important roles in the evolution of dimorphism. In contrast, analyses of adult dimorphism are restricted to the evaluation of a single measure that is a composite of female and male ontogenetic processes. Ontogenetic variables that could be relevant to adult dimorphism include prenatal growth rates, gestation lengths, birth weights, early postnatal growth rates, growth spurt duration and magnitude, and growth cessation age. Clearly, all these variables contribute in some way to adult size and adult dimorphism, and correlates of these (and other) ontogenetic variables must be specified before adult dimorphism can be fully explained. As a theoretical example, there may be strong correlations between the degree of intermale competition and male growth spurt peak velocity, but not duration. Duration of the growth spurt or duration of the total growth period may correlate more closely to other variables (such as ecological factors or diet). These kinds of correlates can obviously be specified only if the growth process can be dissected into its component parts, and these parts require evaluation in light of important socioecological variables.

The necessity of studying the entire growth period is demonstrated by trade-offs that are apparent in growth and development. Trade-offs are partly a consequence of the time-ordering of ontogeny. In other words, factors that influence early stages of ontogeny may constrain the evolution of dimorphism. These trade-offs may help explain the paradox of reduced dimorphism in colobines (and possibly strepsirrhines). Ontogenetic data for colobines suggest that these taxa grow rapidly for comparatively short periods of time (Leigh, 1994). Moreover, colobine growth spurts are of relatively high magnitude and occur relatively early (Leigh, 1996) *(Figure 3).* These attributes are probably adaptations to folivorous diets and risky infant periods (Leigh, 1994). Moreover, such trade-offs probably constrain the evolution of sexual dimorphism by precluding the evolution of long male growth periods. In essence, the only "avenue" to large body size and dimorphism in colobines seems to involve high growth rates. This reflects a compromise between high early growth rates and sexual selection for large male size that colobines may face. A trade-off toward high early growth rates may represent the kind of ecological selection that precludes the operation of Fisherian runaway selection (see Fisher, 1930). It should be emphasized that the distinctness of female colobine growth, as reflected by an early and distinct growth spurt, contributes to limited dimorphism. Specifically, this kind of ontogenetic pattern may limit the degree of dimorphism that can evolve by producing comparatively large female size at young ages. In any case, high levels of intermale competition in colobines do not seem to be matched by comparably high degrees of sexual dimorphism. These cases seem to provide a parallel to gorillas. Consideration of ontogeny thus provides greater insight into the problem of colobine dimorphism than is available from analysis of adult dimorphism. Finally, similar processes may apply to the evolution of dimorphism in strepsirrhines. In these cases, seasonality may limit the amount of time available for growth. Bimaturism, as a way of evolving a dimorphic state, may not be possible given ecological selection for a short growth duration, no matter how intense female mate choice or intermale competition sexual selection might be. Unfortunately, body size ontogeny in prosimians is poorly known, precluding further evaluation of this problem.

AREAS OF FUTURE RESEARCH

Several areas of future research deserve investigation. Perhaps the most pressing problem involves analyzing the

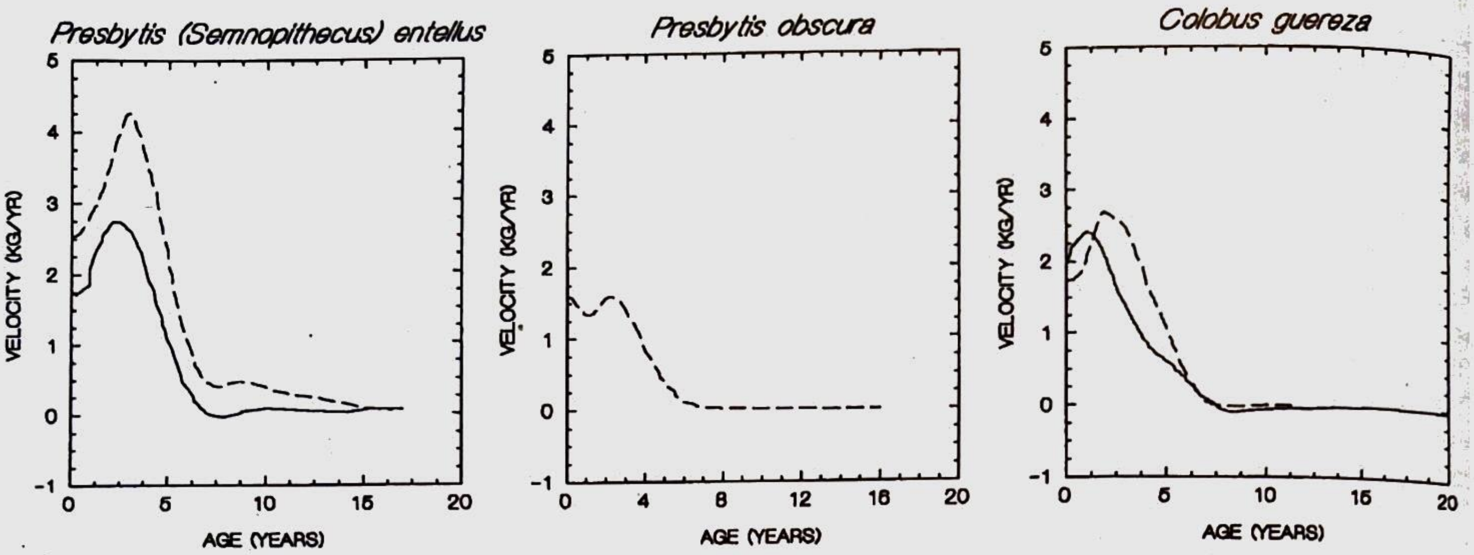

FIGURE 3. Growth rate variation in selected colobine monkey species. These female colobine species show obvious growth spurts that begin and peak relatively early in life. This pattern is unusual relative to other comparably-sized primate species (dashed lines are males, solid lines are females), (see Leigh, 1996).

ontogeny of dimorphism in morphological systems other than body weight. Although body weight is an important variable in sexual selection theory, it represents the sum total of all the organism's morphological systems. Moreover, it is possible that males and females differ significantly in adult body composition and in the ontogeny of body composition. Differential body composition may reflect important differences in metabolic energy budgets by sex, and could be related to ecological and social factors. Consequently, analyses of body composition ontogeny might help explain differences among species in the ontogeny of dimorphism.

The ontogeny of dimorphism in the skeletal system is perhaps the most readily analyzable, but the level of ontogenetic variation in the skeletal system is unknown. Very few species (macaques, baboons, and chimpanzees) have been subjected to studies of skeletal length growth, and these were completed long ago (see Watts, 1986). This is unfortunate, because patterns of skeletal dimorphisms can vary substantially in primates (Oxnard, 1983). At present, it appears that dimorphism in the skeletal system has more conservative ontogenetic foundations than the ontogeny of dimorphism in body weight. Bimaturism, not rate differences in growth, seems to account for skeletal dimorphism (Watts, 1986). However, contemporary analytical methods have not been applied to this problem, and skeletal growth in those species with the largest body mass growth spurts relative to size (male guenons and mandrills) have never been analyzed.

A second critical area of future research includes hormonal analyses of the evolution of dimorphism. The hormonal bases of growth appear to differ between human males and females and among populations (Baumann et al., 1989; Merimee et al., 1991). This may imply that similarly diverse mechanisms influence nonhuman primates. Ultimately, the genes controlling these hormones may be subject to investigation, allowing an understanding of the genetic consequences of natural and sexual selection in primates. Moreover, population differences in human growth may indicate that several alternative hormonal pathways (see Shea, 1992) are involved in the ontogeny of adult size and dimorphism in primates. These potential pathways require specification before our understanding of primate size dimorphism can be considered complete.

The canine complex presents another important system in which the ontogeny of dimorphism should be assessed. Adult canine dimorphism has been thoroughly investigated by Plavcan and colleagues (Plavcan, 1990; Plavcan and van Schaik, 1992). These analyses show a strong correlation between the type of intermale competiton and canine dimorphism. However, the degree to which canine ontogeny differs by competition category is unknown. A lack of interspecific variation in canine eruption schedules might imply uniform action of sexual selection on canine ontogeny, and may help define the age at which the organism responds to sexual selection. Uniformity in the ontogeny of canine dimorphism might also suggest that little information is lost in analyses of adult dimorphism. Typically, anthropoid canines are among the last to fully erupt, although there is some variation in eruption sequences (Fleagle, 1988:41). Late development and eruption of the canine might suggest that sexual selection has favored individuals who "reserve" this weaponry until later in life. This could protect the canine from dietary wear that might reduce its efficacy as a weapon. Dimorphism in eruption schedules might be especially valuable in assessing how sexual selection influences this system. Finally, sexual selection may be minimal in species in which the canine erupts early relative to other teeth. This kind of information has direct application to the fossil record.

Behavioral analyses are crucial to future investigations of ontogeny and dimorphism. Specifically, some assessment of risks and age-related changes in ecological risks are needed. Janson and van Schaik's (1993) theoretical research provides a strong foundation for such analyses, and can be applied to any phase of ontogeny. The ways in which risks of sexual selection change with age should be especially informative in understanding the male component of sexual dimorphism. However, attention to the ontogenetic responses of females both to interfemale competition and to more general ecological risks is required before adult dimorphism can be satisfactorily explained. Obviously, this is most readily applied to body weight, but application to other systems will ultimately be necessary. Clearly, such behavioral investigations must be undertaken over a long term and require morphometric ontogenetic data. Although these objectives will be difficult to attain, it should be noted that Altmann and colleagues have obtained high-quality ontogenetic data from field situations (Moses et al., 1992).

Understanding the ontogeny of sexual dimorphism in fossil samples represents another major area of future research. Persistent debate about the level of dimorphism in *Australopithecus* presents an interesting and important problem. The level of adult dimorphism is difficult to ascertain in this species, and much disagreement exists as to whether or not multiple species are actually represented by this material. If this material represents only one species, then an assessment of adult dimorphism may not be sufficiently informative for behavioral inferences. However, it is possible that ontogenetic inferences may be more informative with regard to socioecology. Such analyses are not yet possible because of the lack of knowledge about the ontogeny of skeletal and dental dimorphism. However, the importance of this taxon to understanding human evolution should motivate much further research into these issues.

CONCLUSIONS

Analyses of ontogeny can contribute to virtually all fields of biology, including analyses of sexual dimorphism. This contribution argues that an ontogenetic perspective must be included in models that seek to explain variation in dimorphism among primate species. The need for including more ontogenetic information arises because studies of adult dimorphism appear to be extremely limited in their ability to resolve controversies about the evolution of dimorphism. On the other hand, an ontogenetic approach provides much more information about the evolution of dimorphism, in part because an adult level of dimorphism is simply a product of developmental trends.

Several areas of investigation in which ontogenetic information has proven useful can be identified. Specifically, ontogenetic analyses show that there is considerable variation in the developmental trajectories that lead to adult dimorphism. Obviously, this variation cannot be appreciated solely on the basis of data about adult size. Ontogenetic data are also critical to evaluating life history correlates of dimorphism. The increasing importance of life history theory in biology will require even more ontogenetic information. The importance of identifying the consequences of female growth patterns on dimorphism offers further impetus for future ontogentic analyses. Specifically, variation among species in female growth can have profound effects on the level of adult dimorphism, independent of influences of intermale competition. Finally, ontogenetic data provide a rich source of comparative data. Dissecting growth curves into component parts offers the chance to relate separate parts of ontogenetic trajectories to social and ecological factors. This provides a potentially productive source of correlative information that will ultimately permit clearer specification of the natural history of primate dimorphism.

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