

# Chapter 13

## Sexual Size Dimorphism in *Australopithecus*: Current Understanding and New Directions

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**Abstract** Sexual size dimorphism in extant and extinct species has often been viewed as a proxy for sexual selection, and by extension, mating system. As a result, various measures of relative size variation have been calculated for australopiths (particularly *Australopithecus afarensis*) as a means to infer mating system and social structure in these extinct hominins. Such analyses are confounded by several factors, including (1) different levels of sexual dimorphism may be present within one species when comparing different systems such as canine size, postcranial size, and body mass; (2) evidence suggests that sexual size dimorphism responds not only to sexual selection acting on both male and female size, but also to natural selection acting differentially on the sexes; and (3) measures of relative size variation within skeletal and/or dental samples of unknown sex are not direct measures of size dimorphism, but rather estimates which are subject to both known and unknown sources of error. This chapter addresses concerns and possibilities for future analyses that relate to these confounding effects, and goes on to present the current understanding of size dimorphism within *Australopithecus*. Specific methodologies for measuring relative size variation within fossil taxa are discussed, particularly newer techniques which incorporate information from across multiple skeletal elements. Finally, the biological and phylogenetic significance of different possible levels of dimorphism within *Ardipithecus ramidus* and various species of *Australopithecus* is discussed in the context of extracting information on selection pressures beyond simple reconstruction of mating systems and social structure.

**Keywords** Size dimorphism • *Australopithecus* • Sexual selection • Skeletal variation

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Sexual dimorphism, the presence of typical, distinctive differences between males and females of the same species, manifests in animals in a number of ways. These include sex-specific differences in the size (or presence) of particular portions of the body (e.g., canines, tail feathers, antlers) or the body as a whole, the shape of anatomical regions (e.g., pelvic shape, cranial crests), and coloration. Here I address sexual *size* dimorphism, as this has been the main focus of dimorphism research in *Australopithecus*, primarily due to the theoretical and empirical support for a relationship between size dimorphism and behavior in living primates. For example, the degree of size dimorphism within *Australopithecus* and the presence or absence of temporal trends in size dimorphism in later hominin evolution has played a key role in discussions of various broad scenarios for the evolution of human behavior from the Early Pliocene to the present (e.g., Lovejoy 1981, 2009; McHenry 1994, 1996).

### Sexual Selection and Sexual Dimorphism

Sexual dimorphism in body size is associated with a number of behavioral features in living primates. For example, in two hominoid genera which show pronounced mass dimorphism, *Pongo* and *Gorilla*, sex differences in locomotor behavior are apparent in degree and type of arboreal locomotion (Galdikas and Teleki 1981; Sugardjito and van Hooff 1986; Remis 1995; Doran 1997) presumably due to males' greater mass and the lack of adequate arboreal support. There are also sex differences in some primate diets that appear to be related to size dimorphism (Clutton-Brock 1977; Demment 1983). However, dietary and locomotor sex differences within primates appear to be the result of dimorphism rather than the cause (Clutton-Brock and Harvey 1977), whereas sexual selection theory suggests that sexual dimorphism results from specific types of mating/social behavior.

The basic explanation for the evolution of sexual dimorphism as suggested by Darwin (1871), and still understood today to be essentially correct, is that dimorphism results from competition for mating opportunities, choice of mates based on particular characteristics, or some combination of the two. More specifically, sexual selection (and thus sexual dimorphism) results from situations which set up reproductive skew such that one sex has greater variability in its reproductive output than the other. For example, if all healthy adult females in a population produce roughly the same number of viable offspring over their reproductive lifespans while some males produce many offspring and others produce few or none, sexual selection will result. Those heritable characteristics that distinguish the males that father the most offspring from those that do not will be preferentially passed on to the next generation. Thus characteristics that allow males to win contests with other males for mating opportunities (male–male competition) or that make them more attractive to estrous females (female choice) will become emphasized in descendant males. Within primates, these characteristics have typically been recognized to be body size and weapon size (i.e., canines in the case of non-human primates), although we also know that reproductive competition among males need not necessarily involve face-to-face conflict. For example, it may occur as sperm competition (Harcourt 1997; Anderson and Dixson 2002) or via alternative mating strategies such as those used by “unflanged” adult male orangutans (Utami et al. 2002). Likewise, female mate choice is not limited to precopulatory choice, but can also involve postcopulatory and even postfertilization mechanisms (Paul 2002), and in some cases males also exhibit mate choice, with high ranking males mating preferentially with those females most likely to be experiencing conceptive cycles (e.g., Alberts et al. 2006).

Decades of research in non-human anthropoid primates has shown that high levels of canine size and body mass dimorphism are usually associated with social structures that produce high intensity competition between males for mating opportunities (e.g., Clutton-Brock et al. 1977; Gaulin and Sailer 1984; Clutton-Brock 1985; Rodman and Mitani 1987; Kay et al. 1988; Ely and Kurland 1989; Greenfield 1992; Plavcan and van Schaik 1992, 1997b; Ford 1994; Martin et al. 1994; Mitani et al. 1996; Lindenfors and Tullberg 1998; Plavcan 1999, 2001, 2004; Barton 2000; Gordon 2004, 2006a; Thorén et al. 2006), and new research is beginning to show that female choice can reinforce or dampen these relationships (Plavcan 2004; Maestripietri and Roney 2005). Within the extant hominoids, high dimorphism is found in gorillas, which live in uni- or multi-male groups with multiple females, and in orangutans, in which one male’s territory typically overlaps with that of multiple females; in both cases high male–male competition is expected. Somewhat less dimorphism is present in chimpanzees and bonobos, which

live in multi-male, multi-female groups in which male–male competition can occur, but where it is presumably more difficult to monopolize access to estrous females. Very little dimorphism is found in gibbons and siamangs, which typically form pair-bonds in which one adult male and one adult female will jointly defend a territory, although “monogamous” gibbons are known to engage in extra-pair copulations (Reichard 1995; Jiang et al. 1999), and an increasing number of hylobatid social groups with more than one adult male are being reported (e.g., Brockelman et al. 1998; Fuentes 2000; Sommer and Reichard 2000; Lappan 2007).

The other extant hominoid, *Homo sapiens*, presents at least two complications for this relatively simple picture: (1) modern human social structure and mating patterns are incredibly varied and defy easy categorization (e.g., Flinn and Low 1986; Marlowe 2003), and (2) canine size, one of the obvious targets of sexual selection in non-human primates, has undergone dramatic decrease in both sexes throughout hominin evolution (Washburn 1971; Plavcan and van Schaik 1997a) as well as a shape reorganization in early hominins associated with the reduction and eventual loss of the canine-premolar honing complex (Lockwood et al. 2000; Kimbel et al. 2006; White et al. 2006). These changes jointly act to reduce the effectiveness of canines as weapons and greatly decrease the likelihood that canines are targets of sexual selection in modern humans or earlier hominins.

## Natural Selection and Sexual Dimorphism

As important as the role of sexual selection is in generating and maintaining sexual size dimorphism, it is unlikely to be the only force acting on size dimorphism. Among the studies mentioned above, the model with the greatest explanatory power for the relationship between sexual selection and body mass dimorphism within anthropoids is that described by Plavcan (2004) with  $r^2 = 0.549$  for a sample of 85 species. While some of the 45% of variation in dimorphism that is unaccounted for is undoubtedly due to an imperfect fit between the proxy for sexual selection (competition levels) and sexual selection itself, and some variation is probably due to noise in the body mass signal, there is likely to be a large portion of the variation in dimorphism that is associated with other forces.

For example, natural selection can also affect dimorphism, and this has implications for the interpretation of size dimorphism in the fossil record. First, there are indirect effects of natural selection on sexual dimorphism. For example, predation risk appears to be correlated with minimum group size in many primates (e.g., Stanford 2002; Lehmann et al. 2007), and it has been shown that predation risk also affects group sex-ratios (Hill and Lee 1998), which

in turn affects reproductive skew and sexual selection intensity. Resource seasonality may also drive changes in group size and breeding seasonality, thus affecting sexual selection and sexual dimorphism (Plavcan et al. 2005b). Second, natural selection may also directly affect sexual dimorphism by differential response of male and female adult size to resource availability. In a study of the ontogeny of sexual size dimorphism in primates, Leigh (1992) found that although sexual selection is the primary driver of dimorphism, female growth rates and duration respond to natural selection, which in turn has an effect on adult dimorphism. Several other studies have shown that growth rates are negatively correlated with ecological risk (i.e., resource availability and seasonality) in primates (sifakas, Ravosa et al. 1993; baboons, Altmann and Alberts 1987; and African apes, Leigh and Shea 1996). In particular, variation in female growth rates between African ape species appears to be due primarily to differences in resource stress (where resource stress is diet-dependent), with species living in habitats with greater resource stress (e.g., *Pan troglodytes*) showing depressed female growth rates relative to species in lower stress habitats (e.g., *G. gorilla*) (Leigh and Shea 1996). Assuming growth durations remain constant (which may not be true), if female growth rates are more responsive to ecological pressures than male growth rates, natural selection in the form of ecological stress may depress female adult body size relative to that of adult males, increasing sexual size dimorphism. Thus interpreting the meaning of size dimorphism in *Australopithecus* is not as simple as inferring high levels of male competition from high levels of dimorphism, since ecological effects may also contribute to dimorphism. This is not a trivial concern, since many models for the evolution of bipedalism invoke a role for increased aridity and reduction of forests; i.e., ecological stress. The flip side of the coin is that dimorphism potentially offers a window into not only the social behavior of extinct taxa, but also the ecological pressures that they experienced.

In order to tease apart the effects of natural selection and sexual selection on sexual size dimorphism, it is necessary to investigate the mechanisms through which ecological stress has a differential effect on male and female body size. Resource pressure probably has a stronger effect on females than males because of the energetic costs associated with reproduction and lactation (Ralls 1976; Emlen and Oring 1977; Wrangham 1980; van Schaik 1989; Isbell 1991; Mitchell et al. 1991; van Hooft and van Schaik 1992; Isbell and Pruett 1998; Boinski et al. 2002). Because larger females have absolutely greater metabolic costs than those of smaller females, healthy small females should be able to develop an energetic surplus for reproduction quicker than larger females during periods of resource scarcity. Larger females will thus reproduce less frequently than smaller

females in times of scarcity because of the required greater investment of internal reserves, and thus greater risk, on the part of larger females, hence a decrease in expectation of future offspring (Pianka and Parker 1975; Pianka 1976).

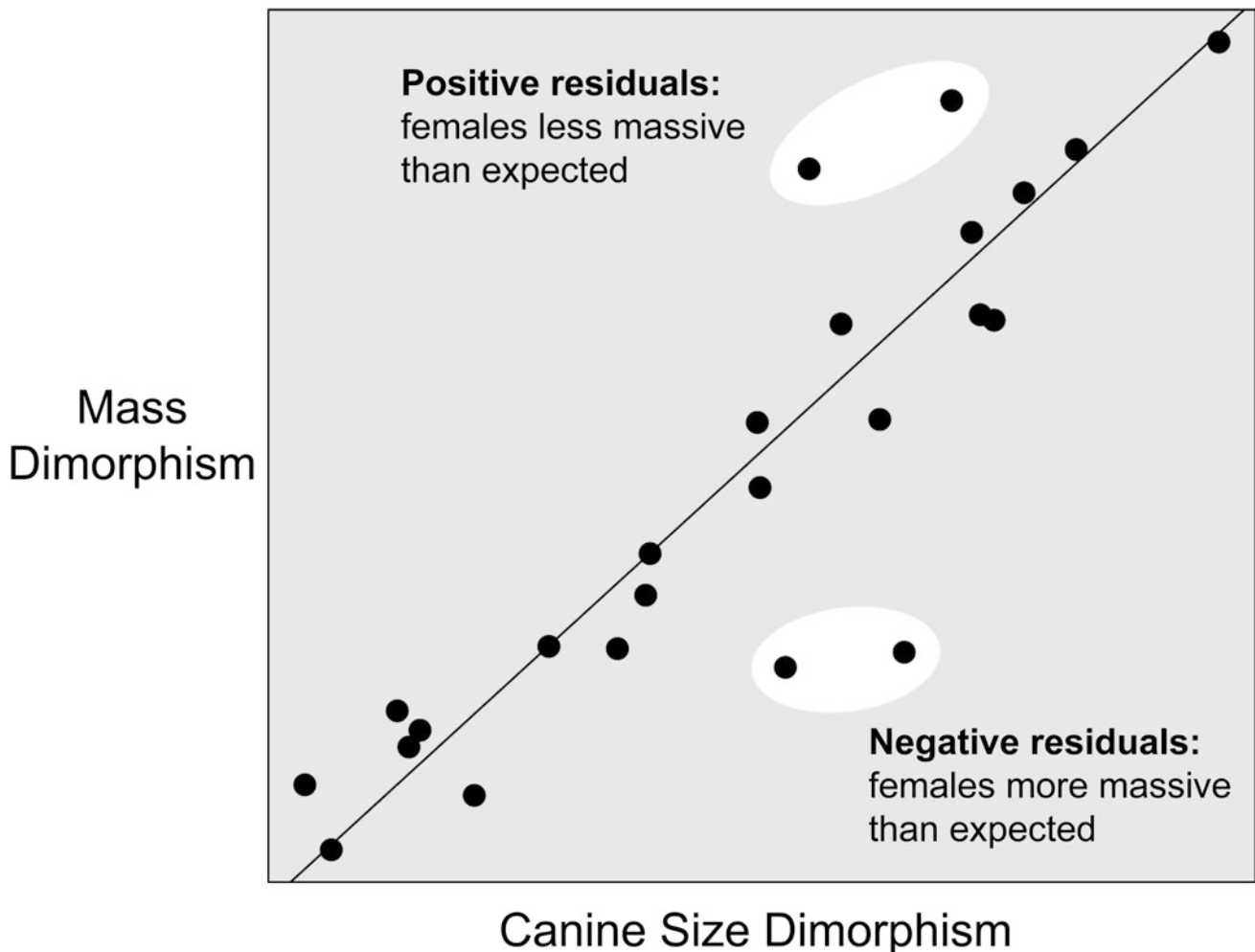
Empirical evidence from Darwin's finches supports these predictions, showing that smaller females breed more often than larger females in variable environments (Downhower 1976). Similarly, a long term study of red deer showed that size dimorphism was negatively correlated with forage quality due to decreased female size, and thus increased dimorphism, when forage quality was low (Post et al. 1999); smaller females were also more likely to breed earlier than larger females and to have more offspring over their reproductive lifespan than larger females (Post and Stenseth 1999). Beehner et al. (2006) found that female baboons in Amboseli were significantly less likely to cycle and significantly less likely to conceive than expected following periods of drought or extreme heat; they argued that this is related to female body condition, and that when females have adequate body reserves, they cycle and conceive. Although Beehner and colleagues did not look at the effect of body size, it follows that healthy smaller females with their lower absolute metabolic needs would be likely to build up the necessary reserves allowing them to cycle and conceive more frequently than larger females during periods of extended resource stress.

Research on the role of resource stress in the evolution of sexual size dimorphism in non-human primates suggests that it can be an important selective force. For example, the application of a quantitative genetics model to identify the forces driving differences in sexual dimorphism among four populations of *Cercocebus pygerythrus*, the African green monkey, showed that these differences are primarily due to negative selection on female body size in more dimorphic populations, counter to the predictions of sexual selection theory; in addition, dimorphism is negatively correlated with food availability, consistent with a differential sex response to resource stress (Gordon 2006a). A comparative analysis looking at the direct effects of resource seasonality on mass and cranial size dimorphism within primates found that increased dimorphism is occasionally associated with increased seasonality, although not consistently so across all taxa (Plavcan et al. 2005b). In addition, a comparative study of the evolution of mass dimorphism across living primates demonstrated that differences in dimorphism between distantly related species are generally due to the effects of sexual selection, but that differences between congeners are as likely to be due to selection (presumably natural) acting on female size as they are to be responding to sexual selection acting on males (Gordon 2006b). Thus there is the potential for any primate species (including fossil hominins) to record an ecological signal in their size dimorphism that is at least partially independent of social behavior.

## Evaluating the Relative Effects of Sexual and Natural Selection on Sexual Dimorphism in Living Primates

One possible way of identifying how strong a selective force resource pressure is for primate size dimorphism, and thus how much care should be taken in inferring particular social behaviors for australopiths based on their dimorphism alone, is to consider the relationship between mass dimorphism and canine size dimorphism in living primates. Although canine size dimorphism is probably not a good indicator of competition levels in hominins because of the change in canine shape and size early in hominin evolution, it has been shown to be an excellent indicator in living non-human primates (Plavcan and van Schaik 1992, 1997a;

Plavcan 2000, 2004), and perhaps more responsive to sexual selection than body mass dimorphism (Plavcan 2000; Thorén et al. 2006). In addition, as Plavcan et al. (2005a) have noted, canine size is less likely than body mass to be directly affected by resource pressure. Therefore canine size might be expected to reflect a strong competition signal, while mass dimorphism could be expected to record a mix of competition and resource pressure signals. By comparing mass dimorphism to canine size dimorphism, the importance of ecological factors in driving differences in mass dimorphism could be evaluated by considering the amount of covariance between the two types of dimorphism. In addition, the relative importance of resource stress on particular populations or species could be determined by analyzing the residuals from regressions of mass dimorphism on canine size dimorphism (Fig. 13.1).



**Fig. 13.1** Hypothetical comparison of mass dimorphism and canine size dimorphism in living primates. Data points may represent species or populations. Line may represent hypothetical scaling relationship (e.g., isometry) or empirically-derived scaling relationship. If deviations from the overall trend are driven by the response of female mass to ecological factors, then those data points which have pronounced positive residuals indicate that mass dimorphism is

unexpectedly high in those populations or species because females are less massive than expected; the reverse is true for pronounced negative residuals. The individual contribution of male and female mass differences to these deviations can be evaluated in more detail by regressing mass against canine size separately for each sex and then comparing the plots and residuals

Of course, there are potential complications to be considered. For example, food distribution may play a large role in determining whether small females gain a selective advantage during periods of resource stress. If resources are uniformly distributed (e.g., leaves, bark), larger females may not have a competitive advantage over smaller females in procuring resources, and thus small size will be at a selective advantage due to the advantage in reproductive frequency enjoyed by smaller females. However, if resources are clumped (e.g., fruit outside of masting events), larger females may be able to competitively exclude small females from feeding patches, thus countering the smaller females' advantage of lower absolute metabolic requirements (Plavcan et al. 2005b). In such a case the implications for directional selection on female body size are unclear. Further research into fallback foods among living primates during periods of resource stress may help identify whether resources are more likely to be distributed uniformly or in clumps at such times. For example, where chimpanzees and lowland gorillas are sympatric, they tend to have similar diets during the wet season, but during periods of food scarcity gorillas rely more on ubiquitously-distributed vegetative foods such as pith and bark while chimpanzees maintain a more patchily-distributed fruit-dominated diet (Wrangham 1977; Sugiyama and Koman 1987; Tutin et al. 1997; Rogers et al. 2004; Yamagiwa and Basabose 2006). Given that these are both large-bodied ape species living in the same habitat, ecological (or paleo-ecological) variables alone are not enough to predict the likely distribution of fallback foods for a given species; dietary information (or dietary reconstructions in the case of fossil hominins) must also be considered.

Another complicating factor is that canines are not only used by males for competition over mating opportunities; they are also used by females for competition over resources (Plavcan 2004). Thus if resources are distributed in such a way that some females can competitively exclude others, selection may favor larger canines in females and thus reduced canine dimorphism, potentially without a decrease in female body size and thus no change in mass dimorphism. When mass dimorphism is plotted against canine dimorphism, this scenario would be indistinguishable from stable canine dimorphism and increased mass dimorphism, since in both cases the population under consideration will have a positive residual. Comparisons between populations of the same species or subspecies where mass and canine size are examined separately for each sex may be able to identify which variables are changing, in which direction, and in which sex.

More broadly, comparative studies can investigate these relationships by determining whether female mass responds more to ecological differences than male mass and whether mass dimorphism is significantly correlated with ecological

variables. Recent work in wild lemurs has shown that within brown lemurs and sifakas, female body size differs more than male body size between closely-related populations and subspecies that live in different ecological zones in Madagascar (Johnson et al. 2005; Lehman et al. 2005; Lewis and Kappeler 2005). Madagascar potentially provides a particularly useful test case because ecological conditions vary widely across the island and lemurs do not appear to respond to sexual selection with changes in mass dimorphism, leaving natural selection as a more likely candidate for producing changes in dimorphism. A complicating ecological factor should be noted, however: anthropogenically disturbed habitats (at forest edges, as opposed to cropland) may actually reduce resource stress if they provide a new food resource (e.g., guava); recent research on fecal cortisol levels comparing lemur populations in undisturbed and disturbed habitats indicates that stress levels are often reduced in disturbed habitats (Tecot 2008, 2013). Ecological variables must be selected with care to reflect actual resource stress.

## Sexual Dimorphism in Extinct Taxa

Of course, before one can begin interpreting the biological significance of sexual dimorphism within the hominin fossil record, one must have a reliable assessment of the degree of dimorphism present within a fossil sample. A major problem in studying sexual dimorphism in extinct taxa is that it is practically impossible to definitively identify the sex of every specimen in a fossil hypodigm. Since sexual size dimorphism is typically measured as a ratio of mean male size to mean female size or the log of that ratio (Smith 1999), sexual dimorphism cannot usually be measured in the fossil record. Instead, relative size variation of the fossil sample is compared to that of extant taxa. Many different techniques exist for measuring relative size variation, including the max/min ratio (e.g., Richmond and Jungers 1995), mean method ratio (e.g., Simons et al. 1999), method of moments (e.g., Josephson et al. 1996), coefficient of variation (e.g., Leutenegger and Shell 1987; Lockwood et al. 1996), assigned resampling method (e.g., Lee 2001), and the binomial dimorphism index (e.g., Reno et al. 2003). Each of these techniques is susceptible to error under various conditions, although simulation studies and studies of actual primate data have shown max/min ratios to be particularly poor estimators while mean method ratios are relatively good estimators (Plavcan 1994; Rehg and Leigh 1999; Kościński and Pietraszewski 2004). Although many of these techniques express relative size variation in a ratio form, it is important to remember that these are not measures of sexual dimorphism and are not directly comparable to sexual dimorphism ratios for living taxa. These measures

tend to be highly correlated with actual dimorphism, but the correlation is typically not completely linear, and taxa with low dimorphism almost always have values of relative size variation that are higher than expected due to size overlap in the sexes (Plavcan 1994; Gordon et al. 2008).

A second problem is the question of what sort of size should be measured. As mentioned above, the two types of sexual dimorphism in size that have been shown to be related to competition levels in living primates are canine size and body mass dimorphism. Canine size dimorphism may or may not provide useful information because of the reduction of canine size throughout the hominin lineage (Plavcan and van Schaik 1997a; Plavcan 2000) and a change in canine shape away from that of a useful weapon (Lockwood et al. 2000; Kimbel et al. 2006). Body mass cannot be measured directly in the fossil record, and although it can be estimated, estimates vary widely depending on the measurement used and the taxon selected to provide the regression model (e.g., body mass estimates for A.L. 288-1 ranging from 25 to 41 kg; Jungers 1988a, 1990a; McHenry 1988, 1992; Hartwig-Scherer 1993; Porter 1995). In addition, body mass estimates are accompanied by prediction errors that are usually so large that estimates are useless for significance tests (Smith 1996). So although some studies have used mass estimates to provide a general sense of the level of mass dimorphism we might expect to see in fossil taxa (e.g., McHenry 1991, 1992, 1996; Plavcan 2000), most research in recent years has focused on comparative studies of relative size variation in various skeletal measurements (e.g., mandibular, craniofacial, femoral, humeral, etc.). These studies incorporate an implicit assumption that the degree of relative size variation present in extinct and extant taxa for a particular skeletal region is proportional to the level of mass dimorphism present in those same taxa—an assumption which may or may not be true.

### Studies of Sexual Dimorphism/Relative Size Variation in *Australopithecus*

Studies of relative size variation in australopith canines suggests that canine dimorphism in *Australopithecus afarensis* and *A. africanus* is most similar to that of monogamous and polyandrous primates (Plavcan 2000). It has been suggested that there might be higher canine size dimorphism in *A. anamensis* (Ward et al. 2001, 2010) although the presence of apparently higher dimorphism in *A. anamensis* than *A. afarensis* is only present in the mandibular canine, and only in tooth root areas, not crown dimensions (Plavcan et al. 2009). It is unclear whether this difference is significant with respect to sexual selection pressures, as it has been shown that the best canine

indicator of competition levels is canine height dimorphism, not canine area dimorphism (Plavcan and van Schaik 1997a; Plavcan 2000). Furthermore, with the well-documented reduction of canine size and relative canine size throughout time in *Australopithecus* (and *Homo*), it has been suggested that canines were similarly less important in male–male contests, and thus high levels of male competition would not be expected to produce high degrees of canine dimorphism (Plavcan and van Schaik 1997a). Thus it is not clear that a hominin species and a non-hominin primate species which were subjected to the same degree of male–male competition would exhibit the same amount of canine size dimorphism, and thus the results of such analyses are difficult to interpret.

A more promising area of research for behavior reconstruction is the study of body size dimorphism. Due to the sparse nature of the hypodigms of most *Australopithecus* species and the comparatively rich hypodigm of *A. afarensis*, the statistical study of body size dimorphism in *Australopithecus* has primarily focused on *A. afarensis*. Although the presence of large postcranial elements combined with the broad size range of cranial material in *A. anamensis* (Ward et al. 2001) suggests high levels of body size dimorphism, no single postcranial element is well enough represented in this species for existing techniques to distinguish between high, gorilla-like levels of dimorphism and low, chimpanzee- and human-like levels of dimorphism in any particular element. The newly-described species *Australopithecus sediba* includes two partial skeletons presumed to be an adult female and a juvenile male; comparison between these specimens suggests a low level of dimorphism, although the juvenile clearly has not completed growth and of course this a comparison of only two individuals (Berger et al. 2010; de Ruiter et al. 2013). The size range of postcranial elements preserved for *A. africanus* indicates at least a moderate level of dimorphism (McHenry and Berger 1998), and some proximal femoral measurements show significantly greater dimorphism in *A. africanus* than in modern humans, but most do not (Harmon 2009). Craniofacial dimorphism in *A. africanus* appears to be intermediate between high gorilla-like dimorphism and low human- and chimp-like dimorphism (Lockwood 1999), but craniofacial dimorphism is of unknown utility in reconstructing social structure and/or competition levels. The reason for this is that comparative studies linking behavior to dimorphism in living primates have been on body mass dimorphism (Clutton-Brock et al. 1977; Leutenegger and Kelly 1977; Gaulin and Sailer 1984; Cheverud et al. 1985; Kappeler 1990, 1991; Leigh 1992, 1995; Ford 1994; Martin et al. 1994; Leigh and Shea 1995; Mitani et al. 1996; Plavcan and van Schaik 1997a, b; Smith and Cheverud 2002; Gordon 2004, 2006b; Plavcan 2004) or canine size dimorphism (Leutenegger and Kelly 1977; Kay et al. 1988; Greenfield 1992; Plavcan and van Schaik 1992,

**Table 13.1** Summary of primary mating systems and levels of dimorphism within some extant hominoids and two australopith taxa with large postcranial hypodigms<sup>a</sup>

Species	Mating system	Canine dimorphism	Mass dimorphism	Postcranial dimorphism
<i>Gorilla gorilla</i>	Polygyny	High	High	High
<i>Pongo pygmaeus</i>	Polygny (noyau)	High	High	High
<i>Pan troglodytes</i>	Polygynandry	Moderate	<b>Moderate</b>	<b>Low</b>
<i>Homo sapiens</i>	Serial monogamy?	Low	<b>Low</b>	<b>Moderate</b>
<i>Hylobates lar</i>	Monogamy	Low	Very low	Very low
<i>Australopithecus afarensis</i>	?	Low	?	High?
<i>Australopithecus africanus</i>	?	Low	?	Moderate?

<sup>a</sup> Levels of dimorphism tend to be higher in species which exhibit more male–male competition for mating opportunities. However, this pattern is reversed within postcranial dimorphism between chimpanzees and modern humans (in bold)

1997a; Plavcan et al. 1995; Plavcan 2004), not craniofacial dimorphism. Furthermore, the relationship between craniofacial dimorphism and body mass dimorphism is highly variable between taxa (Plavcan 2003).

Numerous studies have performed statistical comparisons of skeletal size dimorphism in *A. afarensis* and living hominoids (e.g., Kimbel and White 1988; McHenry 1991, 1996; Richmond and Jungers 1995; Lague and Jungers 1996; Lockwood et al. 1996; Lague 2002; Reno et al. 2003, 2005, 2010; Plavcan et al. 2005a; Harmon 2006; Gordon et al. 2008). Most recent research has found relatively high levels of dimorphism in *A. afarensis*, similar to that seen in orangutans and gorillas, although Reno et al. (2003, 2005, 2010) found that dimorphism in *A. afarensis* could not be differentiated from that of chimpanzees or modern humans (to be discussed in more detail below). All published single-element studies of actual postcranial dimorphism (as opposed to dimorphism in estimated mass or estimated femoral head size) produce an observed level of *A. afarensis* dimorphism that exceeds that of all living hominoids, although the difference in dimorphism between *A. afarensis* and the extant taxon is not usually significant for gorillas and orangutans (Richmond and Jungers 1995; Lockwood et al. 1996; Harmon 2006). Interestingly, these postcranial studies are also distinct in that they construct an overall measure of size for each specimen from multiple measurements using a geometric mean, and thus incorporate more information than univariate analyses. Unfortunately, such measures of overall size cannot be calculated when one or more measurements are missing for a given specimen.

Also, as with craniofacial dimorphism, to date no studies have analyzed the relationship between postcranial dimorphism and social behavior in living primates. While studies linking body size dimorphism to social behavior generally show that higher levels of dimorphism are associated with mating systems where greater competition between males is expected (Table 13.1), all such studies to date have examined body mass, not postcranial size. This is a particular problem within the hominids (African apes and humans),

because chimpanzees are more mass dimorphic than humans, while humans are more postcranially dimorphic than chimpanzees (Gordon et al. 2008; Table 13.1). Notably, researchers who argue for a human-like mating system for *A. afarensis* because their analyses show no significant difference between dimorphism in *A. afarensis* and modern humans (Reno et al. 2003, 2010) have downplayed the fact that those same analyses also show no significant difference between *A. afarensis* and chimpanzees, and thus the dimorphism signal could just as easily be used to argue for a chimpanzee-like mating system in *A. afarensis*.

### Improving Measures of Relative Size Variation in *Australopithecus*

So what can be done to improve these measures of relative size variation in fossil hominins, particularly in relation to the variable which is likely to be the target of sexual selection; i.e., mass dimorphism? Two areas of research are called for: (1) developing new techniques which can include more of the information present in fossil specimens for any particular taxon, and (2) generating a better understanding of the relationship between mass dimorphism and skeletal dimorphism, including both craniofacial and postcranial dimorphism. These topics are explored in more detail below.

### New Techniques for Improving Hypodigm Representation

A source of frustration in the study of size variation in *Australopithecus* is that the hypodigms of both *A. afarensis* and *A. africanus* include relatively large numbers of elements, yet for any given element or set of measurements, the sample size available within each species is usually quite small. Ideally, analyses could be developed which

combine information from all specimens in a species hypodigm, regardless of which elements are present for a given individual. The major hurdle for such analyses is how to handle the missing data problem. In the past several years, two different types of multivariate approaches have been developed to address this issue. The first uses relationships between measurements in a single fossil specimen to estimate the missing data for other fossils, then compares relative size variation in the resulting data set to that in comparative taxa (i.e., template methods). The second uses Monte Carlo resampling techniques to compare sets of measurements from a fossil taxon to sets of measurements from extant comparative taxa in which the extant specimens are sampled in such a manner that they are missing the same measurements as the fossil specimens (i.e., resampled geometric mean methods). These two types of methods are described more fully below.

### Template Methods

These methods first attracted wide attention with Reno et al.'s (2003) analysis of size dimorphism in *A. afarensis*. The basic concept is that if a single specimen preserves many different skeletal elements (e.g., A.L. 288-1), that specimen can be used as a template in which the relationship between the size of various elements is used to predict the size of missing elements for other specimens. For example, the ratio between femoral head size and humeral head size in the template specimen can be used to estimate femoral head size for isolated proximal humeri, the ratio between femoral head size and radial head size in the template specimen can be used to estimate femoral head size for isolated proximal radii, etc. As a result, any specimens that contain elements present in the template specimen can be included in the data set. Researchers can then use their favorite measure of relative size variation (e.g., mean method ratio, binomial dimorphism index, coefficient of variation, etc.) and compare the result against similarly-constructed datasets for extant comparative taxa of interest. Thus template methods are multivariate in the sense that multiple types of measurements are used to estimate one representative measure of size, although univariate methods are used to compare relative size variation between fossil and extant taxa.

One problem with template methods is that as currently applied, the size of absent elements is predicted using the ratio between element sizes (Reno et al. 2003, 2010). Using a ratio implicitly assumes that the two elements in question scale isometrically with each other in *A. afarensis*, an assumption which may or may not be correct. For example, although articular surface areas generally scale isometrically with body mass (and thus each other) in non-human hominoids, many articular surface areas scale allometrically with

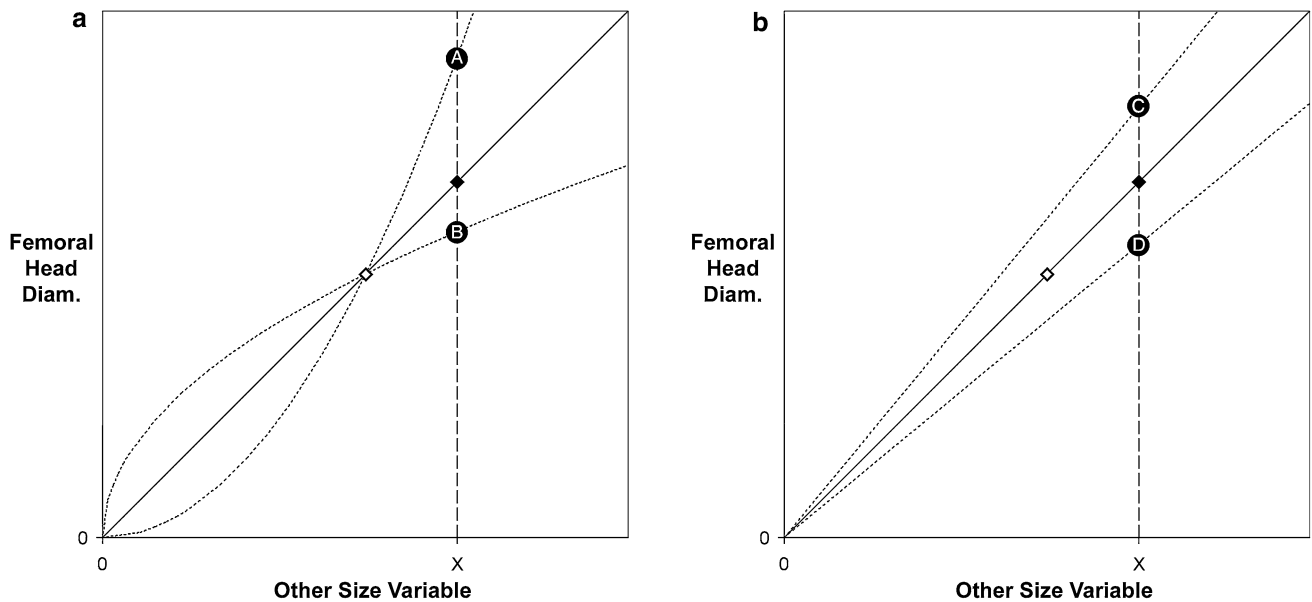
mass and each other in humans, a difference which is likely related to differences in distribution of loads between quadrupedalism and bipedalism (Jungers 1988b, 1990b). Without several relatively complete specimens of *A. afarensis* it is not possible to determine scaling relationships between elements, but it is certainly possible (and likely) that human-like deviations from isometric scaling occur in the australopith skeleton. Deviations from isometry have serious consequences for ratio-based estimates. As Fig. 13.2a shows, using a ratio when the actual scaling relationship is not isometric can seriously under- or over-estimate size, particularly when the template specimen is known to be one of the smallest individuals in the species.

A second problem with template methods is that they do not account for “biological error;” that is, few if any individual specimens will plot directly on scaling lines. Size estimates are affected by biological error in both the template specimen and the estimated specimen. For example, suppose that the relationship between two variables is exactly isometric. Even in this situation, the template specimen will most likely sit above or below the line (i.e., have a non-zero residual from the scaling line). When ratios between the observed sizes in the template specimen are used to estimate size for another specimen, this biological error is multiplied, resulting in an under- or over-estimate of size (Fig. 13.2b). In addition, even if the template specimen happens to sit exactly on the actual scaling line, the real measure of size in the other specimen is likely to also incorporate some biological error, and thus differ from the predicted value.

A third related problem with template methods is that, to date, they have not incorporated prediction intervals for the estimated measurements. As noted earlier, prediction intervals for fossil measurements are often so large as to render predictions practically useless in a statistical sense (Smith 1996). Prediction intervals can be calculated for measurements estimated using templates. The template method is actually a regression technique: predicting an unknown femoral head size using the ratio of femoral head diameter to some other measurement in A.L. 288-1 is mathematically equivalent to using a regression of femoral head size against the predictor variable, where the regression is constrained to the origin (solid diagonal lines in Fig. 13.2) and has a sample size of one (A.L. 288-1 in this case). The number of degrees of freedom in such a regression are zero ( $n-1$ ), and thus 95% prediction intervals for the estimated femoral head measurement include negative and positive infinity.

A fourth problem relates to the susceptibility of template methods to error due to including multiple measurements from the same individual (Plavcan et al. 2005a; Scott and Strok 2006; however, see Reno et al. 2005). For example, if two or more “unassociated” elements that are used to predict separate measures of femoral head size actually





**Fig. 13.2** Examples of possible estimation error through use of a template method ratio. Errors can be due to (a) allometric scaling and/or (b) biological error. Both plots show femoral head diameter (FHD) plotted against another variable for the template specimen in raw (non-logged) data space (*open diamond*), the measured value for the other variable in a second specimen ( $x$  and *vertical dashed line*), and the estimated value of FHD for the second specimen (*closed diamond*), which is based on the ratio of FHD to the other dimension in the template specimen (*solid line*). Examples show a small template specimen as in the case of A.L. 288-1 in Reno et al. (2003). If FHD scales positively allometrically with respect to the other variable, then the template ratio will underestimate the actual value of FHD in the

second specimen (compare the *closed diamond* with A). Likewise, negative allometry means that the template ratio will overestimate the actual value of FHD (B). Even if both variables scale isometrically with each other, biological error (variation of individual specimens about the regression line) can result in estimation error. If the template specimen plots below the actual scaling line, the template ratio will underestimate the true scaling slope (in raw data space; for logged data, this is equivalent to underestimating the intercept) and will underestimate the actual value of FHD in the second specimen (compare the *closed diamond* with C). Similarly, if the template specimen plots above the actual scaling line, the template ratio will overestimate the actual value of FHD in the second specimen (D)

belong to one individual, then that single individual is over-represented in the fossil sample and will affect the observed size variation in the sample. This is particularly a problem in studies of size dimorphism in *A. afarensis*, which typically include specimens from A.L. 333, because there is a high probability that multiple elements from the A.L. 333 site come from fewer individuals than there are elements, perhaps as few as five individuals (Plavcan et al. 2005a).

Despite all of these issues, or perhaps because of them, template methods initiated a renewed interest in studies of dimorphism in australopiths, particularly in developing techniques for incorporating multiple specimens with missing data into a single analysis. It should be noted that Henry McHenry had already developed such a technique 12 years earlier: in his analysis of body size dimorphism in *A. afarensis*, he generated estimates of body mass for fossil specimens representing various skeletal elements based on body mass regressions for extant taxa (McHenry 1991). While McHenry's work might be criticized on the grounds that the reference samples for his regression equations may not be appropriate (given the lack of australopiths of known

body mass), that study did not assume that all measurements scaled isometrically with each other, nor did it base predicted values on regressions with a sample size of one.

### Resampled Geometric Mean Methods

These methods are more traditionally multivariate than template methods and address some of the problems of template methods. Conceptually they are much like the previously described geometric mean methods (e.g., Richmond and Jungers 1995; Lockwood et al. 1996; Harmon 2006) except that modifications have been made to accommodate missing data. For example, it can be shown mathematically that the ratio of mean male size to mean female size for the geometric mean of several variables is equivalent to the geometric mean of those ratios calculated individually for each variable (see the appendix in Gordon et al. 2008). For example, consider the gorilla data presented in Table 13.2. The same measure of sexual size dimorphism, a ratio of 1.26, is found regardless of whether

**Table 13.2** Example showing mathematical equivalence of ratio of GMs and GM of ratios. Measurements are in mm; ratios are unitless<sup>a</sup>

Sex	HUMHEAD	ELBOW <sup>0.5</sup>	RADTV	FEMHEAD	FEMSHAFT <sup>0.5</sup>	DISTFEM <sup>0.5</sup>	PROXTIB <sup>0.5</sup>	DISTTIB <sup>0.5</sup>	GM
F	45.6	34.9	21.1	37.5	29.6	44.7	49.0	24.2	34.4
F	49.3	35.4	26.4	40.0	28.0	48.6	53.2	25.1	36.8
F	47.2	37.9	27.1	40.6	27.0	50.3	56.0	27.1	37.7
F	51.6	38.7	26.7	40.9	31.3	50.3	55.1	27.5	38.9
F	50.7	37.7	28.9	43.6	31.0	52.2	58.9	29.0	40.1
M	54.4	43.1	29.2	47.7	33.9	57.1	67.3	29.5	43.4
M	62.1	46.3	32.1	48.5	37.3	58.5	64.8	34.3	46.5
M	63.0	46.0	36.6	50.6	36.5	62.1	69.4	30.7	47.5
M	65.1	46.5	35.0	52.1	40.0	62.9	71.4	31.0	48.5
M	64.3	49.3	36.6	54.1	39.9	64.9	74.4	34.4	50.4
SD	<i>1.26</i>	<i>1.25</i>	<i>1.30</i>	<i>1.25</i>	<i>1.28</i>	<i>1.24</i>	<i>1.28</i>	<i>1.20</i>	<b><i>1.26</i></b>

<sup>a</sup> Reproduced from Gordon et al. (2008). Values are provided for ten adult gorillas for each of eight linear postcranial measurements. Male:female ratios are calculated for each linear measurement and GMs of all measurements are calculated for each individual. Multivariate dimorphism for this data set can be calculated as either the ratio of average male GM divided by average female GM, or as the geometric mean of the male:female ratios for each linear measurement. In either case the result is the same, the ratio of 1.26 shown in bold italics. Note that in all cases sex-specific means are calculated as geometric means, not arithmetic means; however, ratios of sex-specific arithmetic means are identical to the ratios of sex-specific geometric means shown here at three significant digits

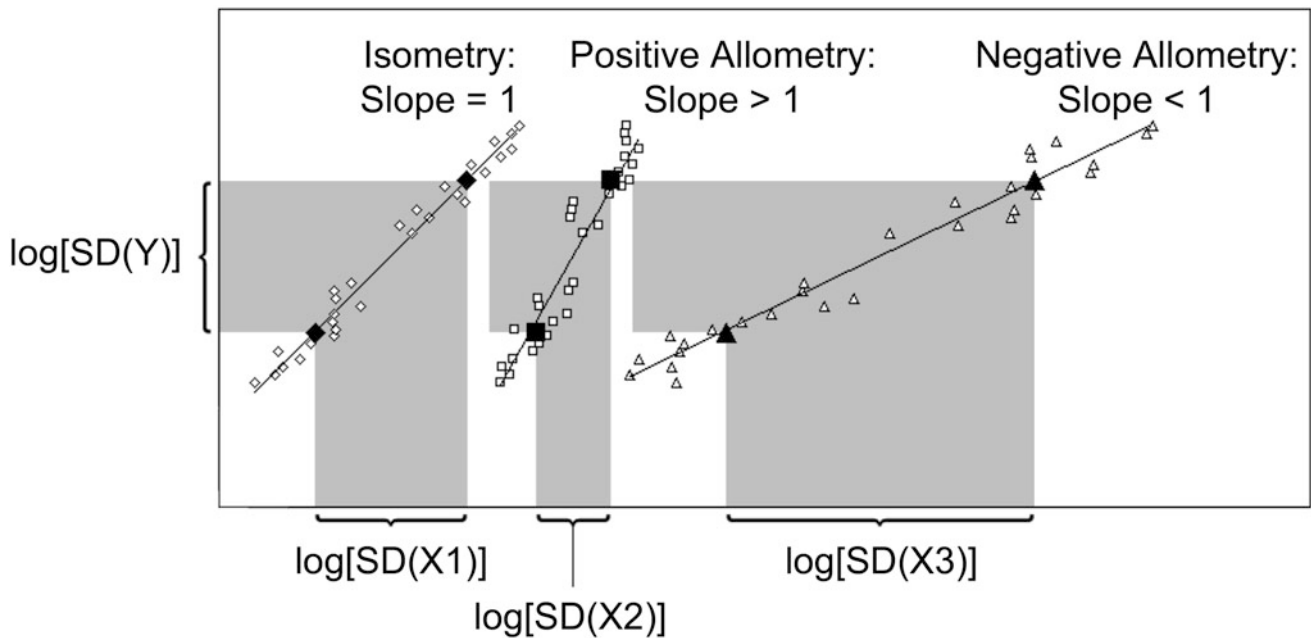
**Table 13.3** Example of *A. afarensis* specimens and postcranial measurements used to calculate overall measure of postcranial size dimorphism. Measurements in mm<sup>a</sup>

Specimen	HUMHEAD	ELBOW <sup>0.5</sup>	RADTV	FEMHEAD	FEMSHAFT <sup>0.5</sup>	DISTFEM <sup>0.5</sup>	PROXTIB <sup>0.5</sup>	DISTTIB <sup>0.5</sup>
A.L. 288-1	27.3	20.5	15.0	28.6	20.9	–	40.3	18.2
A.L. 128-1/129-1	–	–	–	–	21.6	37.5	39.9	–
A.L. 137-48a	–	22.9	–	–	–	–	–	–
A.L. 211-1	–	–	–	–	28.2	–	–	–
A.L. 322-1	–	22.9	–	–	–	–	–	–
A.L. 333-3	–	–	–	40.2	31.3	–	–	–
A.L. 333-4	–	–	–	–	–	45.6	–	–
A.L. 333-6	–	–	–	–	–	–	–	21.7
A.L. 333-7	–	–	–	–	–	–	–	24.8
A.L. 333-42	–	–	–	–	–	–	50.6	–
A.L. 333-95	–	–	–	–	29.1	–	–	–
A.L. 333-96	–	–	–	–	–	–	–	21.0
A.L. 333-107	35.1	–	–	–	–	–	–	–
A.L. 333w-40	–	–	–	–	30.8	–	–	–
A.L. 333w-56	–	–	–	–	–	45.0	–	–
A.L. 333x-14	–	–	22.2	–	–	–	–	–
A.L. 333x-26	–	–	–	–	–	–	52.3	–
MMR:	1.29	1.12	1.48	1.41	1.40	1.21	1.28	1.19

<sup>a</sup> Reproduced from Gordon et al. (2008). Fossil measurements taken from McHenry (1992) and McHenry and Berger (1998). Mean method ratio (MMR) calculated for each measurement. Overall measure of MMR is the geometric mean of these eight values: 1.29

dimorphism is calculated for the overall size variable (the geometric mean of all measurements) or if it is calculated as the geometric mean of dimorphism in each measurement. This property means that geometric mean methods can be applied in cases of missing data. Consider the *A. afarensis* data presented in Table 13.3: although it is impossible for a measure of overall size to be calculated for any one

specimen using the geometric mean, a measure of overall relative size variation can be calculated for the sample as a whole by calculating the geometric mean of the ratios for each variable. This value can then be compared to values from extant comparative samples that have been generated in the same way; i.e., subsamples of equal size as the fossil sample are selected, data is removed from the comparative



**Fig. 13.3** Relationship between scaling and size dimorphism for pairs of variables (hypothetical data). Reproduced from Gordon et al. (2008). When plotted in log space, the log of sexual dimorphism (SD) is the difference between the mean of male values and the mean of female values. For example, the length of the bracket along the Y-axis is equal to the log of the male:female ratio for variable Y, where the *bracket* indicates the distance between the sex-specific means (shown as *closed symbols*). When two variables of the same dimensionality (i.e., linear, area, or volume measurements) scale isometrically with

each other they will have highly similar SD values (compare the length of the *brackets* for Y and X1); these SD values would be identical if there were no variation about the regression line. When there is positive allometry for the scaling of Y on X, the X variable will have a lower SD value than Y (compare *brackets* for Y and X2), while the reverse is true for negative allometry (compare *brackets* for Y and X3). Note that the slope of the scaling relationship can be estimated by the slope of a line passing through the female and male means, which is equivalent to  $\log(\text{SD}(Y))/\log(\text{SD}(X))$

sample so that fossil and extant comparative samples are missing the same number and types of measurements, and then overall relative size variation is calculated for the resulting comparative sample (Gordon et al. 2008).

Resampled geometric mean methods enjoy several advantages over template methods. First, specimens can be included which do not have elements present in a template specimen (e.g., the three specimens with distal femur measurements in Table 13.3, a measurement not available for A.L. 288-1). Second, no measurements are estimated; only values which are measured directly are included. Third, because relative size variation is calculated independently for each variable, only antimeres can result in multiple representation for single individuals for a given variable. Representation of single individuals by multiple elements is not a drawback but a goal in geometric mean methods, and empirical tests have shown that results change very little if supposed unassociated elements are actually drawn from a single individual (Gordon et al. 2008). Fourth, because of the manner in which multiple variables are used to calculate the final measure of relative size dimorphism, fossil sample sizes are generally large enough to calculate distributions of relative size variation for fossil taxa as well as comparative taxa, whereas all previous analyses

(including previous geometric mean analyses) compared distributions for comparative taxa to the single observed value for a fossil sample. Thus resampled geometric mean methods can potentially provide a much more conservative yet more accurate test for significant difference between fossil and extant samples in relative size variation.

One problem that template methods and resampled geometric mean methods share, although to a lesser extent in the latter, is that of the assumption of isometric scaling between variables. As Fig. 13.3 illustrates, the ratio between size dimorphism as measured for two variables within a single sample is directly proportional to the scaling relationship between those two variables. Thus when all variables scale isometrically with each other, all variables are expected to show the same level of dimorphism and thus a geometric mean of those dimorphism levels will be an accurate representation of the overall level of dimorphism in all of the included variables. However, if positive or negative allometry exists between some of the included variables, then the observed level of dimorphism will be expected to differ between variables. In that case comparisons between taxa would only be valid if all taxa included in the analysis shared the same scaling patterns for all variables.

Gordon et al. (2008) circumvented this problem by only including variables that did not differ significantly from isometry in their scaling with the other variables in the analysis as measured within each of the extant species. (Notably, they found that *A. afarensis* exhibited gorilla-like levels of size dimorphism in agreement with most other recent studies, whereas Reno et al. (2003, 2010), who did not demonstrate that their variables scaled isometrically with each other, did not.) However, this problem can also be addressed by using a weighted geometric mean, where the weights are the scaling relationships between each variable and an overall standard. This standard could be one of the variables in the analysis or another variable such as body mass. Multiple sets of weightings could be generated for the fossil geometric means based on the scaling relationships of each of the comparative taxa, with interpretation taking particular notice of the results using the most conservative set of weights.

### **Improving Understanding of the Relationship Between Mass Dimorphism and Skeletal Dimorphism**

This leads into the second area of research, which is the investigation of the relationship between different types of dimorphism. As previous researchers have noted, skeletal dimorphism is not equivalent to body mass dimorphism (e.g., Plavcan 2003; Plavcan et al. 2005a; Harmon 2006; Gordon et al. 2008). Because sexual selection probably targets body mass rather than skeletal size, it is important to understand how the two are related. For example, sexual dimorphism for most postcranial measurements is higher in modern humans than in chimpanzees, but the reverse is true for body mass (Richmond and Jungers 1995; Gordon et al. 2008). However, little work has been done to investigate these relationships. Preliminary research suggests that dimorphism in postcranial measurements may be more variable intraspecifically than is dimorphism in craniofacial measurements among living primates (Plavcan and Gordon 2007), but much more work remains to be done in this area. In particular, the scaling of body mass with measurements used in fossil analyses needs to be identified for those taxa that are typically used in comparative studies, and ideally these should be identified for a broad range of primates and evaluated in the context of variation in positional behavior.

### **Applying New Methods to Other Species**

Aside from the benefit of being able to better evaluate relative size variation in *A. afarensis*, these new techniques also open

up the possibility of applying rigorous statistical approaches to analyzing size dimorphism in other australopiths. For example, recent studies of size and shape variation in *A. afarensis* and *A. africanus* suggest that postcranial size dimorphism is probably greater in *A. afarensis* than in *A. africanus* (Cunningham 2005; Green et al. 2007; Harmon 2009), but this comparison has yet to be directly tested. Fortunately, the hypodigm of *A. africanus* is now large enough to apply the new methods described above. Furthermore, the postcranial hypodigm of *A. afarensis* continues to expand, which will improve estimates of skeletal dimorphism and increase the power of statistical tests. For example, the new postcranial specimen KSD-VP-1/1 from Woranso-Mille, Ethiopia, falls somewhere in the range from mid-sized male to among the largest males of *A. afarensis* (Haile-Selassie et al. 2010). Thus estimates of postcranial dimorphism in *A. afarensis* will likely either go up or stay the same while standard error of the estimates will go down, making it more likely that significant difference in dimorphism will be found between *A. afarensis* and taxa with lower apparent levels of dimorphism. Finally, although *A. anamensis* is lacking in postcrania, it is possible that techniques could be developed which incorporate the relationship between craniofacial dimorphism and body mass dimorphism, taking into account that the connection between male competition and cranial size dimorphism may not be particularly tight. Such techniques may ultimately allow us to make comparisons not only between single fossil species and extant taxa, but among fossil taxa as well.

### **Dimorphism in *Ardipithecus ramidus***

With the long-anticipated publication of the analysis of *Ar. ramidus* in a special issue of *Science* in 2009, it is interesting to consider how dimorphism in this taxon relates to the overall patterns seen in *Australopithecus*. Unfortunately, no direct analysis of postcranial size dimorphism in *Ar. ramidus* has been published to date, but there are arguments made within the special issue of *Science* that body size dimorphism was probably low (Lovejoy 2009; Suwa et al. 2009b). Evaluating this assertion and its implications for evolutionary pressures acting on hominin dimorphism requires consideration of the sex assessment of the specimen ARA-VP-6/500 as well as the phylogenetic placement of *Ar. ramidus*.

### **Ardi or Artie? Sex Assessment in ARA-VP-6/500**

Sex assessment in ARA-VP-6/500 relies on the following argument: the canine of ARA-VP-6/500 is among the smallest

in the hypodigm of *Ar. ramidus*, while the postcranial elements are among the largest. Therefore, either sex is a possibility, but according to Suwa et al. (2009b) ARA-VP-6/500 must be female because the probability of sampling a male canine that is as small as that of ARA-VP-6/500 is very low.

The rank-based sampling procedure of Suwa et al. (2009b) for assessing the probability of a male canine being as small as that of ARA-VP-6/500 relies upon the assumption that there is a moderately high level of variability in canine size in *Ar. ramidus* that is due to significant size difference between the sexes. However, as they themselves note, canine size variation in *Ar. ramidus* is very low. As shown in their Fig. 1e, f (Suwa et al. 2009b), the variability of upper canine metrics in *Ar. ramidus* is less than that seen in modern humans, *A. anamensis*, and *A. afarensis*, all of which are considerably less variable than *Pan troglodytes* and *P. paniscus*. As shown in that same figure, there is substantial overlap in male and female metrics in modern humans (although not in *Pan*), a taxon more variable in size than *Ar. ramidus*. As such, there is a reasonable probability that a male *Ar. ramidus* can have a canine as small as ARA-VP-6/500. The point here is that low canine size variation on the order of that seen in *Ar. ramidus* indicates that no strong statement regarding attribution to either sex can be made for any specimen on the basis of canine size alone.

Furthermore, the assumption in Suwa et al. (2009b) and the accompanying papers is that because canine size variation is low, body size variation must also be low. However, as discussed above, the hominins as a clade demonstrate a decoupling of canine and body size variation with low canine size variation in *A. afarensis* and later hominins, but substantial postcranial size variation. Regardless of whether or not *Ar. ramidus* is a hominin, that same decoupling may be present in this taxon. Unfortunately, these papers do not present any analysis of size variation in the postcranium. However, two possibilities are considered below.

*Low canine size variation, high postcranial size variation:* If this is the case, the large size of the postcranium of ARA-VP-6/500 in conjunction with high postcranial size variation such as that seen in *A. afarensis*, *G. gorilla*, and *P. pygmaeus* could be interpreted as strong evidence that ARA-VP-6/500 is male; i.e., Artie, not Ardi.

*Low canine size variation, low postcranial size variation:* If this case is true, the large postcranium of ARA-VP-6/500 tells us just as much as its small canine, i.e., not much. In the presence of low size variation, no confident assessment of sex can be made.

The implications of these scenarios are clear: depending on how variable postcranial size is in *Ar. ramidus*, it may be possible to make a strong argument for ARA-VP-6/500 being male, but regardless of how much size variability exists in the postcrania, one cannot make a strong argument for ARA-VP-6/500 being female on the basis of size

variation in the canine and postcrania alone. Suwa et al. (2009a) argue that the supraorbital torus in the cranium of ARA-VP-6/500 is thin relative to chimpanzees, thus confirming that this specimen is female. However, the lack of comparison to supraorbital torus thickness in conspecifics makes this assertion dubious. They also note that ARA-VP-6/500 possessed a small compound temporal/nuchal crest, but suggest that since such a crest appears in both male and female chimpanzees, it should not be taken as an indicator that the individual was male (Suwa et al. 2009a). In any event, the case for ARA-VP-6/500 being female is weak. This is important because the argument for low body size dimorphism in *Ar. ramidus* is based entirely on the assumption that ARA-VP-6/500 is a female with some of the largest postcranial elements in the hypodigm (Lovejoy 2009; Suwa et al. 2009a).

### **Canine Size, Canine Dimorphism, and Body Size Dimorphism: Implications for Understanding Evolutionary Pressures on Large-Bodied Hominoids in the Early Pliocene**

When considering canine size, canine size variation, body size variation, and phylogenetic placement of *Ar. ramidus*, there is good evidence that the canines are relatively small compared to extant African apes, and that there is low size variation within the canines (Suwa et al. 2009b). As noted earlier, there have not yet been any rigorous assessments of body size variation in *Ar. ramidus*, and there is some question regarding whether this species is a member of Hominini (e.g., Sarmiento 2010; Wood and Harrison 2011). Thus one could consider four possible scenarios given the data presented for *Ar. ramidus* so far, as shown in Table 13.4. Implications of each of these scenarios are considered in turn.

*Scenario 1: Hominin with relatively small canines, low canine size variation, and low body size variation.* In this case, *Ar. ramidus* would follow the hominin trend of reduced canine size and dimorphism, but would be unusual in that it had low body size dimorphism, contrary to the pattern seen in later fossil hominins, *Pan*, and *Gorilla*. Given the ubiquity of moderate to high body size dimorphism in fossil hominins and the African apes, this low dimorphism would most parsimoniously be interpreted as an autapomorphy of *Ar. ramidus*, implying that either a reversal occurs in later hominins if they are descended from an *Ar. ramidus*-like ancestor, or that *Ar. ramidus* represents a side branch diverging from the main trunk of later hominin evolution.

*Scenario 2: Hominin with relatively small canines, low canine size variation, and high body size variation.* Under

**Table 13.4** Possible scenarios regarding dimorphism and phylogenetic placement of *Ar. ramidus*<sup>a</sup>

Scenario	Canine size	Canine size variation	Body size variation	Member of Hominini
1	Small	Low	Low	Yes
2	Small	Low	High	Yes
3	Small	Low	Low	No
4	Small	Low	High	No

<sup>a</sup> Canine size and measures of variation are relative to living African apes

this scenario, *Ar. ramidus* would indicate that the hominin pattern of decoupled canine and body size dimorphism was established at least 4.2 Ma, increasing the temporal gap between the decoupling of the various types of size dimorphism and the first appearance of stone tools.

**Scenario 3: Non-hominin with relatively small canines, low canine size variation, and low body size variation.** In this case, the existence of *Ar. ramidus* would indicate that there were at least two lineages of large-bodied hominoids with decreased canine size in the Early Pliocene (i.e., hominins and the *Ar. ramidus* lineage). Furthermore, inferred locomotor and postural differences between *Ar. ramidus* and hominins based on their postcranial morphology (Lovejoy et al. 2009a–c) would suggest that those multiple hominoid lineages were exploiting different niches in the changing landscape of East Africa at that time.

**Scenario 4: Non-hominin with relatively small canines, low canine size variation, and high body size variation.** Finally, this scenario would indicate that not only were there multiple East African ape lineages with decreased canine size exploiting different niches in the Early Pliocene, but also that the pattern of decoupled body size and canine size dimorphism occurred in at least two lineages at around the same time. This pattern would argue for some external forcing due to a region-wide selection pressure, presumably related to climatic variables of some sort. Furthermore, note that in this and the previous scenario, the reduction of canine size could not be considered a synapomorphy of hominins.

While all four of the scenarios outlined above are inherently interesting, and three of them represent large changes from earlier models of hominid and hominin evolution in the Pliocene (scenarios 1, 3, and 4), at present there is no way to choose between them. Although the phylogenetic placement of *Ar. ramidus* may be debated for many years to come, the eventual publication of more detailed analyses of postcranial dimorphism in this species will help narrow down the possibilities.

## The Biological Significance of Sexual Dimorphism in *Australopithecus*

At the end of the day, what can we say about dimorphism in *Australopithecus*, and what can we infer from it? Most studies demonstrate strong statistical support for a moderate

to high degree of skeletal size dimorphism in *A. afarensis*. Even assuming human-like scaling patterns for postcranial dimensions with body mass, *A. afarensis* almost certainly exhibited greater mass dimorphism than modern humans, and possibly more than chimpanzees and bonobos, although probably not as much as gorillas or orangutans. A slightly lower level of mass dimorphism is likely for *A. africanus*, while the levels of postcranial and mass dimorphism in *A. anamensis* are hard to evaluate at this point. That said, given the evidence supporting the role of resource stress in selecting against large female size and thus increasing dimorphism, combined with paleoecological reconstructions of high environmental variability at sites where the australopithecine material under consideration is found (e.g., Hadar between 3.4 and 2.9 Ma; Bonnefille et al. 2004), a significant portion of the dimorphism observed in *Australopithecus* species could potentially be due to ecological effects rather than sexual selection. How can we determine what role various selective factors played, and how may we use that knowledge in reconstructing behavior and ecology in fossil hominins?

One possibility relies on the relationship between growth rate variation and ecological stress in producing sexual size dimorphism. It is possible to develop techniques which assess the amount of size variation present at different developmental ages in fossil taxa and compare them to extant species in order to determine whether dimorphism is primarily due to duration differences (in which case relative variation in adult size would be expected to be high, but relative variation at all earlier age stages would be low), indicating a relatively small ecological component, or due to rate differences (in which case relative variation would be expected to steadily increase with developmental age), indicating a significant ecological component. For example, in a recent analysis of *Paranthropus robustus* facial material, Lockwood et al. (2007) compared dimorphism levels at different dental wear stages to demonstrate that facial dimorphism in this species appears to result from extended male growth relative to females. Such procedures are easiest with craniofacial and mandibular size, where developmental age can be inferred from dental eruption and wear, but they might also be developed for postcranial elements based on degree of epiphyseal fusion to identify patterns of size variation at younger developmental ages.

A second possibility is to evaluate australopith dimorphism in a phylogenetic comparative context. For example, Gordon (2004) used a phylogenetically independent contrasts approach to consider the relationship between evolutionary changes in female and male skeletal size in *Pan troglodytes troglodytes*, *P. troglodytes schweinfurthii*, *P. paniscus*, and *A. afarensis* (where female size in *A. afarensis* was represented by A.L. 288-1, and male size by a composite of A.L. 333-3, -x26, -42, -107, and -x14). In that study, differences in size dimorphism between subspecies of *P. troglodytes* were due to differences in female size, consistent with ecological differences between their habitats. Dimorphism differences between *P. troglodytes* and *P. paniscus* were due to differences in male size, consistent with expectations of greater sexual selection occurring in common chimpanzees than in bonobos. Finally, differences in dimorphism between *Pan* and *A. afarensis* were primarily due to differences in female size, suggesting that *A. afarensis* probably experienced similar levels of sexual selection as the genus *Pan*, but exhibited higher levels of dimorphism than *Pan*, perhaps due to the effect of natural selection on female body size in the form of ecological stress. Approaches like this can be adapted to include larger sample sizes, remove assumptions of presumed sex, analyze other species, etc. Ultimately, such approaches may allow us to infer much more than just analogous social structures, and permit us to build new human evolutionary models where paleoecological signals from the environment can be compared against ecological signals preserved in fossil hominin dimorphism.

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