# The Pace and Processes of Early Divergence and Stasis: Morphological Evolution in Isolated Populations of the Sulawesi Booted Macaque, *Macaca ochreata* (Cercopithecidae)

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# Abstract

I conducted a morphological field study of two primate populations (*Macaca ochreata ochreata* and *M. o. brunnescens* of Sulawesi, Indonesia) that have been isolated from one another for approximately 9,000 years, under subtly different ecological conditions. My aims were to (1) determine which morphological traits have undergone evolutionary change during this period, and which have remained stable; and (2) ask which evolutionary processes may have contributed to the observed divergence or stasis, as the case may be.

My results indicate (1) subtle divergence in head breadth, and (2) marked stability in body size, body proportions, limb proportions, and male secondary sexual characters (maxillary canine teeth and testes). Genetic drift is suspected as the cause of divergence in head breadth, due to small population size in the divergent population (*brunnescens*), the small magnitude of change, and the lack of a known effect of head breadth on ecological performance in this taxon.

There is some evidence that strong parallel selection within each population maintains the populations' morphological stability, i.e., their lack of divergence (except in head breadth). First, the femur shows positively allometric growth relative to the other limb segments; furthermore, relative growth of the limb segments (but not the trunk) seems to be highly canalized (resistant to environmentally-induced change). In combination with behavioral evidence from primary-forest populations that this species is highly arboreal, the evidence suggests strong, parallel ecological selection for leaping ability, via faster growth of the femur relative to the other limb segments. Second, strongly positive allometry and a high coefficient of variation in male secondary sexual traits (especially maxillary canine teeth) suggest that on-going, parallel sexual selection may enforce stasis in these traits as well.

The results suggest that some morphological traits (e.g., cranial characters) may be less constrained by selection than are others, and thus more free to diverge by genetic drift, replicating previous studies on New World primates and on Neandertals and modern humans. The results also highlight the possible role of ecological and sexual selection in constraining evolutionary change.

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From the beginning, the field component of this project has been all-Indonesian (except for me). It was my Indonesian friends and research technicians and neighbors of all ages who patiently taught me their language, and thereafter consoled me with conversation, jokes, and kind words during the many months of research away from the land of my birth. They were all too effective; Lanowulu, a town in Tinanggea district, Southeast Sulawesi, became the home of my heart. Now, sitting here in an office in California as I write this, I feel like a foreigner and I yearn to go home.

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I owe so much to Prof. Sandy Harcourt, on so many levels, that even a summary of my debt to him would require a good-sized chapter by itself, so I will necessarily be brief. Sandy's scientific work is well-known to the anthropological and biological communities, of course; but in working with Sandy for many years, one learns about qualities of his that are not listed on his c.v., yet are present in abundance—kindness, patience, humility, and above all, compassion. It is these qualities of his that I am most hopeful to someday pass along to my students and to my children. There is no living man whom I equally respect and admire, my father having passed away long ago.

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In the name of God:

the Most Compassionate; the Most Merciful

There is not an animal that lives on the earth,

nor a being that flies on its wings,

but forms part of communities like you.

Nothing have We omitted from the Book,

and they all shall be gathered to their Lord in the end.

*Qur'an* 6: 38

(interpretation by Yusuf Ali)

For Vina,

the treasure of a lifetime

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# Chapter One

## Evolutionary diversification and stasis: a critical review

New hominin species are discovered ever more often, and with each discovery, the hominin family tree grows bushier. In most cases, a new speciation event is required to explain how the newly-discovered fossil population fits in. Diversification theory—from stasis to divergence of populations, to speciation, through higher-order patterns of diversity—thus has become more and more useful to anthropologists who want to understand human evolution on a deep level (the how as well as the what of it).

The purpose of this dissertation is to contribute to our understanding of some of the details of evolutionary diversification. I therefore begin with a review of work on more foundational issues in the field of diversification.

This is a critical review, and my intent is to be provocative without being pejorative. My intent, furthermore, is to express herein the direction in which I think evolutionary biology is going—some of the ideas that I present here are minority ideas, but they are not my ideas, and many have been around for a long time. I therefore play the role of a reporter, remarking upon interesting developments in my field. In other words, this chapter is a review, not an original theoretical disquisition.

### *1.1: Preliminary considerations*

Since even the most foundational terminology and concepts in evolutionary biology tend to be fraught with ambiguity, misunderstandings and multiple distinct usages (e.g., fitness: Mills and Beatty 1979), I begin with a discussion of fundamental concepts that are needed before I move on to discuss diversification.

*Foundational mechanisms of evolution*—According to population genetic theory, evolutionary divergence between populations may be caused in part by mutation, recombination, natural selection, sexual selection, genetic drift, gene flow, and those forms of non-random mating that do not correspond strictly to sexual selection (such as assortative mating, inbreeding and outbreeding) (Gillespie 1998).

Endler (1986: ch. 1) distinguished between natural selection in the broad sense, and natural selection in the narrow sense. The former includes sexual selection, while the latter excludes it. For convenience, I will henceforth use the term "natural selection" exclusively in its broad sense, while natural selection in the narrow sense will be called ecological selection.

Evolution is driven by heritable variation, including the underlying structure of that variation and its mode of inheritance; and of course by the interaction of variants with their environmental circumstances (i.e., fitness). Darwin, in a letter to Charles Lyell dated September 1860, wrote that he regretted using the term "natural selection," preferring in retrospect the much more accurate "natural preservation" (quoted in Ruse 1979). Natural selection is essentially a passive process that results automatically when certain preconditions (variation, inheritance and fitness differences) are present. As Endler (1986: ch. 2) has reminded his readers, selection no more acts on variation than erosion acts on a sandy hillside.

Thus natural selection cannot truly be the cause of anything, even though biologists (including myself) habitually describe it as a cause. If natural selection is not the cause of anything *per se*, then what is the cause? Is it really just variation and inheritance? Surely if we were to go too far in reductionism while searching for a cause, we would end up with no way to distinguish selection from genetic drift. When biologists talk about natural selection as a cause, we are really talking about differential fitness as a cause. Fitness is a propensity that arises from the genetic and epigenetic constitution of each organismal variant, in relation to the organism's biotic and abiotic environments (Ho and Saunders 1979; Mills and Beatty 1979; Sober 1984: his section 3.2).

Fitness is highly complex; when one tries to precisely specify or predict it in any given case, the number of possible permutations of genotype, phenotype, biotic environment and abiotic environment can become overwhelming. When we know $b$, an organism's genotype, and $c$, its environment (pre-natal to death) in the full ecological, social and physiological sense of "environment," then we can (in theory!) estimate $a \mid (b, c)$, the probability of the organism producing viable offspring. Even the *a posteriori* quantitative specification of $a \mid (b, c)$ is extremely rarely attempted, however.

While Darwin (1859) and the majority of his successors think that variation is random and only differential fitness is non-random, there is currently a need for much more philosophical precision about what is meant by "randomness," and in what sense or senses (if any) variation is truly random (Fox 1984). For example, which homologous chromosome ends up in a particular gamete cell after the first meiotic division is probably more or less random; but can we really then say that variation in the broad sense is random, when the entire meiotic process (indeed the sexual process as a whole) is precisely arranged so as to increase variation, and thus, by Fisher's (1930) fundamental theorem of natural selection, to speed up adaptive evolution?

Furthermore, biochemical experiments with amino acids tend to support the proposition that the underlying structure of biological variation—even of amino acids synthesized in the laboratory—is profoundly non-random and indeed functional from the first (Ho and Saunders 1979; Ho and Saunders 1984). Life is not rendered functional and non-random by natural selection; rather, the fundamental components of life are inherently functional, but the variants that are relatively most functional in a given specific environment will spread via natural selection (more precisely, via differential fitness).

Mendel (1866), Avery et al. (1944), and Watson and Crick (1953a; 1953b), in their turns, contributed a tangible substrate to heredity, making natural selection a much stronger theory than it had been before. Likewise the theoreticians and empiricists of the Modern Synthesis contributed a mathematical sophistication to evolutionary theory that led to, for example, the realization that allele frequencies can and do change drastically, without any need for fitness differences (i.e., via genetic drift), under some circumstances. The Modern Synthesis also pointed to the importance of genetic linkage in sexual selection (Fisher 1930: ch. 6).

Kirschner and Gerhart (2005), however, argue that the Modern Synthesis is useful but incomplete, because it ignores the crucial (and very much non-random, and non-trivial) link between genetic variability and effects on the phenotype. As Kirschner and Gerhart put it, knowledge of this linkage is "needed to explain the feasibility of evolutionary change." Thus it seems that the spread and preservation of random mutations is not quite sufficient to explain the diversification and adaptedness of life, let alone the origin of life (see also Fox 1984; Ho and Saunders 1979; Wagner and Altenberg 1996).

An emerging view, summarized briefly, is that evolution is fundamentally predictable (Morris 2003; Vermeij 2006), and that it therefore must have—like ecology—more self-organization built into it than can be accounted for by natural preservation of random mutations (Groves 1989: ch. 2; Ho and Saunders 1979; Wagner and Altenberg 1996). For example, recent work (summarized in Gibbs 2003) suggests that non-coding or "junk" DNA may actually have any of several biological functions—for example, one possibility is that non-coding DNA could function as a vast reservoir of genetic variability, perhaps left over from the distant past, that could provide potentially useful genetic code (see also ENCODE Project Consortium 2007 for evidence of widespread transcription of the human genome). Such a possibility challenges the assumption that random point mutations in coding genes are the main source of new genetic variants.

A deeper understanding of the nature and workings of fitness can come from study of its two interacting components: (1) the structure of genetic variation and of the processes that produce and maintain it; and (2) ecological influences upon the fitness of organismal variants, referred to recently as the source laws of ecology, as opposed to the consequence laws of natural selection (Endler and McLellan 1988; Nakajima 1998; Sober 1984). In the case of sexual (as opposed to ecological) selection, the source laws that interact with the variants themselves to determine fitness would probably be based upon sensory biases in other animals' nervous systems, or other physiological or anatomical factors (Endler and Basolo 1998).

*Definition of species*—In order to evaluate fairly the potentialities of the various causes of evolution (enumerated above) to cause divergence between populations, we need to employ a definition of species that does not create an *a priori* bias in favor of a particular cause or causes of divergence. The popular biological (isolation) species definition of Poulton (1904), Dobzhansky (1937) and Mayr (1942; 1963) is biased in that it excludes, by definition, any mechanism of divergence that does not include complete cessation of gene flow. We can see, however, that in many organisms—including several pairs of Sulawesi macaque species, such as *Macaca tonkeana* and *M. ochreata*—there are parapatric populations that maintain bimodal trait distributions within their contact zones, in the face of limited gene flow. Introgression of certain traits occurs without any change in the overall bimodal distribution (Camperio Ciani et al. 2005; Mallet 1995; Watanabe et al. 1991a; Watanabe and Matsumura 1991; Watanabe et al. 1991b).

Aside from the sheer methodological difficulty of a mortal being actually gathering enough field data on interbreeding and gene flow to establish the absolute genetic independence of parapatric populations, the isolation species definition seems possibly circular, defining species in terms of one of the major phenomena (gene flow, or lack thereof) that is supposed to be under study as a potential cause of divergence (Mallet 1995; Wallace 1865).

Yet another problem with the isolation species concept is that, as Cracraft and Prum (1988) put it, "Patterns of reproductive cohesion and disjunction among populations do not necessarily parallel phylogenetic patterns of differentiation." In other words, non-sister populations often interbreed to some extent, while not interbreeding with their true sister populations, depending upon the current geographical and ecological situation. Thus the isolation species concept can not only obscure early and intermediate stages of diversification, but can obscure true phylogenetic relationships as well.

A particularly interesting example of the paraphyly to which the isolation concept can lead, is given in Godfrey and Marks (1991: their fig. 1). A species with a vast range is divided into several parapatric subspecies (as in the case of, e.g., a ring species) which are genotypically distinct and discontinuous (bimodal in contact areas), but do interbreed to some extent, hence they are classified as one species or superspecies. A peripheral isolate population then forms and becomes reproductively isolated from all the rest of the parent species—but the new isolate is most closely related to only one of the populations within the parent species. Hence the peripheral isolate is now considered a separate species (under the isolation concept), yet is nested phylogenetically within the larger parent species.

Darwin (1859: ch. 2) defined a species as a set of individuals that share a cluster of morphological traits in common, and that are not (unlike races or varieties) connected to other such clusters of traits via a continuum of intermediate populations. This definition was of course applied to populations in contact; fully allopatric populations' distinctiveness was to be judged subjectively.

Mallet (1995) defined species using Darwin's and Wallace's favored definition, but replaced the morphological criterion with a genetic one, so that species are defined as clusters (modes) of genotypes. Mallet points out that his species definition is neutral with respect to the various hypothesized causes of divergence, and is not at all circular when the question of speciation comes up. A critical test of species status, under Mallet's definition, is the distribution of genotypes in contact zones between populations; a unimodal distribution indicates that the two populations are races within a single species; a bimodal distribution (unless the contact zone is of very recent, perhaps anthropogenic, origin) indicates that the two genotypic clusters are temporally stable, and that any limited introgression (gene exchange) that may occur between them has not been sufficient to collapse the populations together in terms of overall allelic frequencies.

Finally, the new genotypic definition sidesteps some of the difficulties that led to adoption of the reproductive-isolation definition of species in the first place. When purely morphological criteria were used to classify butterfly species around the turn of the twentieth century, such criteria led to the classification of males and various female morphs within mimetic butterfly species as different species; this impression was overturned only when (monomorphic) males were observed mating with the various female morphs (Mallet 1995). That observation led Poulton (1904) to propose an interbreeding-based species definition. The modern, genotypic-cluster definition of species, however, avoids the problem of intraspecific polymorphism by classifying organisms based upon *overall* genetic similarity, a criterion that allows for intraspecific polymorphism in a few arbitrary and eye-catching morphological traits, just as it allows for modest genetic introgression between species.

It may be objected that Mallet's (1995) definition of species would split into separate species those populations that may, in the future, collapse together again due to environmental change; Mallet answers that the future is unknown to us anyway, and that secondary introgression after some degree of divergence has occurred is itself an interesting and potentially creative source of evolutionary divergence and change (see also Mallet 2007). While the isolation species definition is conceptually very clean, field biologists are quite well aware of the messiness and fuzzy boundaries of nature, and the inherent diversity-generating potential of such seeming disorder. One can think of meiosis as a metaphor for the reality of population divergence on the ground—in truth, meiosis (as viewed via time-lapse photography) is quite a sticky, messy process, full of crossing-over and inversions and non-disjunctions; but it is just these complications that fuel much of the variation that allows evolution to occur.

## *1.2: Early vs. late diversification, and speciation*

I have explained in the previous section why I prefer to use Mallet's (1995) simple definition of species, one that encourages us to see speciation as a long-term process, all of whose phases are equally interesting. Accordingly, then, I use herein the term "diversification" as a blanket concept that embraces everything from the earliest divergence of populations to the evolution of full reproductive isolation (at whatever point that occurs), and beyond. I thus avoid the potential quibbling that may arise as to whether early diversification counts as subspeciation or speciation. Until very recently, the focus in diversification research was firmly placed upon the latest stages of diversification—that is, the evolution of reproductive isolation and isolating mechanisms (Coyne and Barton 1988; Coyne and Orr 1998; Dobzhansky 1937; Endler 1989; Ortiz-Barrientos et al. 2004). In laboratory model-organism research on organisms such as *Drosophila*, the emphasis has been placed especially upon post-mating or post-zygotic means of isolation, Haldane's rule, and reinforcement—although the last of these has recently been the subject of many field studies (reviewed in Servedio 2004).

Reinforcement is by definition the outcome of secondary contact between previously-isolated populations, and that fact has two important implications. First, reinforcement must be a very late stage of diversification, and one that need not really occur at all (its prevalence in nature remains little-known: Servedio 2004). Second, due to the necessity for allopatric isolation followed by broad secondary contact, reinforcement requires the establishment of a highly effective barrier, followed by the complete elimination of that barrier. As with all scenarios of fully-allopatric speciation, this requirement introduces an unparsimonious geological requirement which, although it undoubtedly has occurred in many instances throughout the earth's history, cannot possibly explain all of the biodiversity on Earth (Bridle et al. 2004; Endler 1982; Schneider et al. 1999).

Reinforcement, and reproductive isolation in general, are undoubtedly highly effective and important mechanisms of diversification (Turelli et al. 2001), but these processes are not at all necessary to generate biodiversity (Endler 1989).

### *1.3: Geography, gene flow and diversification*

In this section I will argue that while allopatric speciation (speciation by full isolation) is an important and highly effective means of population divergence, its assumed ubiquity, and perceived greater plausibility, are unjustified. It is becoming clearer that we really don't know very much about how speciation usually occurs in nature—although an explosive surge in research is greatly adding to our understanding.

*The non-necessity of isolation in diversification*—For decades, biological research has emphasized the allopatric speciation model, which is usually attributed to Mayr (1942; 1963) who popularized it and provided much evidence in its favor. In fact, the allopatric speciation model goes back to the biogeographical research of Gulick (1890, cited in Irwin et al. 2001 as 1890a). In allopatric speciation, gene flow (or rather its cessation) is accorded the central and indispensable role. As Turelli et al. (2001) point out, complete cessation of gene flow enables divergence of any pair of populations by any potentially effective mechanisms that might occur within the respective populations—natural selection, drift, and so on.

The undoubted and virtually undisputed effectiveness of complete isolation at facilitating divergence between populations has sometimes led to a certain lack of interest in what processes might be occuring within the respective populations—and in seriously testing alternatives to isolation-based speciation. The obvious effectiveness of full isolation has also led to a confusion of potential effectiveness with necessity and prevalence in nature, to the extent that genetic isolation has come to be considered the predominant mode of speciation in nature, though many authors over the years have contested that still-prevalent view (Bridle et al. 2001; Endler 1982; Endler 1989; Orr and Smith 1998; Schneider et al. 1999).

If any within-population evolutionary mechanism has received attention under the allopatric speciation model, it is genetic drift, as Mayr (1963) proposed the model of peripatric speciation, i.e., divergence of peripheral isolates via drift in small populations. This rather complete model is quite parsimonious genetically since it requires no fitness differences (it does not necessarily invoke selection), yet does not neglect within-population processes in favor of an exclusive focus upon gene flow. Peripatric speciation requires, however, a nearly complete cessation of gene flow, since Wright (cited in Gillespie 1998: 99) with his island model showed that even a single migrant each generation would be sufficient to prevent divergence of populations, in the absence of divergent natural selection (see also Lynch 1988).

One difficulty with the broad applicability of the peripatric model, however, is the phenomenon of extraordinarily long-distance dispersal, even over broad expanses of unfavorable habitats (e.g., Sweanor et al. 2000, cited in Thompson and Jenks 2005), in which animals sometimes engage (humans: Hudjashov et al. 2007; *Puma concolor*: Sweanor et al. 2000, cited in Thompson and Jenks 2005; *Macaca fuscata*: Yoshimi and Takasaki 2003). Slatkin (1976) has shown that, while local dispersal causes only extremely slow advance of advantageous alleles into a neighboring population, rare long-distance dispersal events can have a significant impact on the genetic constitution of populations otherwise isolated (whether by distance or by a physical barrier). Since the peripatric speciation model relies upon genetic drift (caused by small effective population size in peripheral isolates), it seems likely that peripatric speciation occurs only under very specific circumstances. I argue in chapter three of this dissertation, however, that the Tiworo and Buton Straits have essentially isolated the booted macaque populations *Macaca ochreata ochreata* and *M. o. brunnescens* during the Holocene—a situation that could be accurately described as peripatric, since the latter population could be considered a peripheral isolate.

It is often pointed out that future environmental changes could—without the benefit of isolating mechanisms—cause currently selection-maintained populations to collapse together and become homogenized. Thus Coyne and Barton's (1988) contention that "reproductive isolation can perpetuate local adaptations that would normally disappear with ecological change and gene flow." But if ecological change were to remove whatever differences in ecological selection maintained the populations' distinctiveness, would isolating mechanisms alone be enough to maintain the local adaptations in the long term? Non-neutral variability is, moreover, unlikely to be homogenized by gene flow (Endler 1973; Endler 1977; Endler 1989; Nosil and Crespi 2004; Rice and Hostert 1993). Aside from that, secondary hybridization on a moderate scale (short of panmixis) can introduce increased variability to a population, which can in fact speed up evolutionary divergence between the populations, and can even lead to speciation—quite the opposite of homogenization (Endler 1989; Mallet 1995; Mallet 2007).

When it is conceded that gene flow does not automatically erase non-neutral differences between populations, one must also admit that full reproductive isolation—and hence isolating mechanisms—are not necessary to maintain long-term distinctiveness of populations (Endler 1989). It then follows that significant, long-term diversification need not rest upon interpopulational epistasis—i.e., the evolution of a genetic trait that is adaptive against the genetic background of one population, but maladaptive, if not fatal, against the genetic background of a sister population (see Coyne and Orr 1998: their section 4a). Thus the possibility of non-allopatric, non-isolation-based speciation renders speciation as a whole more parsimonious and credible, since fewer special assumptions are required.

*The prevalence of allopatric speciation in nature*—Obviously full isolation must be quite effective at causing divergence of populations, when full isolation does indeed occur. But how common is allopatric speciation in nature? One barrier to the widespread applicability of the allopatric model has been the current distribution of sister species' ranges, which tend to be parapatric; that is, most sister species share narrow hybrid zones with limited introgression (e.g., White 1968). Diamond (1980) noted that many biologists who work in temperate regions suppose that there must be unseen ecological barriers in the tropics that maintain the patchy distributions of tropical animal species. Diamond (1980) went on to show, however, that the unseen-barriers hypothesis is inconsistent with the distributions of bird species in Papua. Diamond argues instead that patchy distributions in the tropics are better explained by the distribution of competitor species.

Haffer (1967; 1969), in a study that remains highly influential, proposed that the currently contiguous (parapatric) ranges of most Amazonian bird species could have originated via allopatric, indeed peripatric, speciation. He argued that Pleistocene fluctuations in temperature and sea levels, and especially in local levels of rainfall, led to contraction of tropical forest into small patches. Endler (1982) questioned the refugia concept of Haffer by pointing out that the current contact areas of Haffer's (1967; 1969) proposed Amazonian avian refugia are not necessarily where they should be under Haffer's model.

It is unclear, moreover, exactly what forest changes occurred during Pleistocene ice ages (Colvinaux 1987), and thus, what the consequences of such changes might have been for species that specialized to varying degrees upon various types of forests. What little paleoecological data are available suggest that invasion of the lowlands by montane tree species is more likely than expansion of grasslands and contraction of lowland tropical forest into several clumps (Bush et al. 1992; Colvinaux 1987). Recent work that questions the applicability of the refugia model to Amazonia has been ably reviewed by Knapp and Mallet (2003).

Among North American songbirds, whose speciation rates should have been more sharply affected by the most recent glacial maximum than were the species of the Amazon basin, Klicka and Zink (1997) found that only one pair of avian sister species show the lack of reciprocal monophyly (lineage sorting) and extremely low sequence divergence (in mitochondrial DNA) expected for populations that were isolated from one another in the terminal Pleistocene, assuming a 2% per myr rate of mtDNA sequence divergence (references cited in Klicka and Zink 1997: note 11). Many populations seem to have separated from one another during the Pliocene, a relatively dry period; but Klicka and Zink (1997) note that no particular pulses of diversification are evident in their mtDNA data.

On the other hand, there remains some evidence that refugial isolation could have occurred, and could have led to some differentiation of populations, in the temperate zone. Hofreiter et al. (2004) found that mitochondrial DNA of brown bears that lived in adjacent areas of central Europe at about the last glacial maximum was not differentiated, yet today their mtDNA is differentiated, suggesting that the last ice age did lead to some genetic divergence between bear populations, and hence must have had at least some effect upon gene flow (though not necessarily complete isolation: Irwin 2002). Ancient DNA studies have the advantage of providing a direct glimpse into the past, so that one is not restricted to inferring past events from present patterns of biogeography or phylogeography.

Even if the reality of ice-age refugia is assumed, the impact of refugia upon gene flow would have to have been a function of three factors: (1) the degree of habitat-specialization of the species in question; (2) the distance between the refugium in which an individual finds itself caught after forest contraction, and other such refugia in the surrounding area; and (3) the maximal dispersal capabilities of that species. There is no argument here that, when these three factors are balanced just so, peripatric speciation via refugial isolation could have been highly effective.

Water barriers, on the other hand, clearly exert some influence upon divergence of populations. Rivers in the Amazonian region clearly play a role in the maintenance, and probably the origin, of distinctiveness among many animal species, as expected under both the parapatric and allopatric models (Ayres and Clutton-Brock 1992; Beven et al. 1984; Hershkovitz 1968; Jacobs et al. 1995). On the other hand, rivers should not be assumed to function as absolute barriers to gene flow, as some introgression seems to occur across them (Froehlich et al. 1991).

Mercer & Roth (2003) suggest that a burst of diversification in southeast Asian tree squirrels at about 10-12 mya corresponds to a massive drop in sea level, after which sea levels rose again and squirrel populations on southeast Asia's many islands were then isolated (more or less absolutely) from one another.

Mercer & Roth's (2003) data seem to provide some support for allopatric diversification, but the use of molecular clocks to place precise dates on phylogenetic nodes is a doubtful proposition (Pulquério and Nichols 2006), and they give no error term for their dates. Aside from that, although minimal sea levels seem to occur just before the burst of diversification, there have been many sea level fluctuations before and after the sea-level minimum which, while less extreme, would have left many islands connected. Because of the need for precision in reconstruction of the timing of phyletic events with respect to geological events, studies such as Mercer and Roth's (2003) that rely upon genetic data from Recent populations are somewhat difficult to evaluate.

*Allopatric speciation theory and biological reasoning*—The allopatric speciation model has sometimes been perceived as so well-established—and its alternatives so implausible—that it can safely be assumed to have caused diversification in every case. For example, Cracraft and Prum (1988) assert in the introduction to their paper that the evidence in favor of allopatric speciation as the "predominant" mode of speciation is so unassailable that one can simply ask which particular sub-type of allopatric speciation has occurred in each case: *viz.*, vicariance vs. rare, long-distance dispersal across a barrier.

The review papers cited by Cracraft and Prum (1988), however, simply collect evidence that allopatric speciation could conceivably have been possible in any given case; there are no tests against alternative hypotheses using independent lines of evidence.

Cracraft and Prum (1988) select a subset of their data for analysis, based upon its (partial) agreement with an allopatric interpretation: "The four clades discussed in this section [Results] were chosen because they exemplify congruence in their spatial pattern of differentiation." Even so, they then lower the reader's expectations for fit of the data to the model: "Theoretically, conflicting general patterns such as these are to be expected, inasmuch as all continental biotas have had a long complex history...." The key consideration is that the data fit the dominant model of speciation: "The key...is to delineate these different congruent patterns and then seek to resolve any conflicts among them...." (Cracraft and Prum 1988). My intent here is not to unfairly single out Cracraft and Prum, but merely to use their paper as one among many possible examples of the extent to which the dominance of the allopatric model has affected biological reasoning. Within the currently-dominant biological paradigm (in which speciation-by-isolation is considered vastly more plausible, on theoretical grounds, than the alternatives), their interpretation is perfectly reasonable and appropriate.

In assuming allopatric speciation by default, Cracraft and Prum (1988) follow predecessors such as Haffer (1969): "On the basis of the theory of geographic speciation, let us assume that most or all of the Amazonian forest [avian] species originated from small populations which were isolated from their parent populations...." Even before the publication of Haffer's study, the stage was already set, as noted by White (1968): "Cases where no paleontological or cytogenetic data exist are automatically interpreted in terms of the allopatric model, even if the particular interpretation seems somewhat forced." Also note that, well before Haffer (1969), Brown (Brown 1957) assumed *a priori* that some sort of speciation-by-isolation must be required to explain present biogeographic patterns. Evidence that barriers cause or maintain differences between species is often lacking, however (Diamond 1980; Ehrlich and Raven 1969; Groves 1989; Groves 1990). In addition, the possibility of isolation by distance is often not seriously considered (Endler 1989).

*The allopatric-parapatric distinction vs. dynamic balance*—While the term "allopatric" is conventionally reserved for situations in which gene flow is zero or very near zero, while "parapatric" is used to refer to all other points along the continuum of possible levels of gene flow, the semantic discontinuity does not imply an actual discontinuity. Zero is no less a number than is 0.0001. Therefore the "balance of forces" (gene flow vs. selection) applies even when one of them (gene flow or selection) equals zero; in fact, the efficacy of complete isolation only serves to reinforce the importance of the gene flow-selection ratio. Allopatric speciation is, then, a special case of parapatric speciation in which one of the parameters in the balance (gene flow) happens to equal zero. Allopatric speciation is not truly a separate entity.

On the other hand, for my argument to be consistent, I will have to admit that for a population to essentially split down the middle with none of the attenuation of gene flow afforded by geographic distance or by microhabitat specialization, while not impossible, is likely very unusual (except perhaps in certain parasitic insects that seem often to form host races)—for the same reason that fully allopatric speciation (0% gene flow) is highly effective when it does occur. Complete gene exchange between diverging morphs can retard divergence by means of what Felsenstein (1981) calls the selection-recombination antagonism, i.e., a tendency of recombination to break apart the linkage between alleles that increase ecological adaptation to different habitats, and those that cause divergence in assortative mating (and hence pre-mating isolation)—although it should be noted that non-genetic pre-mating isolating mechanisms such as sexual imprinting (Lorenz 1937; see below) could avoid this problem.

Thus, the isolation (so-called biological) species concept and the interlocking model of allopatric speciation together tend to distract our attention from much of the fascinating, ambiguous diversity of life, directing the spotlight away from the critical early stages of diversification, instead fixing it permanently upon certain final stages which may be unnecessary (e.g., reinforcement), and upon isolating mechanisms, which are commonly thought to be necessary to absolutely stop gene flow from occurring (e.g., Coyne and Orr 1998). The preceived importance of, and research focus upon, isolating mechanisms comes from the mistaken view that gene flow swamps all other evolutionary causes such as differential fitness and selection, when in fact it does not (Endler 1977).

I pause here, however, to note that when a particular trait has little if any fitness consequence and its divergence can therefore be affected by genetic drift (as can be the case with cranial shape: Marroig and Cheverud 2004; Weaver et al. 2007), then gene flow can indeed much more easily overwhelm genetic drift than it can selection; thus allopatric speciation may be the only reasonable model where divergence via genetic drift is concerned (Lynch 1988). Divergence by genetic drift may be quite widespread; aside from the case of traits with no effect upon fitness, even those that do have fitness consequences can diverge by genetic drift under certain circumstances. For example, a phenotypic trait can diverge between two populations via genetic drift even when the same trait is under similar stabilizing selection in both populations (Estes and Arnold 2007; T. D. Weaver, pers. comm.).

*Parapatry: divergence with moderate gene flow*—The conservative, restraining influence of gene flow can be attenuated by an absolute barrier, by a partial barrier that is relatively difficult to cross, or simply by a long distance relative to a species' dispersal ability or vagility (i.e., isolation by distance) (Turelli et al. 2001). The "characteristic length" of Slatkin (1973), or $\sigma / \sqrt{2}s$ (where $\sigma$ = mean dispersal distance per generation, and $s$ = selection), is proportional to the minimum distance required to enable parapatric divergence starting at extreme ends of a population's range, no matter how free gene flow may be between neighboring populations (Slatkin 1973; Turelli et al. 2001). The greater the ratio cited above, the greater the geographic distance required for divergence to occur. Since gene flow is in the numerator, the greater the gene flow, the larger the population's geographic range must be to allow parapatric divergence; since selection is in the denominator, stronger selection at a given rate of gene flow means divergence can occur within a smaller geographic range. Slatkin's (1973) model and Endler's (1973; 1977) theoretical and empirical research together form the basis of parapatric speciation theory.

Gavrilets et al. (1998) extended Slatkin's (1973) analysis to a more complex (and more realistic) multi-locus model, and found that divergence to the point of full reproductive isolation (via pleiotropy) is quite likely to evolve in parapatry, although subdivision of populations (i.e., attenuation of gene flow over a population's range) does of course increase the likelihood of divergence. Gavrilets et al.'s (1998) result is quite what is expected under the selection-gene flow balance model of speciation (Slatkin 1973) and agrees with numerous laboratory experiments (Rice and Hostert 1993).

Parapatric divergence by distance, once known only from theory and the laboratory, has recently gathered more empirical support from the field—e.g. Irwin et al.'s (Irwin et al. 2005) study of divergence in an avian ring species, the greenish warbler *Phylloscopus trochiloides* (Phylloscopidae). Irwin et al. (2005: fig. 2) reported a linear relationship between genetic distance, using nuclear DNA (amplified fragment length polymorphisms, AFLPs), suggesting a pattern of isolation-by-distance with continuous gene flow around the ring. Other ring species that show evidence for selection-based divergence, or at least the maintenance of such divergence whatever its origin, over long distances in spite of gene flow include South American spider monkeys, *Ateles* (Atelidae) (Froehlich et al. 1991) and Sulawesi macaques (Cercopithecidae, *Macaca* spp.) (Camperio Ciani et al. 2005; Watanabe et al. 1991a; Watanabe and Matsumura 1991; Watanabe et al. 1991b).

In sum, there is no doubt that gene flow between populations exerts a powerfully conservative influence upon diversification, and there is likewise no doubt that (at least in animals), absolute reproductive incompatibility is eventually achieved at some point during the higher-order divergence of any two lineages; but that said, the lack or near-lack of gene flow and the presence of isolating mechanisms must no longer be considered necessary concomitants of diversification and stasis, respectively.

### *1.4: Ecology, adaptive radiation and diversification*

*Ecological selection balanced by gene flow*—As mentioned in the previous section, most diversification probably proceeds according to the balance of differential natural selection vs. gene flow (Endler 1973; Endler 1977; Rice and Hostert 1993; Slatkin 1973). It should be noted that most of the divergence-with-gene-flow models are based upon differential ecological selection, whether clinal or discontinuous. This is because it is easy to imagine how ecological selection (as opposed to, say, sexual selection) regimes could vary over geographical space, and because genetic drift is generally thought to be weaker than selection, though drift might cause divergence between populations if gene flow between them is quite weak (Lynch 1988).

Perhaps the most powerful ecological selection regime is geographically discontinuous (Rice and Hostert 1993), which may be why ecotones (sharp boundaries between habitat types) can become centers of diversification (Smith et al. 1997). Mathematical models suggest, however, that even gradual changes in ecological selection intensity along a cline, however, can lead to a sharply-stepped genetic and morphological cline (Endler 1973), though the steepness of the cline also depends upon the degree of over- or underdominance, the latter favoring a steeper cline (May et al. 1975). Thus, stepped clines in genes or morphology need not result from secondary introgression following allopatric isolation, as is usually supposed, nor even from an abrupt change in the direction of selection.

Endler (1973) conducted a classic laboratory experiment with *Drosophila* flies that confirmed the potentiality of modest levels of ecological selection, varying gently over an artificial cline, to cause divergence between populations in the face of significant gene flow. Endler set up two series of artificial subpopulations. In one of the series, each subpopulation exchanged 40% of each generation with the two neighboring subpopulations (20% to each side), simulating strong gene flow. In the other series, no gene flow was allowed. All subpopulations differed in (manipulated) fitness of the *Bar* allele, according to a gentle cline, with differences in fitness between neighboring subpopulations of only 0.04. Thus gene flow was very strong, yet selection varied only slightly.

Endler (1973) found that different levels of gene flow did not change in the slope of the cline in *Bar* allele frequency over time—only the presence or absence of selection affected the slope. While changes in the frequency of a single allele are not sufficient to meet even Mallet's (1995) species definition, let alone to cause full reproductive isolation, Endler's result does demonstrate that at least initial diversification is easy to achieve in parapatry, even with weak differential selection along a cline and strong gene flow.

Rice and Hostert (1993) reviewed several laboratory studies on flies, primarily *Drosophila*, which collectively indicate that diversification to the point of full reproductive isolation is quite possible in parapatry, provided that selection is strong (relative to gene flow) and discontinuous, and that pleiotropy exists between selected characters and those employed in mate recognition. The laboratory experiments reviewed by Rice and Hostert (1993) provide strong empirical support for the theoretical models of ecological selection-gene flow balance that have been advanced by Slatkin (1973) and Gavrilets et al. (1998).

Recently, many examples from the field have supported the hypothesis of ecological selection causing divergence in spite of substantial gene flow (reviewed in Orr and Smith 1998; Schluter 2000b). For example, Schneider et al. (1999) reported that body size of skink lizards (Scincidae, *Carlia rubrigularis*) differed between habitats, in spite of presumed dispersal and gene flow between habitats: rainforest-dwelling skinks were substantially larger than those that live in open woodlands. Mitochondrial DNA clades, on the other hand, were arranged on either side of a barrier to dispersal, the Black Mountain Corrdior, yet there were no morphological differences on either side of this barrier.

Schneider et al. (1999) suspected that greater avian predation of lizards in the open-woodland habitat was causing lizards in that area to diverge in terms of timing of maturation—stopping growth at an earlier age (and smaller size) in order to reproduce sooner, due to high extrinsic mortality from predation. Schneider et al. (1999) tested that hypothesis experimentally by placing fake lizards in both habitats; those placed in the open-woodland habitat were attacked by birds far more often.

Where Schneider et al. (1999), compared discrete sets of populations, Smith et al. (1997) conducted a more quantitative study of morphological divergence vs. gene flow in populations of a bird, the little greenbul (Pycnonotidae, *Andropadus virens*) in Cameroon. The populations under study were located in either closed tropical forest, or in transitional regions (ecotones) characterized by mosaics of either savanna and fragmented forest, or savanna and gallery forests. Smith et al. (1997) measured overall gene flow between pairs of populations by using $G_{ST}$, a version of the coefficient of population subdividsion $F_{ST}$ that is generalized for multiple loci with multiple alleles, to estimate

*Nm*, the number of migrants per generation. They measured divergence in certain key morphological traits, such as wing length, via comparisons of multivariate Euclidean distance between populations. A plot of pairwise gene flow ($G_{ST}$) comparisons vs. pairwise morphological distance shows a linear correlation between level of gene flow (specifically, estimated *Nm*) and divergence in morphology—but only for pairwise comparisons of ecotone populations vs. forest populations (Smith et al. 1997: their fig. 2). Thus divergence is coincident with habitat differences and seems to be balanced or retarded by gene flow, in quite a linear fashion, suggesting the gene flow-ecological selection balance that has been demonstrated in the laboratory.

Various theoretical models, beginning with that of Maynard Smith (1966) but including many more recent examples, have argued that sympatric speciation should be possible. Sympatric speciation is, as explained in the previous section, really just (as with allopatric speciation) a special case of parapatric speciation. The terms with suffix "-patric" refer to the macrogeographical situation, however, not gene flow, nor microhabitat, niche, and so on. This unfortunate choice of terminology, centered as it is on gross geography, can obscure more important issues. Due to the confusion that can result from an exclusive focus upon gene flow—let alone upon geography as such—one might consider using more descriptive and specific names to models of ecological speciation, such as microhabitat-based diversification by ecological selection or (which I will call here the microhabitat-ecological model), rather than simply sympatric speciation, and geographical diversification by ecological selection (which I will call here the geographic-ecological model), rather than parapatric speciation.

Most of the so-called sympatric models invoke ecological selection, not sexual selection or drift, as is also the case with the parapatric models (for reasons to be explained in the next section). The sympatric speciation models also tend to envision a reduction in gene flow that increases via positive feedback, concomitant with an increasing degree of resource (and hence microhabitat) specialization of two morphs within a population. It is possible that disruptive ecological selection within a single population can lead to polymorphisms related to resource specialization, and that full reproductive isolation can eventually evolve partly via the reduced gene flow that results (Maynard Smith 1966; Skúlason and Smith 1995; Smith et al. 1997). In some taxa such as certain fish, a continuum of reproductive isolation and reduction of gene flow has been observed between life-history or resource morphs (reviewed in Hindar 1994; Skúlason and Smith 1995), as predicted by the microhabitat-ecological model.

One of the first sources of empirical support for the microhabitat-ecological model was a study by Rice and Salt (1990) that subjected laboratory populations of *Drosophila* flies to divergent ecological selection. The flies' experimental environment included a complex maze, which facilitated divergence in spatiotemporal habitat preferences. The maze simulated microhabitat differences by establishing light and chemical odor gradients, thus allowing the possibility of divergence based upon photo- and chemotaxis. Rice and Salt found that divergence to the point of reproductive isolation occurred within 35 generations, based upon simulated microhabitat preferences.

The main limitation of Rice and Salt's (1990) study, however, is its highly manipulative nature. The complexity of the habitat maze, and the sharp differentiation of the light and chemical environments, may have been more exaggerated than any situation found in nature. Aside from the issue of ecological realism, it seems to me that a certain bias toward divergence may have been unintentionally built into the experiment, in that each maze included twelve one-way funnel traps which "were used to prevent flies from choosing more than one habitat in a single generation" (Rice and Salt 1990: 1142). Thus the study is suggestive of what is possible under rather extreme circumstances, but its external validity may be somewhat limited.

*Natural experiments*—A natural experiment on microhabitat-ecological diversification was reported by Carroll and coauthors (Carroll and Boyd 1992; Carroll et al. 1997), who studied in great detail populations of soapberry bugs (Rhopalidae, *Jadera haematoloma*)—a group of North American bugs that adaptively radiated to exploit various plant species that were introduced to the continent within the past fifty years, or about 100 generations. Carroll and Boyd (1992) documented the match between host races' phenotypes and their hosts, with mouthpart length changing to match the new host plants' fruit capsules, while body size decreased (see also Carroll et al. 1997). Carroll et al. (1997) then used cross-rearing experiments to show that the divergent phenotypic traits have a genetic basis, and the divergence is not the result of phenotypic plasticity or environmental effects.

Notwithstanding the inherent interest and relevance of overall morphological and genetic divergence (Endler 1989), reproductive isolation remains the coin of the realm in speciation research; therefore ecological-speciation researchers are keen to demonstrate that ecological divergence can result in full isolation. While Carroll and coauthors focused upon morphological divergence (and its apparently genetic basis) apparently caused by recently-introduced plant hosts, Hendry et al. (2000) tested for reproductive isolation resulting from another recent introduction. At the time of Hendry et al.'s study, sockeye salmon (Salmonidae, *Oncorhynchus nerka*) had been introduced to Lake Washington (Washington, USA) at most 56 years, or approximately 13 generations, earlier; the lake population first colonized the Cedar River, a tributary of the lake, then apparently colonized one of the lake's beaches.

Hendry et al. (2000) found that the beach and river subpopulations had already diverged morphologically in body depth, and cite evidence that this trait tends to be exaggerated by sexual selection; in river populations, however, they argue that sexual selection on body depth is opposed by ecological selection for greater swimming efficiency due to river currents and predators. Overall female body size, on the other hand, tends to be greater in the river subpopulation, possibly because larger female salmon are able to dig deeper and therefore can make more flood-resistant nests (flooding is not a problem in the beach environment). In the beach habitat, selection for large female body size may be relaxed, perhaps allowing females to stop growth and begin reproduction earlier; beach-living females were indeed shorter-bodied than river-living females.

Hendry et al. (2000) used an indirect method to test for reproductive isolation. Fluctuations in temperature during incubation of salmon eggs occur only in riverine, not beach, environments, and these fluctuations leave marks on otoliths (ear stones) of adults; therefore Hendry et al. were able to determine which currently beach-living individuals were immigrants. Fully 39% of the beach-living salmon were immigrants from the river, yet analysis of presumably neutral microsatellite genetic markers revealed significant divergence between natal beach-living salmon on the one hand, and river-living and beach-immigrant salmon, collectively, on the other. Hendry et al. reasoned that reproductive isolation must have begun to evolve between the river and beach populations, since any recent gene flow would have prevented divergence in presumably neutral genetic markers. Reduced gene flow, then, seems likely to be the end result of strongly-divergent ecological selection and reduced reproductive success of beach-immigrant fish relative to beach-natal fish, rather than being a cause of divergence from the beginning, since obviously there were no barriers to immigration of river fish to the beach fifty years ago, any more than such barriers exist now.

Hendry et al.'s (2000) study is interesting not only in terms of ecological selection, morphological divergence and reproductive isolation, but because of the extremely short time scale involved (13 generations or fewer), relative to the geological time scale over which evolution is generally thought to take place; I will return to this issue in more detail in the section on phylotemporal patterns of evolution. Although the research of Carroll and coauthors' work on soapberry bugs (Carroll and Boyd 1992; Carroll et al. 1997) focused mainly on morphological divergence, it is interesting to note that here there is also some potential for the rapid evolution of reproductive isolation, inasmuch as subsequent research on their part (Carroll et al. 2003) suggested the beginnings of epistasis among some of the divergent traits; epistasis can of course form the basis of reproductive isolation (Coyne and Orr 1998).

*True field experiments*—The empirical ideal remains the true field experiment—conducted in a natural environment, yet incorporating replicated treatments with random assignment of subjects thereto. Losos et al. (1997) collected anolis lizards (*Anolis sagrei*) from a relatively large island in the Bahamas and randomly assigned them to several smaller, lizard-free islands, in propagules of five or ten lizards per island. The large island of origin had small to medium-sized trees whereas the experimental islands were dominated by shrubs, with no trees. Previous research (Losos et al. 1994, cited in Losos et al. 1997) showed that among extant natural populations of this lizard species, hindlimb length tends to be correlated with average perch diameter, probably for reasons of biomechanical efficiency. Losos et al. (1997) reasoned that, if the limb length-perch size pattern evolved by ecological selection, it should be possible to replicate it experimentally, given the imposition of appropriate environmental pressures.

After ten to fourteen years had passed (depending on the island), morphological difference from the source population was negatively correlated with vegetation height (the experimental islands had shorter vegetation than the source island) (Losos et al. 1997: their fig. 2), and the experimental populations were arranged non-randomly in the multivariate space laid out by a principal-components analysis, relative to the source population's centroid. In other words, the experimental populations' body shaped tended to cluster in one region within the larger range of source-population variability (Losos et al. 1997: their fig. 1a).

It should be noted, however, that the error in Losos et al.'s vegetation-morphology regression was quite large, and the linear relationship seems to be sustained by one or a few points; the error distribution along the regression line is by no means uniform either (Losos et al. 1997: their fig. 2). Meanwhile, it is uncertain whether the morphological differences observed count as divergence *per se*, since in terms of multivariate morphology, the experimental populations fall within a subset of the range of the populations of origin (Losos et al. 1997: their fig. 1a).

In contrast to Losos et al.'s (1997) work on allopatric divergence, Bolnick (2004) conducted a field experiment on threespine stickleback fish (Gasterosteidae, *Gasterosteus aculatus*) to test whether increased competition (which Bolnick manipulated by increasing density in certain enclosed areas) can lead to disruptive selection and morphological divergence in full sympatry. Bolnick places his work in the context of Rosenzweig's (1978) model of density-dependent adaptive peaks: a modified version of Wright's adaptive landscape model in which fitness peaks can be depressed through negative density- and frequency-dependence. That is, no matter how successful a given ecological strategy may be (e.g. exploitation of a very abundant and high-quality resource), the lower the fitness will be of those who pursue that strategy, as more and more individuals pursue it. Thus as fitness of an originally-successful resource-exploitation strategy decreases with increasing density, those who pursue divergent, non-modal strategies have an advantage. It is just such a tension that might enable niche width to evolve in full sympatry (Macarthur and Levins 1967; Roughgarden 1972), thus making room for greater morphological diversity, as suggested by the extensive literature documenting prevasive character displacement (divergence of adaptive traits, especially trophic morphology, in zones of sympatric overlap) in nature (e.g., Schluter 2000a).

Bolnick (2004) claims to have documented evolutionary divergence in gill raker length, a form of trophic (feeding-related) morphology in this species, in his high-density enclosures. He therefore claims that the high-density conditions depressed the fitness of intermediate phenotypes, increasing the reproductive success of divergent phenotypes.

While the theoretical aspects of Bolnick's exposition are interesing, the empirical evidence remains incomplete, for two main reasons.

First, Bolnick (2004) was unable to directly measure density in any of his fish enclosures, using a rough maximum-likelihood method instead (which is less accurate than the mark-recapture method). Second, the cubic spline regressions presented by Bolnick (2004) remain rather unconvincing when one simply examines the scatterplots, notwithstanding their significance by conventional statistical criteria. While Bolnick states that p-values from statistical tests represent "the probability of the null hypothesis that the estimated [regression] coefficient is zero" (Bolnick 2004: caption to his table 3), non-Bayesian tests cannot in fact give probabilities of hypotheses; they can only give the probability of obtaining the data if the null hypothesis were true (Gigerenzer et al. 2004).

The influence of experimentally-manipulated density on diet breadth and divergence in feeding behavior in the same species was again studied by Svanbäck and Bolnick (2007). Rather than testing for incipient population divergence, Svanbäck and Bolnick (2007) used a series of smaller enclosures ($9m^2$ each) within a different lake. Rather than estimating density indirectly with a statistical model, they began with the small, fishless enclosures and then stocked them manually with either low- or high-density treatments. They were able to measure diet breadth of individuals and of treatments by identifying stomach contents to generic or familial levels, and used geometric morphometrics rather than linear measures to quantify morphology. While their enclosures were small, they also sampled free-swimming fish from the lake as a whole as a control or baseline group. Notably, Svanbäck and Bolnick (2007) concentrate on the earliest possible stage of diversification—inter-individual differences within a more or less undifferentiated population.

Svanbäck and Bolnick (2007) found no difference between their low- and high-density (low- and high-competition) treatments in terms of survival or of average morphology, nor of morphological variance, nor did they find any differences between experimental and free-swimming (control) lake fish. This seems unsurprising given the 14-day duration of the study. Their results suggest that the high-density treatment resulted in reduced prey density (which was sampled independently, the day before the fish were removed), reduced stomach contents, and a lower RNA/DNA ratio (interpreted as indicating less somatic growth), relative to low-density treatment and control fish.

While Svanbäck and Bolnick (2007) found no morphological divergence, they did find behavioral divergence correlated with pre-existing morphological differences, especially under high-density conditions. Increased competition for food is expected under basic ecological theory and substitution of fallback foods is certainly unsurprising (as Svänback and Bolnick 2007 admit), but the divergence of behavior along axes of pre-existing inter-individual morphological differences is at least interesting and suggestive. Further research might then test whether morphological as well as behavioral differences will then be evolutionarily exaggerated under sustained high-density conditions.

A particularly strong experimental study, though it included neither replication nor random assignment of subjects, was performed by Herrel et al. (2008). Five male-female pairs of lizards (Lacertidae, *Podarcis sicula*) were moved in 1971 from a source island to an experimental island; the experimental island was previously inhabited by a different species of lizard (*P. melisellensis*), but this species had since become extinct. In a span of 36 years since the introduction, the lizards on the experimental island evolved larger heads and much stronger bite forces, particularly in males, than those from the source island. The lizards on the experimental island also seem to rely much more heavily on plant foods—particularly cellulose-rich plant parts such as leaves and stems—than do the source-island lizards, while the source-island lizards tend to rely on arthropods. It is likely that differences in available, unexploited food resources (i.e., niche) may have changed the direction of ecological selection, resulting in a rapid morphological shift (see section 1.10).

*Character displacement*—One of the most venerable arguments for the role of ecology in morphological divergence has been the frequently observed pattern of greater differences between two species when they occur sympatrically than where they occur allopatrically (Schluter 2000a), a phenomenon that was first extensively documented by Lack (1945, cited in Schluter 2000a). Overdispersion (that is, non-randomly even spacing) of mean phenotypes among sympatric species is also a fairly commonly-observed phenomenon, one that is consistent with ecological character displacement by competition (Schluter 2000a).

One difficulty, however, with observational evidence for character displacement is that mechanisms other than ecological resource competition within or between (nascent) populations can conceivably cause the same pattern; Day (2000), for example, suggested that Fisherian runaway sexual selection could result in a character-displacement-like pattern.

Experimental studies of ecological character displacement have a different kind of disadvantage, as compared to more general studies of ecological divergence. Experimental studies of character displacement generally place populations of one species with a closely-related species and observe the effect of competition between trophically similar species upon morphological and other divergence (Schluter 1994). The problem is that the species have already diverged; as with naturalistic observations of character displacement, we do not know whether competition in sympatry between similar forms caused the initial divergence, or merely exaggerates existing differences.

Certain types of experiments on character displacement examine the effects of long-term sympatry with a closely-related competitor, vs. allopatry, upon incipient divergence within a population (e.g., Pfennig and Rice 2007). Thus while divergence is generally just beginning to occur, and speciation (however it may be defined) may never occur, studies of this nature at least demonstrate the possibility of initial divergence due to ecological selection (Losos et al. 1997), with no apparent attenuation of gene flow.

*Maintenance of diversity by predators*—Character displacement generally involves competition between congeneric populations. Interactions among more distantly-related species, however, in many cases predatory interactions, may cause divergence by ecological selection, even without resource competition (Vamosi 2005). Among the species in which character displacement has been documented, moreover, carnivores are greatly over-represented, suggesting that a species' trophic level within its food web may have an impact on propensity to ecological diversification (Schluter 2000a), or at the least, predation may help maintain diversity, leading to stasis.

In a now-classic study of intertidal invertebrates on the coast of California, Paine (1966) removed the top predator, the starfish *Pisaster ochraceus* (Asteriidae), to examine the effects of top-down control on diversity at lower trophic levels. Contrary to the theory of character displacement and niche separation via competition among individuals pursuing the same resource (Macarthur and Levins 1967; Lack 1945, cited in Schluter 2000a), Paine (1966) found evidence for top-down maintenance of diversity by the top predator.

More recently, Gurevitch et al. (2000) conducted a meta-analysis of 39 experiments (from 20 published papers) that compared the effects of and interactions of predator-removal vs. competitor-removal on the growth, mass, density, and survival of prey species. They found that experimental removal of competitors led to modest increases in growth, mass and survival. On the other hand, experimental removal of predators resulted in decreased growth and mass in the prey species, but greatly increased survival. Both competitor removal and predator removal had similarly positive effects on density (Gurevitch et al. 2000: their fig. 4).

*Diversification caused by differential predation?*—A recent review of the impact of predators on diversity found empirical evidence that predators can both increase and reduce diversity among their prey, a result also predicted by theoretical models (Vamosi 2005). Not only predators, in fact, can affect diversification—enemies defined broadly, to include parasites and pathogens, can have the same effect (Nunn et al. 2004; Rundle et al. 2003; Vamosi 2005). Nunn et al. (2004), for example, noted that the most diverse primate clades are also the most parasitized. While suggestive, such comparative results must be supplemented with smaller-scale studies that include fewer species, yet more detail on ecology and functional morphology.

A study by Langerhans et al. (2007) of ecological speciation in Bahamas mosquitofish (*Gambusia* sp.) compared allopatric populations living in various natural underground pools (blue holes). Langerhans et al. (2007) begin with the engineering-based *a priori* prediction that in fish, a shallower tail-region of the body (the peduncle) is more efficient for sustained cruising, while a deeper peduncle is more effective for rapid acceleration (of the type needed, of course, to escape a predatory attack). They then compare peduncle morphology in blue holes where there are predators vs. those that are predator-free. Using a large sample size (> 600 mosquitofish), replication (12 blue holes) and precise methodology (geometric morphometrics), Langerhans et al. (2007) found that morphology of mosquitofish followed the prediction—deeper peduncles in predator-infested blue holes, and shallower ones in predator-free blue holes.

Beyond purely methodological considerations, however, the greatest strength of Langerhans et al.'s (2007) study is that fitness was not measured as an outcome but was predicted (as a propensity or property of a specific morphological trait) based upon simple, easily-understood engineering principles.

In summary, recent field research in ecological diversification seems to provide strong support to the microhabitat-ecological model of ecological divergence, which incorporates some spatial assortment but little attenuation of gene flow (Carroll and Boyd 1992; Carroll et al. 2003; Carroll et al. 1997; Hendry et al. 2000; Schneider et al. 1999), apparently in spite of predicted selection-recombination antagonism (Felsenstein 1981).

Indeed, microhabitat-ecological divergence seems capable of leading to, or at least approaching, reproductive isolation (Carroll et al. 2003; Hendry et al. 2000).

Given the theoretical work of Slatkin (1973) and Felsestein (1981), laboratory work on the subject by Endler (1973) and Rice and Hostert (1993), and biogeographic patterns (Endler 1982; Groves 1990; White 1968), it seems all the more likely that geographic-ecological (what is commonly called "parapatric") diversification must be important in nature.

### *1.5: Diversification by sexual selection*

There is no doubt that extant sister species often differ in mating preferences and in secondary sexual or sexual-attractant traits (Darwin 1871; Endler and Houde 1995; West-Eberhard 1983). It is therefore often supposed that sexual selection might have driven divergence of the two populations in question, especially when there are no apparent ecologically adaptive differences between them. There has been much less empirical work on this question than there has been on diversification by ecological selection, though, for an obvious reason: it is difficult to imagine the process by which divergence might occur via sexual selection alone—without environmental effects (i.e., sensory drive, clines, or ecological discontinuities). For example, Irwin et al. (2001: 227) suggest that "ring species can form in the absence of ecological divergence only when effective gene flow between the terminal forms is small."

Populations undergoing ecological diversification are often exposed to differing selective regimes due to their locations along environmental gradients, which create clines of increasing or decreasing selection intensity; discontinous selection regimes may also exist, as with ecotones, rain shadows, and so on. Mating preferences, however, and the sensory biases that underlie them, are likely to be constant throughout a species' range; thus, no spatially-varying sexual-selection regime is expected to exist (Price 1998). Thus there are many models for the spread of traits throughout a population via sexual selection, but few that demonstrate how diversification by sexual selection might work.

*Mechanisms of sexual selection*—While ecological differences (interacting with specific variants) are the source of ecological selection (Endler and McLellan 1988), sexual selection must also have source laws. Where sexual selection by mate choice is concerned, these source laws are based upon the sensory system of the signal-receiving sex (Endler and Basolo 1998). (Here I use the term "signal" in the broadest sense, without any special assumption of honest signaling or information content.) For example, Ryan et al. (1990) investigated the source laws of sexual selection in Túngara frogs by examining the sensory superstructure of the receiving sex (females); thus a great deal is known, in that species, about the causal basis of sexual selection.

The Fisherian runaway sexual selection model (Fisher 1930: ch. 6; Kirkpatrick 1982; Pomiankowski and Iwasa 1998) is highly parsimonious (relative to honest-signaling models), in that it does not require fitness advantages for the (usually) female preference, nor does it require a specific, sustained history of selection for signal-sending in one sex and a history of selection for signal-evaluation in the other. It merely requires mutation, meiosis, linkage disequilibrium and time, yet it produces quite powerful results (Lande 1981; Pomiankowski and Iwasa 1998). It should be noted that, unlike Zahavi's (1975; 1977) honest signaling model, Fisher's model also does not require the fitness benefit of inheriting good genes to outweigh the fitness cost of inheriting a survival-handicapping trait. Hence Fisher's is the more parsimonious model.

While Fisher's model has been criticized for its unrealistic assumption of cost-free female preferences, Day (2000) has recently produced a model showing that the incorporation of two-dimensional space eliminates the need for the aforementioned assumption. It is true that Fisher's (1930: ch. 6) model is a model of the exaggeration, not the origin, of sexually-selected traits; but then, neither is the "honest signaling" hypothesis an hypothesis of origin, since it is based upon selection, which affects the spread of traits only (Endler 1986: ch. 1).

Fisherian sexual selection can cause initially similar populations to diverge, but in many models the process is initiated by genetic drift or by chance initial differences between populations in the structure of genetic variance and covariance, or may also be initiated by ecological differences, however slight (Lande 1981). Indeed, the potential for diversification via sexual selection seems vast, since as Lande (1981) points out, "In species with complex morphology and behavior, the diversity of possible outcomes could be enormous, with a hyperplane rather than a line of equilibria."

*Can sexual selection alone cause divergence between populations?*—Because of the frequent and obvious geographical gradients in environmental conditions that clearly affect ecological selection, the potential for ecological selection to cause geographic diversification is fairly obvious. Can sexual selection alone, without piggybacking on ecological-selection clines (Lande 1982), cause populations to diverge? Evidence for sexual selection alone leading to diversification is rather limited; a change in the balance of sexual and ecological selection is more often observed to lead to divergence in the wild (Svensson and Gosden 2007).

Svensson et al. (2006) conducted a field study on an enormous sample (> 3,000) of male damselflies (Calopterygidae, *Calopteryx splendens*) from a pair of parapatric populations in Sweden. The populations had diverged morphologically, though they were not reproductively isolated and exchanged a moderate number of genes each generation. Svensson et al. separately plotted multivariate morphological selective surfaces for survival and for mating rate, and found much stronger—and more divergent—sexual than natural selection in the two populations. (While damselflies obviously are not primates, this sort of research simply cannot be done in the field with large vertebrates.)

A study of crickets (Gryllidae, *Gryllus* spp.) by Gray and Cade (2000) is interesting in that it examined early divergence by sexual selection—i.e. between a pair of cryptic sister species that differ in call characteristics. In addition to inter-population differences in acoustic trait and preference, Gray and Cade found a strong genetic correlation between trait and preference, which is a key prediction of the Fisherian sexual selection model. Since these two populations are still capable of producing viable hybrid offspring, it seems they have differentiated based on mutual non-recognition, perhaps due to Fisherian sexual selection on call characteristics. Gray and Cade also found no evidence for character displacement in areas of sympatry, which helps to narrow the range of possible explanations.

Moving to the vertebrate world, and a bit closer to primates, Wilson et al. (2000) compared the degree of structuring of mtDNA variation among groups of neotropical Midas cichlid fishes (Cichlidae, *Amphilophus citrinellum*), which are known to show color polymorphism with associated assortative-mating patterns, as well as divergence in trophic morphology and behavior. Wilson et al. found that divergence in mtDNA was more closely associated with color differences than with trophic differences, and concluded that in this case at least, sexual selection may have had a stronger influence than ecological selection upon overall genetic divergence. They also remarked that in this neotropical cichlid group, trophic ecotypes seem to be much older than they are in the rapidly-radiating African cichlids.

Even in African cichlids, however, sexual selection may be very important in early diversification. Knight and Turner (2004) tested five populations of the Lake Malawi *Pseudotropheus zebra* (Cichlidae) species complex for signs of assortative mating based upon male color. Males and females from the five populations were allowed to mingle, and the parentage of the resulting clutches (> 1,900 juveniles) was then determined by mtDNA typing. Knight and Turner found strongly assortative mating (or at least, assortative fertilization—which one is not clear) based upon population-of-origin, the populations being differentiated by body color: assortative mating by population-of-origin occurred more than three times as often as expected by chance. The study is particularly interesting, and rare, because it involves populations that appear to be at a very early stage of divergence, because it features a large sample, and because it is minimally manipulative yet conducted under controlled conditions.

*Sensory drive, sexual selection and diversification*—Sensory drive is essentially natural or sexual selection for effective communication in environments that differ in their propagation of light and sound (Endler and Basolo 1998). Fish populations that live at various depths in bodies of water with various degrees of penetrability to light, may exemplify sensory drive. For example, Seehausen et al. (1997) found that divergent mate choice caused by just such stratification of light intensity within lakes maintained a great deal of diversity in body color among sympatric populations. Likewise, differences in predation regimes between environments can have an impact upon sexual selection.

It should be emphasized that the most critically important aspect of environment-dependent sensory drive is that it provides a geographic, or at least microgeographic, structure to mating preferences that would probably otherwise be absent. Thus this spatial structuring of mating preferences (or rather mate choice patterns) can serve as an analog to spatially varying ecological regimes (e.g., clines: Endler 1973; Endler 1977), possibly causing divergence between populations by sexual selection alone.

Sensory drive can also enable parapatric (macrohabitat) divergence via sexual selection, without necessarily involving ecological selection. Irwin (2000) has observed parallel divergence in song complexity, correlated with latitude, separately in two branches of an avian ring species in Siberia, on either side of the Tibetan plateau. Irwin (2000; Irwin et al. 2001) raises the possibility that song complexity may have increased in parallel in both sets of populations along a latitudinal gradient, due to changes in forest characteristics (also correlated with latitude) that might affect sound transmission and hence alter sexual selection pressures for song complexity.

Recent mathematical models have provided further theoretical support for the contention that divergence of populations by sexual selection on body color, even in sympatry, can occur when a single habitat is divided into microhabitats with varying levels of light penetration (Chunco et al. 2007; Kawata et al. 2007).

*Mutational order plus sexual selection and sexual imprinting*—Sexual imprinting is the molding of future mating preference through exposure to a model individual early in life, usually a parent (Lorenz 1937). Mutational order is the spatiotemporally stochastic appearance of mutations in a population (Clarke et al. 1988; Mani and Clarke 1990). It is possible that a combination of mutational order in a species whose range is large relative to its dispersal capabilities, and sexual imprinting, could lead to parapatric divergence by sexual selection, against a background of constant but generalized sexual selection. The sexual selection regime (caused by sensory biases in the recipient or choosing sex) would have to be broad and general, such as a generalized bias for large objects (Andersson 1982; Basolo 1990) or bright colors. The more specific form or elaboration of the trait in the chosen or displaying sex (usually males) would then depend upon the random order of mutations that appear in various areas of the ancestral, unitary species' range (Clarke et al. 1988; Mani and Clarke 1990).

Of course, mutational order generally leads to phenotypic convergence and genotypic divergence among populations, under the convergent selection modeled by Clarke et al. (1988) and Mani and Clarke (1990)—but such selection is normally ecological selection (see, e.g., Livingstone 1961), and points toward a very specific adaptive optimum. Sexual selection (and social selection—see below) pressures can, on the other hand, be much more general (West-Eberhard 1983); any one of a wide range of broadly similar sensory inputs (such as large or brightly-colored objects, as mentioned above) can be equally effective at stimulating a positive sexual response in the receiving or choosing sex.

In spite of the very broad receiver bias and sexual selection pressure, however, the members of the receiving sex in one particular part of the ancestral species' range can come to prefer a particular, very specific manifestation of a trait (in the chosen sex) by means of sexual imprinting.

Mutational order in sexually-selected traits could conceivably lead to diversification in parapatry. The respective alleles (in each regional population) that code for each of the new traits will then expand outward toward each other, in advancing fronts, from their respective centers of origin (Fisher 1937; Slatkin 1976). During their advance, however, as the traits' frequency increases within their respective local areas, sexual imprinting (which is positively frequency-dependent) will cause the specific traits to be preferred by the "choosing" sex within each respective region (Laland 1994; Price 1998). Such a receiver preference should have no problem keeping pace with the advancing wavefront of display-trait alleles, since sexual imprinting is a non-genetic phenomenon, and thus should occur in a single generation wherever trait frequency is high enough. Thus the advancing waves of specific sexual traits, and specific sexually-imprinted (learned) preferences, will eventually collide but sexual imprinting should prevent mutual introgression of traits, thus preventing homogenization of the newly-distinct populations.

### *1. 6: Diversification by social (signal) selection*

Sexual selection depends upon the rate of mating, while ecological selection results from differences in survival or fertility that are unrelated to the rate of mating. Thus the traditional ecological selection-sexual selection distinction is based upon consequence laws of evolution (mating, survival, fertility). Morphological (or chemical) characters that function in social communication but not in sexual attraction nor sexual competition are therefore usually thought of as resulting from ecological selection. West-Eberhard (1983), however, pointed out that social selection—i.e., selection of communication-related but non-sexual traits—can be similar to sexual selection in interesting ways. Social selection can favor essentially open-ended signals that are elaborated until they are finally limited by ecological selection—a characteristic that is similar to sexual selection—as opposed to ecologically-selected morphology, which tends to evolve toward an environmentally-determined engineering optimum. This is because, from a source-law viewpoint (Endler and McLellan 1988), both sexual and social selection result from stimulation of psychophysical biases (whatever the origin of those biases, adaptive or not) in the brain of the receiver of the signal (Endler and Basolo 1998).

Social selection would help to explain the widespread variation in sexually-monomorphic but species- or subspecies-typical display traits that do not seem to have an ecological function, such as colorful patches on the body, among species and especially subspecies or populations in nature (e.g., Fooden 1969; Guthrie 1971; West-Eberhard 1983). Guthrie (1971) argues that white rump patches that occur in a great many artiodactyl species could have evolved to enhance submission displays. Similar rump patches occur in several primate species. Macaques from the southern parts of Sulawesi island (Cercopithecidae; *Macaca ochreata, M. maura, M. tonkeana*) have conspicuous white rump patches, which are sexually monomorphic but species-typical. Some such patches are more elaborated than others: that of *M. tonkeana* features longer hair in addition to its bright color (Fooden 1969). Guthrie (1971) presented evidence that elaboration of the rump patch varies among artiodactyl species as well. Macaques of northern Sulawesi lack white rump patches, but have very bright, hot-pink-colored ischial callosities in the same region of the body (pers. obs.).

The possibly socially-selected variability among Sulawesi macaques is not by any means restricted to the rump, but includes the facial region and the length and form of hair on the crown of the head as well. Notably, the face and rump are the most frequently- and prominently-used body areas in social displays among mammals (Guthrie 1971). Bright red colors are also seen in the gluteal fields of several papionin primate species, such as mandrills and drills (*Mandrillus* spp.), and it is well known that submission displays in primates, as in artiodactyls, often involve presentation of the rump—an "indecorous habit" described by Darwin (1876).

### *1.7: Interaction of ecological and sexual selection*

As noted by Svensson and Gosden (2007), most of the solid evidence for diversification by sexual selection points to an interaction between ecological and sexual selection—or as they put it, a change in the balance between the two. I might add, however, that sensory drive (causing divergence in sensory characteristics between microhabitats or parapatric habitats) could equally well provide the geographical heterogeneity needed for parapatric divergence by sexual selection, without any interaction with ecological selection *per se*.

Ecological and sexual selection can interact in complex ways, often with sexual selection further exaggerating differences that were initiated by ecological selection. Formal models strongly suggest that Fisherian sexual selection on a male secondary sexual trait—when the same trait is also subject to spatially varying ecological-selection optima—can substantially exaggerate geographic differences in the male trait far beyond the aforementioned optima, even in the absence of any geographical barriers (Lande 1982: esp. his fig. 1). Such a process of geographical exaggeration, especially under a model of byproduct speciation where the selected trait is also important in species recognition, could interact with well-known processes of ecological parapatric speciation to hasten divergence (Endler 1973; Endler 1977).

Lande (1982) also argued that Fisherian sexual selection (when coupled with clinally-varying ecological selection) should be more effective at generating marked morphological differences between populations than would selection against interbreeding (e.g., hybrid disadvantage) after secondary contact between previously-allopatric populations. Reproductive isolation might be particularly likely to evolve quickly, if sexual selection were subserved by sexual imprinting. A stepped morphogenetic cline can result relatively quickly, then, when the same trait is subject to both ecological and sexual selection, provided that the characteristic length criterion of Slatkin (1973) is met (Endler 1973; Endler 1977; Lande 1982).

Pomiankowski and Iwasa (1998) extended Lande's (1982) analysis to multiple traits evolving simultaneously, and confirmed that Fisherian sexual selection can interact with small differences in ecological selection among allopatric populations, leading to full reproductive isolation.

## *1.8: Diversification by genetic drift*

*Short-term divergence between populations*—Lynch and Hill (1986) constructed a population-genetic model that generalized Kimura's (1983) molecular neutral model to the phenotypic level. Lynch and Hill argued that two allopatric populations can diverge in neutral characters through mutation and drift alone. At some point, the populations reach mutation-drift equilibrium, after which point the rate of divergence is independent of effective population size (Lynch and Hill 1986). Genetic drift is much less effective at causing divergence between parapatric populations (with significant gene flow); Wright's (cited in Gillespie 1998) island model applies here since there is no divergent selection between populations. Two populations can still diverge rapidly via drift when there is extremely weak gene flow between them, but the ultimate equilibrium level of difference between them should ultimately be reduced relative to fully-isolated populations (Lynch 1988). On the other hand, Gavrilets (2003) in a review of speciation models, concluded that speciation by drift is quite possible but takes much longer than speciation via a selection mechanism.

Lande (1976) was one of the first evolutionists to explicitly test the divergence-by-drift hypothesis with empirical data. Lande predicted the maximum effective population size (N*) that could produce, with a probability of 5%, a certain amount of morphological change ($z$) within an arbitrary number of generations ($t$). He reasoned that if the observed effective population size ($N_e$) is higher than N*, the hypothesis of divergence by drift can be rejected with 95% confidence. Lande (1976) argued that rates of change in horse molar dimensions were so small that divergence could have occurred by drift, even with effective population sizes of up to 10,000. One difficulty with Lande's (1976) analysis, however, is that his constant-heritability model may have made inappropriate assumptions given the time period of his study. It is at least as likely that the slow rate of divergence observed by Lande (1976) was due to stabilizing selection rather than genetic drift (T. D. Weaver, pers. comm.).

*Genetic drift, complexity, and the long-term propensity for diversification*—Lynch (2007) pointed out that prokaryotes generally have much larger effective population sizes than eukaryotes, and prokaryotes are thus more insulated from the effects of genetic drift than are eukaryotes; and yet the genomes of eukaryotes seem capable of evolving ever-greater complexity. Perhaps surprisingly, the vulnerability of eukaryotes to genetic drift may create the opportunity for greater evolutionary diversification. As Lynch (2007:

8601) puts it, "a long-term synergism may exist between nonadaptive evolution at the DNA level and adaptive evolution at the phenotypic level."

Lynch (2007) also argues that natural selection should be even less stringent in advanced vertebrates than it is in more basal eukaryotes, since the former are generally more capable of phenotypic and behavioral plasticity. Lynch's argument can easily be extended even further in the case of *Homo sapiens*, in which phenotypic and especially behavioral plasticity is enormous—thus natural selection should be very weak indeed. This realization—along with the diversity of modern hunter-gatherers' ecology, group sizes and so on (Foley 1995)—should give pause to those evolutionary psychologists who suppose that the human mind was precisely and inexorably shaped by natural selection in the Pleistocene "environment of evolutionary adaptedness" or EEA (e.g., Barkow et al. 1992).

Lynch (2007) further points out that developmental systems may evolve (toward greater modularity) neutrally under a constant phenotype, thus changing, as it were, under the radar of selection. He thus criticizes those who suppose that modularity (an aspect of evolvability), for example, is necessarily a naturally-selected trait of an organism.

Lynch's (2007) ideas about the role of non-adaptive evolution in facilitating later adaptive evolution are significant largely because they strengthen our understanding of the integrated functionality through time of the evolutionary process, and weaken the case that evolution is a random process in the broadest sense, that succeeds in spite of all sorts of senseless wastage (see also Gibbs 2003). According to Lynch, even duplication of genes within a species' genome—the formation of paralogs—can lead to partitioning of gene functions among the paralogs, and thus to modularity, relief from pleiotropy, and greater future evolvability. Evolution is usually supposed to be a blind process without foresight (see, e.g., Dickinson and Seger 1999), and it is doubtless true that natural selection is such a process. But evolution is not natural selection; the latter is one component process, albeit a very important one, within the former.

Lynch (2007) argues that "the origins of biological complexity should no longer be viewed as extraordinarily low-probability outcomes of unobservable adaptive challenges, but expected derivatives of the special population-genetic features of DNA-based genomes." Thus complexity, modularity and evolvability emerge passively from the design of DNA itself (see also Fox 1984; Ho and Saunders 1979; Ho and Saunders 1984).

The critical importance of genetic drift in diversification is that, while natural selection is capable of responding only to spatiotemporally localized needs, genetic drift to some extent frees the evolutionary process from the constraints imposed by the selective tracking of the immediate environment. Thus perhaps Wright's (cited in Gillespie 1998) shifting-balance model of evolution has been vindicated, in the broadest sense, but at a far deeper and more integrated level than that of epistasis among genetic loci.

### *1.9: Interaction of genetic drift and sexual selection*

One fascinating possibility is that morphological differences may be established at first by genetic drift, and then maintained by sexual selection or assortative mating, which could even lead to full reproductive isolation in many cases. Sexual imprinting is a particularly interesting form of assortative mating, and highly parsimonious evolutionarily, because the particular preference of mate (as opposed to the capacity to have such preferences) need not have a genetic basis. Most models of isolation-concept speciation (which requires full isolation, pre- or post-mating or both, when populations are in contact with one another) require linkage between an allele for a trait, and an allele at a separate locus for assortative-mating preference for that trait (e.g., Felsenstein 1981). The drift-plus-imprinting model of speciation avoids that requirement, as well as the requirement of epistasis of post-mating isolation to occur, thus making isolation-concept speciation more likely. As with genetic drift, no fitness differences among variants are required either. Therefore the conbination of genetic drift and subsequent sexual imprinting can be an appealingly simple, parsimonious and powerful mode of diversification, provided that the process is not opposed by ecological selection.

### *1.10: Phylotemporal dynamics of evolution*

*Fluctuating evolution and long-term stasis*—Any adequate account of diversification must also explain its reciprocal—stasis, or the maintenance of specific distinctiveness—with equal precision. Studies of evolutionary rates in nature show that average rates of evolution tend to decrease, the longer the time scale over which evolution is measured (Gingerich 1983; Kinnison and Hendry 2001). It seems to be the case that while strong short-term selection and rapid responses to selection are often observed in nature (Hoekstra et al. 2001), in the long term, these rapid evolutionary rates fluctuate up and down, leading to little or no net change over time (Grant and Grant 2002). Eldredge et al. (2005) suggest that long-term fluctuations in evolutionary rates, combined with the establishment and extinction of many simultaneously evolving metapopulations, can explain the long-term stasis that is observed in the fossil records of many lineages.

It is not merely temporal fluctuations in selection that result in long-term stasis; spatially fluctuating regimes of ecological or sexual selection, combined with gene flow among the divergently-selected populations, will tend to suppress long-term responses to selection in a given species. For example, the study of Svensson and Gosden (2007: see esp. their fig. 4) on geographic mosaics of sexual selection in damselflies demonstrates spatial fluctuation in the intensity and direction of sexual selection, coupled with moderate gene flow between the regional populations.

On the other hand, fluctuating directional evolution among metapopulations is certainly not the only evolutionary mechanism that can account for long-term stasis. Estes and Arnold (2007) compared the performance of several quantitative models of long-term stasis for degree of fit to a large set of empirical data on evolutionary rates in nature. Estes and Arnold obtained the best fit from a model of stabilizing selection around a fitness optimum. Under this model, the mean phenotype in the population is maintained by a balance of stabilizing selection and genetic drift, but occasional directional selection can move the optimum within a limited range. Thus Estes and Arnold's study explains the tendency for long-term evolutionary divergence to occur at a rate slower than would be expected under genetic drift alone (while short-term divergence often occurs faster than expected under drift); their work also implies that natural selection more often constrains than promotes evolutionary divergence (see chapter five of this dissertation).

It should be noted, however, that the study of Estes and Arnold (2007), like all studies, has certain limitations. The data set is quite large and heterogeneous, to the extent that anagenetic rates of evolution within lineages are lumped with rates of divergence between lineages; aside from that, Estes and Arnold did not consider spatially varying evolution in metapopulations, unlike Eldredge et al. (2005). It would be interesting to attempt to replicate the results of Estes and Arnold using a smaller sample of evolutionary rates, while making use of more detailed information about the ecological contexts of divergence and stasis.

*Evolutionary rate and ecological opportunity—*Studies of evolutionary rate in island-living mammals have found greatly increased rates of evolution after island colonization, probably due to the combination of strong ecological selection in the new environment, the opportunity for population growth, and the lack of gene flow from the mainland population (Lister 1989; Millien 2006; Pergams and Ashley 2001; Reznick and Ghalambor 2001). While Pergams & Ashley's (2001) study of microevolution found the most rapid evolution in smaller and more distant islands, a study by Anderson and Handley (2002) of sloths inhabiting Holocene-age islands found no separate effect of distance from mainland when the age of each island was taken into account; Anderson and Handley likewise found a slow, steady rate of evolution toward dwarfed body size rather than the predicted rapid burst of evolution close to the time of colonization. It is possible that dwarfism tends to evolve on a different time scale than does, for example, trophic morphology, for reasons that remain unknown.

Invasion of new habitats is not the only possible opportunity for restructuring of ecological niches and renewed adaptive radiation; catastrophic mass extinctions, such as those caused by asteroid impacts, can likewise reopen ecological niches long filled, leading to adaptive radiation of newer phyletic groups (such as mammals, which radiated mostly but not entirely after the K-T extinction event; or dinosaurs, which radiated after the P-T extinction event) (Ho and Saunders 1979; Morris 1998). Any circumstance that offers open ecological niches (that is, unexploited food resources) combined with the possibility for rapid population growth, or perhaps a novel predator (Herrel et al. 2008; Reznick and Ghalambor 2001), will tend to facilitate adaptive radiation by ecological selection; absent those circumstances, divergence by drift and by sexual or social selection—or, of course, stasis—may well dominate.

*Sequential divergence by ecological and sexual selection*—The form of and targets of selection (if any) are likely to differ throughout the history of an evolutionary lineage, depending upon its history and current circumstances. Vitt and Pianka (2005) found that in a speciose lizard radiation, ecologically-selected traits (trophic morphology and behavior) tended to diverge first, at ancient nodes; communication-related traits such as body color, subject to sexual and perhaps social seletion, diverged later, after the major ecological niches had already been filled. A similar pattern has been noted in many fish species (Streelman and Danley 2003). On the other hand, invasion of a new habitat (such as an island) with many empty niches (i.e., unexploited potential food sources) tends to create the opportunity for massive adaptive radiation by ecological selection; this would explain the massive ecological diversity found in even very recent radiations on islands.

*Is evolution by ecological selection predictable, or does historical contingency dominate?—* While the phenomenon of convergent evolution is well-documented (Morris 2003), its degree of prevalence in the fossil record has been somewhat unclear. Vermeij (2006), however, shows that, among living molluscans, many repeated and convergent evolutionary innovations occur in small clades—clades that will be underrepresented or absent in the early fossil record. That could lead, argues Vermeij, to the appearance of uniqueness of evolutionary innovations in the fossil record, leading to an overriding impression of the importance of historical contingency in determining the long-term course of evolution. Vermeij argues instead that evolution—at least, evolution by ecological selection (as opposed to sexual selection or drift)—is a fundamentally predictable and law-like process.

Recent work on living species has tested the relative importance of historical contingency vs. ecological determinism in evolution. A laboratory study of bacteria by Travisano et al. (1995) suggested that traits that are strongly correlated with fitness tend to evolve predictably and convergently in replicate environments, regardless of initial conditions. Losos et al. (1998) treated *Anolis* lizards on four islands of the Greater Antilles as a natural experiment; he found that all ecomorphs occur on all four islands, and a phylogenetic tree reconstructed from molecular data indicated frequent, convergent transitions from one ecomorph to another throughout the history of the radiation.

Thus variation in traits that strongly affect ecological performance, combined with the availability of unexploited food resources and the opportunity for population growth (Reznick and Ghalambor 2001), can lead to a response to selection sufficiently strong to overcome the effects of some historical contingencies. This area of investigation may improve our understanding of ecological source laws (Endler and McLellan 1988; Nakajima 1998).

## *1.11: Conclusion*

Diversification is an extremely complex process whose major causes and consequences are being actively investigated. While divergence of populations results from a dynamic balance of selection, genetic drift and gene flow—with full isolation being one end of a continuum of possibilities—stasis is by no means a passive or easily-understood process either, as some divergence is expected to occur by chance. As a step toward understanding the complexity of diversification, it is clearly profitable to explore the dynamics of diversification and stasis in populations that are still in the early stages of divergence (such as subspecies), hence the focus of this dissertation.

The very complexity of diversification necessarily implies that the process will play out in very different ways with respect to various different traits, taxa, and ecological circumstances. On the other hand, while complexity leads to a wide variety of possible interactions and outcomes, this does not however mean that evolution is somehow fundamentally unpredictable or lawless. Field studies of a wide range of taxa in the wild are therefore of greater than merely supplementary value, relative to laboratory studies of model organisms—especially given that the genetics and development of many of the morphological traits under consideration tend to be highly conserved among animals (e.g., ENCODE Project Consortium 2007). Nature can, and will, still yield surprises.

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# Chapter Two

# Field methods and research localities

## *2.1: Populations sampled*

This study was conducted in the southeastern peninsula of the island of Sulawesi, in Indonesia. Indonesia is part of Malesia, the archipelago that includes Indonesia and parts of Malaysia and Brunei (fig. 2.1). Sulawesi, which is the eleventh largest island in the world, is located in the Wallacea transitional region between the Oriental and Meganesian (Sahul) faunal zones, between Borneo (to the west) and Papua (to the east) (fig. 2.1). Throughout the remainder of this dissertation, the initial letter in research site designations (e.g. the *O* in O-1 or the *B* in B-1) indicates subspecies: O = *Macaca ochreata ochreata*, B = *M. o. brunnescens*. The *O* sites are in peninsular Southeast Sulawesi, while the *B* sites are on Buton Island, the largest of three islands off the southern coast of peninsular southeast Sulawesi (see fig. 2.2). *M. o. brunnescens* is also found on Muna Island, which is the second-largest of the three islands. Please see table 2.1 for a summary of research localities.

Some of the data obtained (e.g., ecological data from transects; photographic data on color and facial shape) will not be incorporated in this dissertation due to the limited time available for data analysis. Details of methods used and the research sites at which all data were obtained (including data used in subsequent chapters of this dissertation, and data not used) are given here anyway, since I plan to cite this chapter in future published works that will incorporate data not analyzed in the dissertation itself.

*Site O-1: Trapping in disturbed, fragmented roadside forest*—From Aug.-Dec. 2002, 51 *M. o. ochreata* were trapped at two locations (traps 1 and 2) in and near Lanowulu, Tinanggea county, Konawe Selatan regency (known as Kendari regency in 2002), Sulawesi Tenggara province, at the southeast edge of Rawa Aopa Watumohai National Park (figs. 2.2, 2.3; see table 2.1 for coordinates). Site O-1 featured highly disturbed and fragmented secondary forest, but without orchards; however, a small rice paddy (*sawa*) was within the trap 1 group's range, and monkeys from this group would sometimes eat raw rice (*beras*) from this field during the short time each year just before the rice harvest. Thus the monkeys' diet was almost entirely obtained from secondary forest with very minimal supplementation from domesticated food. The district head forest ranger, who lives at the edge of the group's range (M. Tayeb, pers. comm.), confirmed (in late 2006) that the monkeys did not raid the small gardens behind the forest rangers' houses until after the 2002 research season had been completed (probably due to the taste the monkeys had developed for domesticated crops used during pre-baiting and trapping).

The pre-baiting period did last for several weeks before trapping began, however, and may have had some morphometric effect (i.e., possibly increased fatness and body mass) on the animals, especially the males. During the trapping period (after pre-baiting), we finally had to start confining the males for short periods so that we could trap females and larger juveniles, indicating that the males had probably consumed most of the bait during the pre-baiting period.

Toward the end of the research season, we constructed a second trap but only had time to trap two animals, both young adult males; 49 of our animals came from trap 1. We counted a total of 53 individuals in the group that we trapped in trap 1 (count by S. Sal Amansyah in 2002, when macaques crossed the main road); hence we trapped 92% of this group.

*Site O-2: Observations in secondary forest*—In summers of 1999 and 2000, and in March 2002, I conducted preliminary observations of monkeys in the interior of Rawa Aopa Watumohai National Park (figs. 2.2, 2.3). I walked along a trail that started near the eastern edge of the southeastern extreme of the park, just west of trap 2 from Site O-1, and continued more or less westward for several km. The trail was not a randomly-placed transect, but a pre-existing trail that local people had made for the purpose of illegally manufacturing boats from felled trees. The southern part of peninsular southeast Sulawesi has a long history of forest disturbance, reflected in the vast secondary grasslands found throughout the area.

The grasslands have been maintained and expanded through repeated burning, which is done by local people to encourage the growth of new, tender grass shoots, which attract deer (Cervidae, *Cervus timorensis*). The deer are then either shot with a firearm, slashed in the throat with a machete while driving by on a motorcycle, or tripped and crippled by long ribbon-like snares woven through the grass. I was told by a local man that it is not unusual for soldiers to "borrow" military weapons for hunting deer, and I once found a 7.62 mm (military caliber) cartridge casing in the middle of the grassland. Homemade firearms that are made to accomodate black-market military ammunition are also reputedly used for hunting.  Macaques are not hunted in Sulawesi, however (except in the northern peninsula), for religious reasons.

The macaques seem to do quite well in disturbed forest—the group trapped in trap 1 (site O-1, roadside forest) may have increased by about 20 individuals from 2000 to 2002, based upon counts made in 2000 (by RRS: 32 individuals) and in 2002 (by S. Sal Amansyah: 53 individuals) when the macaques crossed the main road.  Pigs (*Sus celebensis*), however, are less abundant than they are in primary forests (e.g. site B-3); when pigs (Suidae, *Sus celebensis*) are found they are rarely found in large family groups, and wallows are rarely encountered.  Anoa (Bovidae, *Bubalus depressicornis*) footprints were found only twice at site O-2, and one of the two trackways (an adult and a juvenile) was found relatively deep within the park, near the old Mor'nene village of Huka'ea, along the bank of a creek.  At the same location we made our only observation of an entire family group of pigs at site O-2 (these groups were commonly sighted at primary-forest sites such as O-3 and B-3).

I made observations of forest stratum use (vertical microhabitat—arboreality vs. terrestriality) and obtained location data when possible, whenever my guides or I heard macaques vocalizing, as we walked along the boat-builders' trail through the forest. Upon hearing the vocalizations we would leave the trail and attempt to find the macaque group.

*Site O-3: Random transects in primary upstream forest*—In 2007, two local guides, two research technicians, and I cut and collected data from random transects on the Ambekairi River, far upstream from the nearest town (called Ambekairi). The town itself is at the confluence of the Ambekairi River and the Konaweha River; the latter is the major drainage of peninsular southeast Sulawesi, while the Ambekairi is one of its major tributaries (figs. 2.2, 2.4). The macaques' diet at this site should have been entirely natural, as the nearest human-cultivated crops downstream are probably out of the upstream monkey groups' range, as booted macaques seem to have relatively small ranges (unpub. data from site O-2), and the nearest downstream crops are *sagu* palms, which are probably not eaten by macaques. Chocolate orchards are located much farther downstream (fig. 2.4).

Most of the local people do not venture this far upstream in the rainy season (which is when we were there), as the river becomes impassible when it floods, and there is no other way back to the town. People enter this forest to search for rattan, mostly in the dry season, but up to the time of our research activities the forest was structurally pristine—although we did observe a chainsawed tree stump near one of the transects, deep within the upstream forest site. Apparently selective logging had been tried there by someone but was quickly abandoned, since there was no practical way of transporting logs out of the forest at that location; at this site the river is shallow and rocky, though it has a very strong flow. Local people are also frightened of *raksasa* (giants or "bigfoot") whose footprints are said to have been found farther upstream.

The prognosis for forest conservation in this area is not good, however, since at the time of our departure there was a mobile chainsaw camp just downstream from our research site (see fig. 2.4), which had not been there when we entered the site. Supplemental transect work is still needed in peninsular southeastern Sulawesi, but it is difficult to imagine where it could be accomplished, as the local people are extraordinarily efficient at exploring the territory on foot (the loggers less so than the rattan-gatherers), despite the lack of navigable waterways, and people have penetrated quite far upstream.

Population densities of vertebrate species at this site seemed somewhat low relative to the other sites (see also section 2.3, final paragraph, for an important note), but we nonetheless encountered pigs (*Sus celebensis*), tracks of anoas (*Bubalus depressicornis*), Sulawesi red-knobbed hornbills (Bucerodtidae, *Aceros cassidix*), and other typical Sulawesi forest vertebrates.

*Site B-1: Trapping in primary forest*— From Dec. 2004-Jan. 2005, 5 *M. o. brunnescens* were trapped near my base camp in northern Buton Island along the Soloi Creek, along the Maligano-Ronta-Ereke road in North Buton Wildlife Sanctuary, Muna regency, Sulawesi Tenggara province. This site (figs. 2.2, 2.5, 2.6; see table 2.1 for coordinates) was located 10 km from the edge of the nearest towns (Maligano to west, Ronta to east) and 15 km from the coast, and was characterized by primary lowland broadleaf forest with very light selective logging near the road only. The monkeys' diet was entirely obtained from primary forest.

At this site we frequently heard anoas (*Bubalus depressicornis*) in the forest, and my technicians saw one of them come to the creek to drink when I was away in the city. We found anoa trackways along the creek, something that I had also observed at site O-2.

We also often encountered large family groups of pigs (*Sus celebensis*) and the usual birds such as Sulawesi red-knobbed hornbills (*Aceros cassidix*).

Large strangler figs (Moraceae, *Ficus* sp.) were sometimes found within the forest, though these were at low density and never very far from the creek. One such large strangler fig was a popular sleeping site of a large macaque troop as long as the fig produced fruit; as soon as the fruit was gone, however, the troop moved on and was not seen or heard in that area again. Indeed, most trees that seemed to produce food favored by macaques (moist fruit such as berries and drupes) were located near the creek (or near the road), perhaps due to availability of water or sunlight. For example, pandanus trees (Pandanaceae, *Pandanus* sp.) produce fruit that can be eaten by macaques, and tend to be found in edge habitat near rivers or roads as they are shade-intolerant. Trees found along ridges located relatively far from the river were noticeably different, with few moist-fruit-producing species present, and indeed these ridgetop areas far from the creek were notable for low vertebrate density, including birds, though we did not assess density quantitatively.

The anoa trackways and pig encounters near the river and the road suggested that many vertebrates prefer such edge habitats, as they may be more productive than interior ridge forest—I cannot confirm that impression, however, since my work at this site was mainly focused upon trapping, and I spent far more time near the river and the road than I did in the ridge forests. An additional area that we visited in northern Buton that was near the creek, but a few km farther downstream, also had apparently low vertebrate density and few moist-fruit-producing trees; in that area, pine trees (Pinaceae, *Pinus* sp.)

were found quite close to the creek. There were no signs of macaques there except for some scat.

Therefore my qualitative impression is that the primary forests of northern Buton Island may be quite heterogeneous, possibly due to local variation in soils as well as microclimates, and not all of the habitat will be suitable for macaques, except possibly as sink habitats. Another researcher who visited areas of northern Buton confirmed that certain areas in the north seemed to have low vertebrate density relative to southern Buton (J. Burton, pers. comm.). The possible effects of soil, vegetation, hydrology, microclimate and other factors on vertebrate density in southeast Sulawesi are deserving of much more detailed study. Collection of random transect data in different areas of northern Buton will be necessary in order to test the qualitative impression of heterogeneity in habitat quality and density of vertebrates.

For the moment, however, density estimates obtained near rivers should be treated as upper bounds, since macaques and many other vertebrates seem to favor riverine areas; there is a possibility that vast interior areas far from year-round streams have very low vertebrate densities, which could lead to a gross overestimate of population density if estimates made in riverine areas are extrapolated to the remaining forested areas of an entire island, for example. Most field studies are of course conducted near rivers or creeks, since human researchers are if anything more water-limited than other vertebrates (due to the additional need for cooking and bathing). The use of small seasonal streams during the rainy season as base camps could help to partially alleviate this problem; the combination of random transects on the ground (in as many areas as possible, including seasonal streams) with remote sensing on a larger scale also seems a promising approach.

*Site B-2: Trapping in an orchard-secondary forest mosaic*—In April-May 2007, my technicians and I trapped 26 *M. o. brunnescens* on southern Buton island, approximately 1 km south of Lawele, Lasalimu county, Buton regency, Sulawesi Tenggara province (fig. 2.7). One trap (trap 4) was located on the boundary between orchards (mostly chocolate with smaller plots of *kadondong* (fam. Burseraceae: A. J. Marshall, pers. comm.) and a secondary forest mosaic (see table 2.1). Trap 5, built later, was located between secondary forest and a newly-cleared field, where crop-raiding (by a different monkey group) had only very recently begun (see table 2.1). Monkeys were observed to spend time in both environments, but often crop-raided in the orchards. The orchards also supported other diurnal forest species such as Sulawesi warty pigs (*Sus celebensis*), monitor lizards (Varanidae, *Varanus* sp.), and Sulawesi red-knobbed hornbills (*Aceros cassidix*) at seemingly high densities.

*Site B-3: Random transects in primary forest*—We constructed our camp along Kendoli Creek in southern Buton island (fig. 2.8), just south of our orchard trapping site, B-2. The location is an island between two streams, in an area where the Kendoli creek splits into three streams. The Kendoli creek flows year-round, though it is lower in the dry season. The site is called "Bala" by Operation Wallacea. A liana attached to the largest tree in camp served as the common origin datum for all three random-direction transects at this site (TR-1, TR-2 and TR-3). While Operation Wallacea personnel reputedly had cut transects at this site, my observations indicated that the transects were neither straight nor in random directions, indeed they used pre-existing man-made rattan and honey trails. Therefore we cut our own transects at this location (see section 2.3).

The forest site was far enough from the town of Lawele and from orchards that it seemed unlikely that the macaques' diet was anything but natural. We frequently saw pigs (*Sus celebensis*), often in wallows, including large family groups. We also encountered monitor lizards (*Varanus* sp.), occasionally saw snakes (though we saw no pythons at this site), and often encountered anoa (*Bubalus depressicornis*) tracks. A variety of birds were present, prominently including Sulawesi red-knobbed hornbills (*Aceros cassidix*) and yellow-billed malkohas (Cuculidae, *Phaenicophaeus calyorhynchus*), which live symbiotically with the macaques. The symbiosis of macaque and malkoha was originally observed in *M. nigra* of northern Sulawesi; the birds are thought to follow macaques in order to consume arboreal insects stirred up by the monkeys (Heinrich, in Fooden 1969: 50). The phenomenon was later observed in *M. maura* of southwestern Sulawesi (Matsumura 2001) and in other Sulawesi macaque species including *M. ochreata* (pers. obs.).

At site B-3, the trees that grew in riparian areas were noticeably different from those that grew atop nearby hills and in the interior. Many tree species that produced moist fruit favored by monkeys, such as berries and drupes, seemed to be restricted to riparian areas. *Soni* (Indo.) trees (Dillenniaceae, *Dillennia* sp.), which produce berries, and *kamba'u* (Butonese) trees, which produce drupes, are two examples. *Orawa* (Tolaki; = *maniaga*, Butonese) trees are found both near creeks and at moderate distance from them in low areas. After *orawa* fruit falls it quickly rots and gives off a strong odor that attracts pigs; monkeys will eat the fruit before it falls, when they encounter it in the canopy.

*Eha* (Tolaki; = *ngasa*, Butonese; Fagaceae, *Castanopsis* sp.) trees, meanwhile, were quite commonly found atop hills at site B-3, as were *ra'u* (Tolaki; = *kase*, Butonese; Sapindaceae, *Pometia pinnata*) trees, both of which produce a hard, but primate-edible and nut-like fruit. *Eha* fruit dehisces around the time it falls to the ground, at which time the nuts are usually eaten by pigs; macaques in southern Buton seem able to open the spiny casing of the fruit, however, before it dehisces and falls to the ground (Basrun, pers. comm.). *Eha* trees normally have a large central trunk, usually dead and termite-eaten, with several smaller, younger stems sprouting up around the dead trunk—possibly an adaptation to the extremely active termite community in this forest, which probably limits the age and stature of the trees in southern Buton.

### *2.2: Field methods: Morphometrics*

*Trapping protocol*—The sample obtained via trapping consisted of 82 *M. ochreata*, including *51 M. o. ochreata* and 31 *M. o. brunnescens* from five trapping locations in three regions and three habitat types, between Aug. 2002 and May 2007. Our trapping protocol combined the pre-baiting method and squeeze-cage specifications of C. J. Jolly and colleagues (pers. comm.) with a traditional wooden trap of a type historically used by the indigenous Tolaki people, designed and built by my research technician, Mr. Kisman of Roraya, Tinanggea, Southeast Sulawesi. The trap featured a falling door triggered when monkeys pulled on bait (bananas or corn). Before construction of the trap, we pre-baited a number of test areas for a few to several weeks, then continued pre-baiting as the trap was built. After one or more monkeys were inside the wooden trap, we tied a locally-built iron squeeze cage (built by Mr. Victor of Kendari, Southeast Sulawesi) to the door of the wooden trap, then opened the wooden trap and the iron squeeze cage, facing one another. An assistant stood well behind the squeeze cage, holding a thin cord attached to the squeeze-cage's door trigger. When the monkey had fled the wooden trap and entered the squeeze-cage, we triggered the squeeze-cage's door. We then carried the squeeze-cage to the nearby tent that was used for morphometry and photography.

We used the squeeze cage's mobile inner panel to confine the animal so that it was unable to move; we then checked to make sure the animal was able to breathe and that its ribcage was not compressed. (If the animal was agitated and seemed likely to hurt itself, we used the squeeze cage to restrict its movements to avoid self-injury by the animal, before moving it to the tent.) Ketamine HCl at 10-15 mg/kg i.m. (Sapolsky and Share 1998) was used for anesthesia, injected intramuscularly in the quadriceps if possible, or in the triceps if the quadriceps is not accessible. Before insertion of the needle, I expelled any bubbles from the syringe. After inserting the syringe but before injecting the anesthetic, I aspirated the syringe slightly to ensure that it was not in a blood vessel.

We took most measurements on only the right side of each animal's body. Canine tooth dimensions, testicular dimensions, and dermatoglyphic prints were taken on both sides. Cheek tooth impressions were taken on the right side, and dental wear was field-scored either on the right side only (2007) or on both sides (earlier seasons), but relative-age assessment was conducted using only field-scored dental eruption and wear from the right side of the mouth.

Although repeatability of measurements was not separately assessed for this study, all caliper measurements were performed by the author (RRS), who achieved high repeatability with sliding calipers in earlier morphometric studies on human subjects at the University of New Mexico.

*Field morphometric protocol, 2002*—The data sheet used is provided in the Appendix of this chapter.

Mass was measured to the nearest 0.05 kg using a hanging digital scale (Intercomp model CS200) and crown-rump length was measured using a steel anthropometer (GPM Gneupel, Switzerland). Length and width of canine teeth (gumline to tip), length of testes, and maxillary bicanine breadth were measured with analog sliding calipers (Mitutoyo, Japan). I attempted to measure bizygomatic (bimalar) breadth with the sliding calipers but was unable to do so accurately with larger animals (in later seasons I switched to spreading calipers for that measurement). I measured circumferences of the right forearm and right thigh, and of the scrotum, with a locally-bought steel measuring tape. I made impressions of the right upper and lower cheek teeth with distortion-resistant polysiloxane vinyl (Exaflex Putty, 2-min. set time, GC America) for assignment of age class based upon molar wear, and for measurement of molar dimensions.

We took a series of eight standardized photographs with a digital camera (PowerShot G2, Canon, Japan) with a 4x5-inch 18% reflectance gray card (Kodak) as a size and reflectance standard (see table 2.2a), inside a large tent with windows shut (to block most reflected sunlight) and a brown tarp overhead oriented east-west that blocks direct sunlight. In photographs of the first few subjects, before the Kodak card arrived, a different size and relfectance standard was used (the "stick"—see table 2.2b). Both standards were then included in several subsequent photographs so that the reflectance of the two standards could be reconciled later.

The photographs taken were: dorsal, ventral, genitals (ventral), "mugshot" (face), profile (lateral head), caudal, lateral (right side), and cranial (top of head). The lateral and caudal photos were taken when the animal was positioned on a sawhorse. I used the camera handheld with the flash locked on, auto exposure, and RAW (.crw) file format (maximum size). We made an effort to maintain camera-subject distance at approximately 110 cm, and to hold the camera orthogonal to the plane of interest (sagittal, coronal, etc.). The weather and sunlight conditions were noted in order to further control for ambient light conditions. It should be noted, however, that field conditions make exacting standardization of photographs difficult.

We obtained palmar and plantar dermatoglyphic prints from both sides of the body. We first cleaned the animal's palm or sole with alcohol, then dusted the skin surface with fine graphite powder using a soft cosmetic brush. Trained research technicians placed two overlapping strips of packaging tape sticky-side-down on the dusted palm or sole, then carefully lifted the tape and placed it sticky-side-down on white card stock, noting the subject number, side of body, and hand or foot on each card. These dermatoglyphic prints were taken primarily to assess dermatoglyphic asymmetry and as a means of identification, to ensure that each individual was trapped, and represented in the database, only once.

For males, I scored pubertal status by palpating testes—subadult males generally had undescended testes.  For females, I scored pubertal status by noting presence or absence of reddened sexual skin.  Female parity was scored via obvious differences in nipple length between parous and nulliparious females.  I tested each female for advanced pregnancy by simultaneously palpating the inferior abdomen with the left hand, with simultaneous intrarectal digital palpation with one finger of the right hand.  In a few cases, intrarectal palpation had to be abandoned when it seemed to cause the animal discomfort in spite of anesthesia.  Female menstrual-cycle status was assessed by noting the state of the female's sexual skin.

Finally, I obtained buccal (inner cheek tissue) cells with a sterile applicator wand and smeared them on an FTA Classic card (Whatman Bioscience, USA) for later genetic analysis.  FTA cards permanently bind DNA nucleotides while lysing blood cells and neutralizing pathogens.  If the animal's gums were bleeding, I dabbed some blood on the card as well.

*Field morphometric protocol, 2004-05*—Data collection was conducted as in 2002, with the following exceptions:  JPEG format photos rather than RAW photos were taken.  We added measurements of testes width (rather than only length), tail length, achilles tendon width (at narrowest point), palmar and plantar lengths, digit lengths (pollex, manual digit III, hallux, pedal digit III), and limb lengths.

Limb legths were measured as follows; all measures taken with limbs flexed at 90-degree angle. Humerus: superior aspect of distal clavicle to olecranon process. Ulna: olecranon process to distal end of ulna (palpated). Femur: proximal end of greater trochanter to distal patella (leg flexed at 90-degree angle). Tibia: tibial plateau to inferior aspect of lateral condyle.

Palmar, plantar and digit lengths were measured as follows. Palmar length: from distal edge of skin between outspread digits III and IV to proximal margin of largest palmar pad. Plantar length: from distal edge of skin between outspread digits II and III to posterior margin of heel, foot flexed at 90-degree angle. Digit lengths: lateral midpoint of palm-digit fold to end of digit, not including nail.

*Field morphometric protocol, 2007*—Data collection as in 2004-05, with the following exceptions. Cranial measures were added, including cranial length, intermeatal breadth, cranial vault, and height of supraorbital torus (right side). Cranial length: glabella to posteriormost point of cranium. Intermeatal breadth: distance between external auditory meati. Cranial vault: right external auditory meatus to superiormost point of interparietal skull.

In 2007, all cranial measures (including bizygomatic breadth) were performed with spreading calipers (GPM Instruments, Switzerland) (previously sliding calipers were used for bizygomatic breadth). Palm, sole and digit lengths were measured with sliding calipers (Mitutoyo, Japan).

In 2007, one RAW and one JPEG photograph were taken of each view of each subject, to ensure that the JPEGs from 2004-05 could be properly standardized and interpreted via regression, if necessary. In 2007, the tent was no longer available; we still used a brown tarp overhead with the same east-west orientation, but substituted woven plastic rice-bag material (*karorong*) on 3½ sides of the photography area to block reflected light from the forest.

*Ethics*—All trapping was done humanely. We used a safe anesthetic (ketamine HCl, 10-15 mg/kg i.m.) that is resistant to overdosing (Sapolsky and Share 1998). Our research protocol was approved before each field season by the University of California, Davis' Animal Use Committee (latest protocol, no. 05-12105, approved June 2006). Our procedures were also evaluated in the field in 2002 by Dr. Made Supartha, a veterinarian from Kendari, Sulawesi Tenggara. Appropriate medication and first-aid equipment for personnel were always kept on hand.

### *2.3: Field Methods: Ecology*

*Construction of random transects*—We assessed the habitats within *M. o. ochreata*'s and *M. o. brunnescens*' ranges via random sampling of trees (DBH > 5 cm), using two-meter-wide belt transects placed randomly throughout each subspecies' range. We recorded only local names of trees, and photographed parts of some trees to aid in subsequent identification. We also walked the same transects repeatedly to obtain animal-density data (to reduce within-transect estimation error), and measured orthogonal distances from transect to animal (or to center of animal group, if > 1 animal sighted) using a 50m-long forester's measuring tape (Buckland et al. 2001; A. J. Marshall, pers. comm.). We counted individual animals rather than groups. We walked animal transects in numerical sequence within each site, and we recorded animal data only when outbound on a transect, not when returning to camp. We also recorded animal data while we worked on tree transects, but only when outbound on a portion of the transect where tree data was still unfinished (to avoid over-representation of portions of the transects closest to the base camp). We obtained 1.7 ha of data on trees and > 60 km of animal density and distribution data, although we obtained far more data in *M. o. brunnescens*' range than in *M. o. ochreata*'s range. The transects were 2 km in length in *M. o. brunnescens*' range (site B-3: TR-1, TR-2 and TR-3; see fig. 2.8), and as long as the rugged topography permitted in *M. ochreata*'s range (site O-3: TR-4 = 0.25 km, TR-5 = 1.05 km, and TR-6 = 1.2 km).

At site B-3, all transects originated from a single data point near our original base camp there; at site O-3, transects (except one) could not begin next to our base camp as the topography was too rugged (sheer rock walls); therefore the origin datum for the last two *ochreata*-range transects (TR-5 and TR-6) was placed as close as possible to our riverside base camp after the steep rocky ridges next to the river had been left behind.

I chose the direction (compass bearing, 0-359 degrees) of each transect using a random number generator (RANDBETWEEN function, Microsoft Excel). As an assistant cut the transect, I supervised the direction and straightness of the transect, sighting almost continuously through the upper edge of my compass which was set to the transect's predetermined bearing.

We made every effort to ensure the straightness and randomness of each transect in order to avoid biased sampling. The GPS coordinates that we were able to obtain along each transect confirmed that each transect was straight, when plotted in the field on a topographic map. At site B-3, on two occasions we were unable to safely traverse a certain part of the forest that lay in the transect's predetermined direction, due to steep and slippery conditions in these areas. In these cases, we made a 100m-long "hole" in each transect (in which neither tree, nor animal, nor light data was recorded), and added an extra 100m at the end of the same transect. Site O-3 was even more rugged and challenging, and the "hole" method did not work—we had to terminate each transect when the forest that lay in its direction became too dangerous to traverse.

*Light penetration measures*—We directly measured the degree of light penetration through canopy and understory in primary forests within each subspecies' range (B-3: 13 points; O-3: 10 points), at randomly-selected points along our transects. The objective of these comparisons is to evaluate the possibility that sensory drive caused divergence between the two subspecies.

A random number generator (RANDBETWEEN function, Microsoft Excel) was used to obtain random numbers between 0 and 2000. Each day during tree and animal transects, we would attempt to obtain (weather and time permitting) measurements of light along whichever transect was being walked on a particular day (the transects were walked in order: 1, 2, etc.). The random number was used as the point along the transect, in meters, at which light was measured. First we would walk to the point along that day's transect where light was to be measured—for example, if the day's light point was

1,223m, we would walk to the nearest 50-m marker (1,200m) and would measure ahead 23m using a forester's tape measure.  Having arrived at the light point, we would lay out the tape measure perpendicular to the transect, first to the right and then to the left side; on each side we sampled light at sub-points 17m and 50m from the center line of the transect, which gave us four sampling sub-points within each light point, each about 33m apart.  We did this to ensure that our data would reflect real, repeatable differences or similarities in light penetration, and so that all our data at a single light point would not have been obtained under a single tree.

We also controlled for moment-to-moment fluctuations in light levels (due to, e.g., tree branches swaying in the wind, and movements of clouds relative to the sun) by taking five measurements at each sub-point (e.g. 17m right, 50m right, etc.), 30 seconds apart.  The timing of these samples was controlled using a wristwatch; after 30 seconds had elapsed, the measurer flipped the "data hold" switch on the light meter without looking at the light meter's readout; he then would look at the readout and record the data. Before measuring light at each sub-point, we cut down all ground cover vegetation (DBH < 5cm) so that only light penetrating the canopy and understory layers would be measured (we did this because our observations suggest that these macaques are largely arboreal, not terrestrial).

*Vertical microhabitat*—Whenever possible (on- and off-transect) we opportunistically obtained data on vertical microhabitat (forest stratum—canopy, understory, ground) use and feeding behavior, and I also built a database of information about which fruit species are consumed by macaques (and pigs) and which are not, according to long-term casual observations by two local research assistants, both of whom have spent several years working in local forests.

One limitation to this data that should be kept in mind is that, although the portion of *M. o. ochreata*'s range that we sampled (site O-3) was essentially undisturbed primary forest, it may be somewhat atypical relative to the average habitat that was available before the arrival of large human populations in *M. ochreata*'s range. Deforestation in peninsular southeast Sulawesi (as compared to Buton Island) has been extreme, especially recently, and the only primary forest that we could find in *M. o. ochreata*'s range was quite far upstream in a rocky and somewhat vertebrate-depauperate area (1½ days' walk upstream from the nearest village). The same was not true of *M. o. brunnescens*' range, as deforestation there is not yet as extensive. Therefore any differences in animal density, forest structure and light environment should be interpreted with care, in the context of soil and geomorphological differences between the areas sampled.

### *Tables*

Please see the following pages.

| Site | Traps | Description | Habitat | Coordinates | Data obtained |
|---|---|---|---|---|---|
| O-1 | 1, 2 | Rawa Aopa Watumohai National Park (roadside) | Disturbed, fragmented forest | Trap 1: S 4° 27' 32", E 122° 27' 40"<br>Trap 2: S 4° 26' 5", E 122° 7' 49" | Morphometrics (N = 51) |
| O-2 | | Rawa Aopa Watumohai National Park (interior) | Secondary, continuous forest | Main trail (entry point):<br>S 4° 26' 16", E 122° 7' 32" | Vertical microhabitat use |
| O-3 | | Ambekairi River | Primary forest on rocky substrate | Base camp:<br>S 3° 36' 9", E 121° 43' 54" | Random transects & light levels: TR-4, 5, 6 |
| B-1 | 3 | North Buton Wildlife Preserve (interior) | Primary forest | Trap 3: S 4° 42' 12", E 122° 56' 2" | Morphometrics (N = 5, all male) |
| B-2 | 4, 5 | South of Lawele, southern Buton | Orchard-secondary forest mosaic | Trap 4: S 5° 14' 17", E 122° 57' 22"<br>Trap 5: S 5° 13' 57", E 122° 57' 38" | Morphometrics (N = 26) |
| B-3 | | Kendoli Creek, southern Buton | Primary forest | Base camp:<br>S 5° 16' 32", E 122° 57' 33" | Random transects & light levels: TR-1, 2, 3 |

**Table 2.1.** Summary of research localities and their characteristics.

| | edge 1 | center | edge 2 |
|---|---|---|---|
| length, 2002-05 | 12.914 | 12.892 | 12.893 |
| width, 2002-05 | 10.183 | 10.184 | 10.174 |
| length, 2007 | 15.073 | 15.066 | 15.095 |
| width, 2007 | 10.176 | 10.173 | 10.157 |

**Table 2.2a.** Measurements of Kodak gray cards (cm) performed after completion of all field research, 22 November 2007, using Mitutoyo sliding calipers. Measurements corrected for zero of calipers (+ 0.01 mm) by subtracting 0.01 mm. Some white observed in corners of 2007 gray card where gray coating had been lost; therefore perhaps better to avoid extreme edges of card when calibrating light reflectance or size. Much discoloration of 2002-05 gray card observed, especially near edges.

| | edge 1 | center | edge 2 |
|---|---|---|---|
| length, gray stripe | 4.982 | 4.973 | 4.985 |

**Table 2.2b.** Length of gray (center) stripe on wooden stick with black, gray and white stripes that was used in early photos in 2002. Measured on 22 November 2007 with Mitutoyo sliding calipers. Length = parallel to long axis of stick. Color of gray stripe still intact as of 22 November 2007, except small spot of black paint observed near edge.

## *Literature cited*

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Fooden, J. 1969, Taxonomy and Evolution of the Monkeys of Celebes: Bibliotheca Primatologica, v. 10. Basel, S. Karger.

Matsumura, S. 2001. Yellow-billed malkohas (*Phaenicophaeus calyorhynchus*) following moor macaques *(Macaca maurus)* in South Sulawesi, Indonesia. Journal of Tropical Ecology 17:619-623.

Sapolsky, R. M., and L. J. Share. 1998. Darting terrestrial primates in the wild: a primer. American Journal of Primatology 44:155-167.

## *Figures*

**Figure 2.1**: Indonesia, showing Sulawesi at the center. (Courtesy Google Earth™ mapping service).

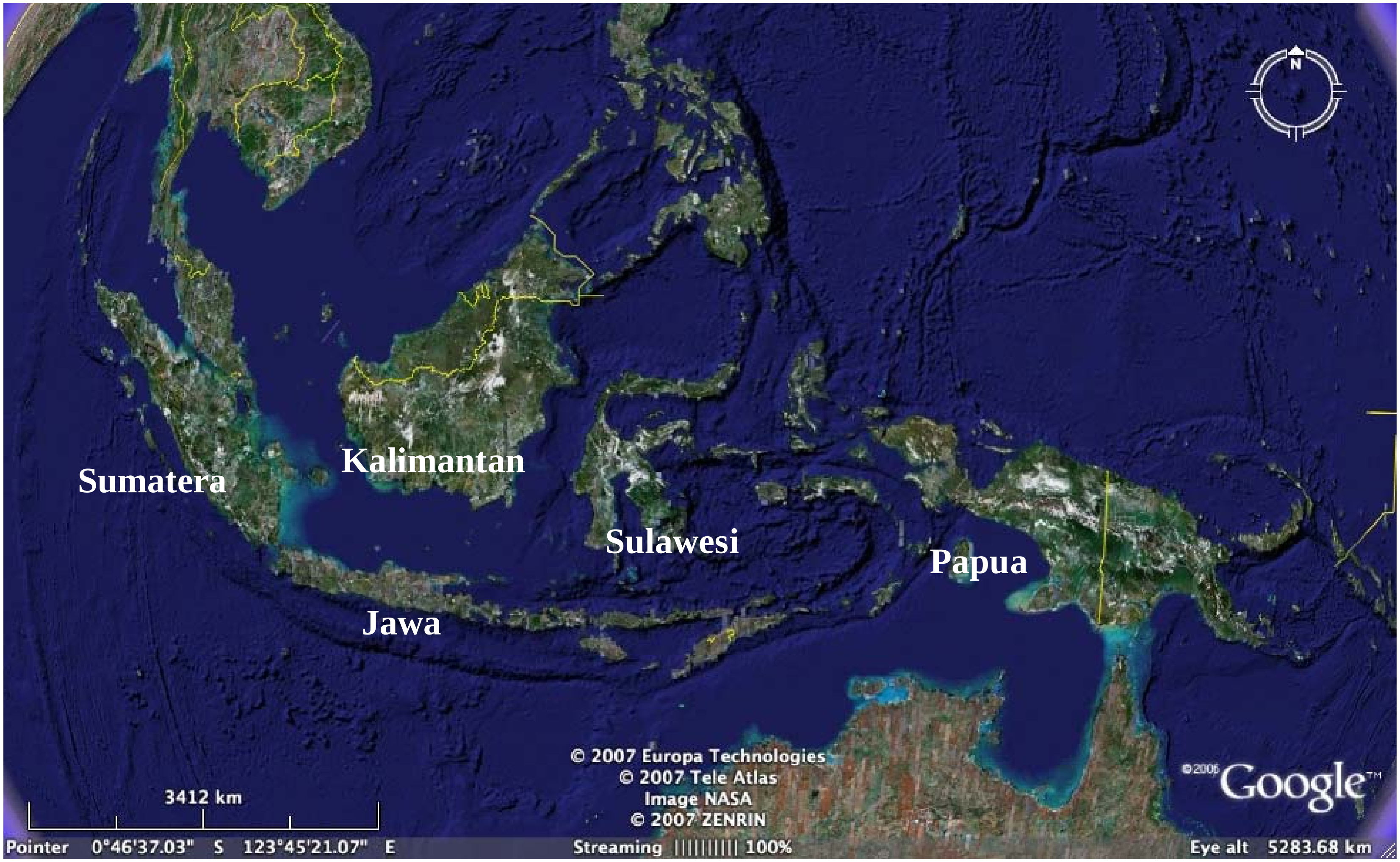
Sumatera
Kalimantan
Sulawesi
Jawa
Papua
N
© 2007 Europa Technologies
© 2007 Tele Atlas
Image NASA
© 2007 ZENRIN
©2006 Google™
3412 km
Pointer 0°46'37.03" S 123°45'21.07" E
Streaming |||||||||| 100%
Eye alt 5283.68 km

Figure 2.1

**Figure 2.2**: The southern part of Sulawesi, with research sites indicated (see table 2.1).

(Courtesy Google Earth™ mapping service).

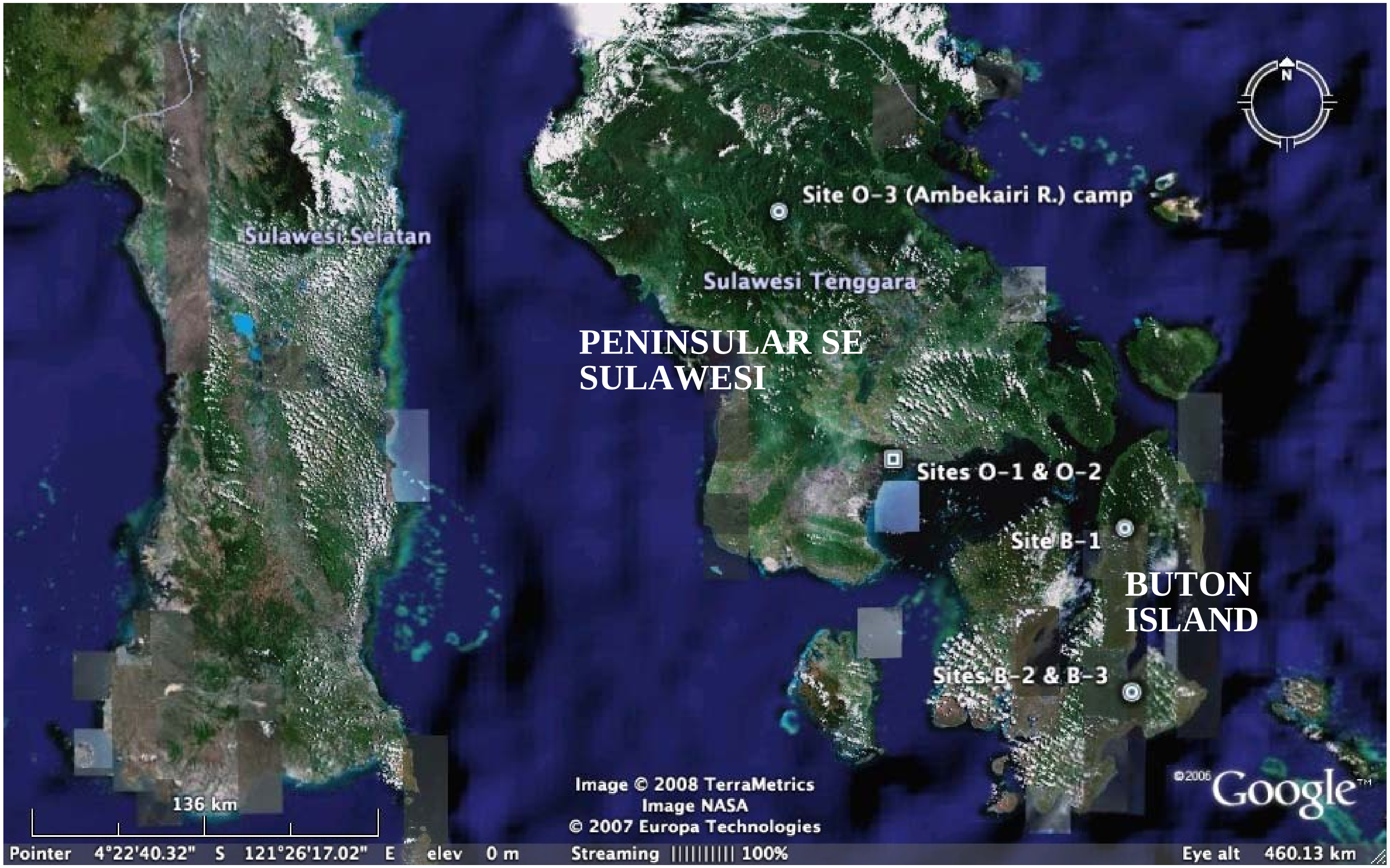
Sulawesi Selatan
Site O-3 (Ambekairi R.) camp
Sulawesi Tenggara
PENINSULAR SE SULAWESI
Sites O-1 & O-2
Site B-1
BUTON ISLAND
Sites B-2 & B-3
N
136 km
Image © 2008 TerraMetrics
Image NASA
© 2007 Europa Technologies
©2006 Google™
Pointer 4°22'40.32" S 121°26'17.02" E elev 0 m
Streaming ||||||||| 100%
Eye alt 460.13 km

Figure 2.2

**Figure 2.3**: Sites O-1 and O-2, Rawa Aopa Watumohai National Park, near the town of Lanowulu. Large transmigrant towns surround the southeastern portion of the park (forested area in dark green). Traps 1 and 2 are at site O-1; the trail used for site O-2 (forest interior) begins just west of trap 2, and continues west through the forest. This forest is surrounded on its north and east by large transmigrant villages, and on its south by a vast *alang-alang* (Poaceae, *Imperata cylindrica*) secondary grassland that is periodically re-settled by local people. The forest is highly disturbed and fragmented at site O-1 but still supports a growing macaque population; it is secondary but continuous in site O-2. (Courtesy Google Earth™ mapping service.)

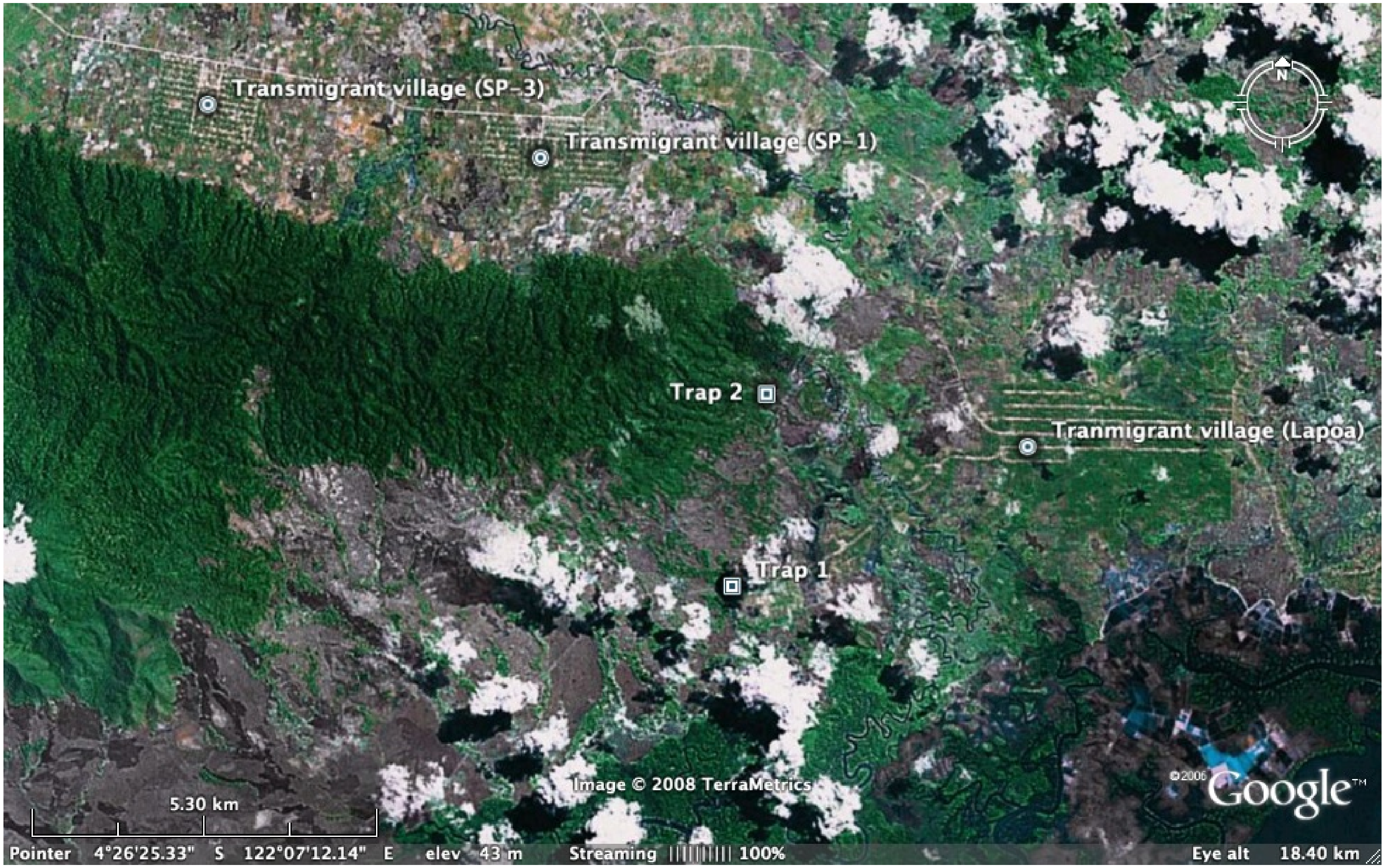
Transmigrant village (SP-3)
Transmigrant village (SP-1)
N
Trap 2
Tranmigrant village (Lapoa)
Trap 1
Image © 2008 TerraMetrics
©2006 Google™
5.30 km
Pointer 4°26'25.33" S 122°07'12.14" E elev 43 m Streaming |||||||||| 100%
Eye alt 18.40 km

Figure 2.3

**Figure 2.4**: Site O-3, showing base camp location along the Ambekairi River, a tributary of the Konaweha River, the latter being the main drainage of southeast Sulawesi. Unlike the other figures, this view "faces" south (south at top of image). This image shows the GPS-measured locations of the nearest occupied structures, the encroaching chainsaw camps that were located just downstream from the still nearly-pristine research site, and in the distance, the town of Ambekairi, which lies next to the confluence of the Ambekairi and the Konaweha. (Courtesy Google Earth™ mapping service).

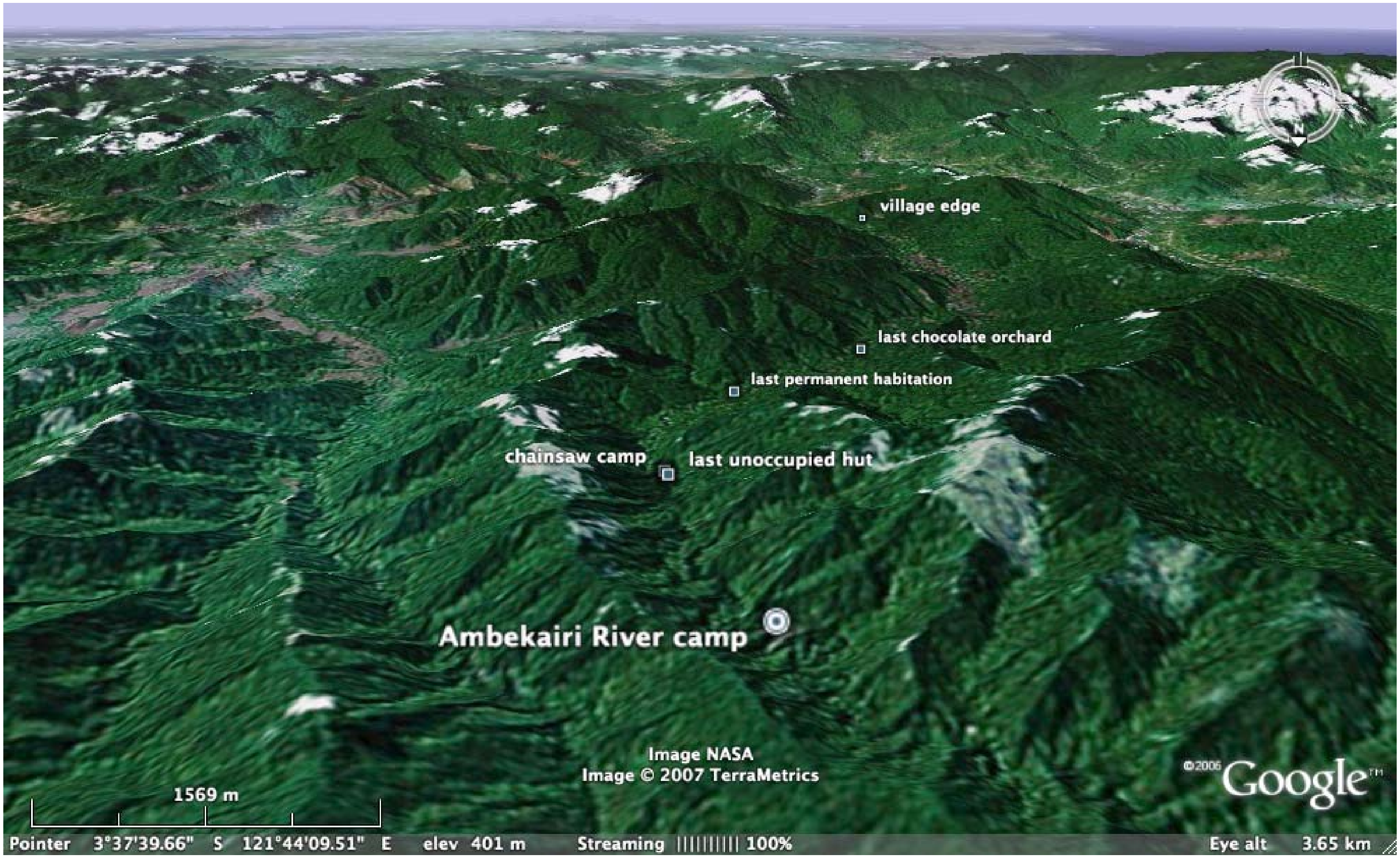
village edge
last chocolate orchard
last permanent habitation
chainsaw camp
last unoccupied hut
Ambekairi River camp
Image NASA
Image © 2007 TerraMetrics
©2006 Google™
1569 m
Pointer 3°37'39.66" S 121°44'09.51" E elev 401 m
Streaming |||||||||| 100%
Eye alt 3.65 km

Figure 2.4

**Figure 2.5**: An overview of site B-1, showing its position in North Buton Wildlife Sanctuary, with the nearest settlements indicated. The ocean lies along the western edge of the image. (Courtesy Google Earth™ mapping service).


N
Maligano (E edge)
Site B-1
Maligano
Ronta (W edge)
Image © 2008 TerraMetrics
©2006 Google™
4.94 km
Image © 2008 DigitalGlobe
Pointer 4°43'26.33" S 122°54'55.93" E elev 158 m Streaming |||||||||| 100%
Eye alt 16.71 km

**Figure 2.5**

**Figure 2.6**: A closer overview of site B-1 ("Kali Soloi camp") along the Soloi Creek, showing the main west-east road that connects the villages of Maligano and Ronta (and, farther east near the ocean, Ereke). The bald-looking area to the east of the camp (which also shows up somewhat in Fig. 2.5) is not deforested; it is a hilltop (not apparent in two dimensions) with sparse, stunted vegetation that is typical of high ridges (relative to local topography) on Buton Island. Very limited selective logging sometimes occurs, but only very close to the road. (Courtesy Google Earth ™ mapping service.)


N
Kali Soloi camp
Image © 2007 DigitalGlobe
Image © 2007 TerraMetrics
©2006 Google
350 m
Pointer 4°42'10.01" S 122°56'11.47" E elev 132 m Streaming ||||||||| 100% Eye alt 1.34 km

**Figure 2.6**

**Figure 2.7**: An overview of site B-2, showing traps 4 and 5. The town of Lawele is north of trap 4. Another (smaller) town, just east of Lawele, is just north of trap 5. Trap 4 is at the boundary of orchard and secondary forest, but the orchards are vast and relatively old. Trap 5 is located in a small, newly-cleared orchard, surrounded by secondary forest. (Courtesy Google Earth™ mapping service.)


N
Trap 5
Trap 4
Image © 2007 DigitalGlobe
©2006 Google™
1736 m
Pointer 5°14'16.33" S 122°57'07.55" E elev 27 m
Streaming |||||||||| 100%
Eye alt 6.05 km

**Figure 2.7**

**Figure 2.8**: A view of site B-3 (foreground) and B-2 (background), with the town of Lawele in the distance. The endpoints of transects TR-1, -2 and -3 are indicated. Deforestation in Buton's interior is not very advanced, and the primary forest at B-3 is nearly pristine. (Courtesy Google Earth™ mapping service.)

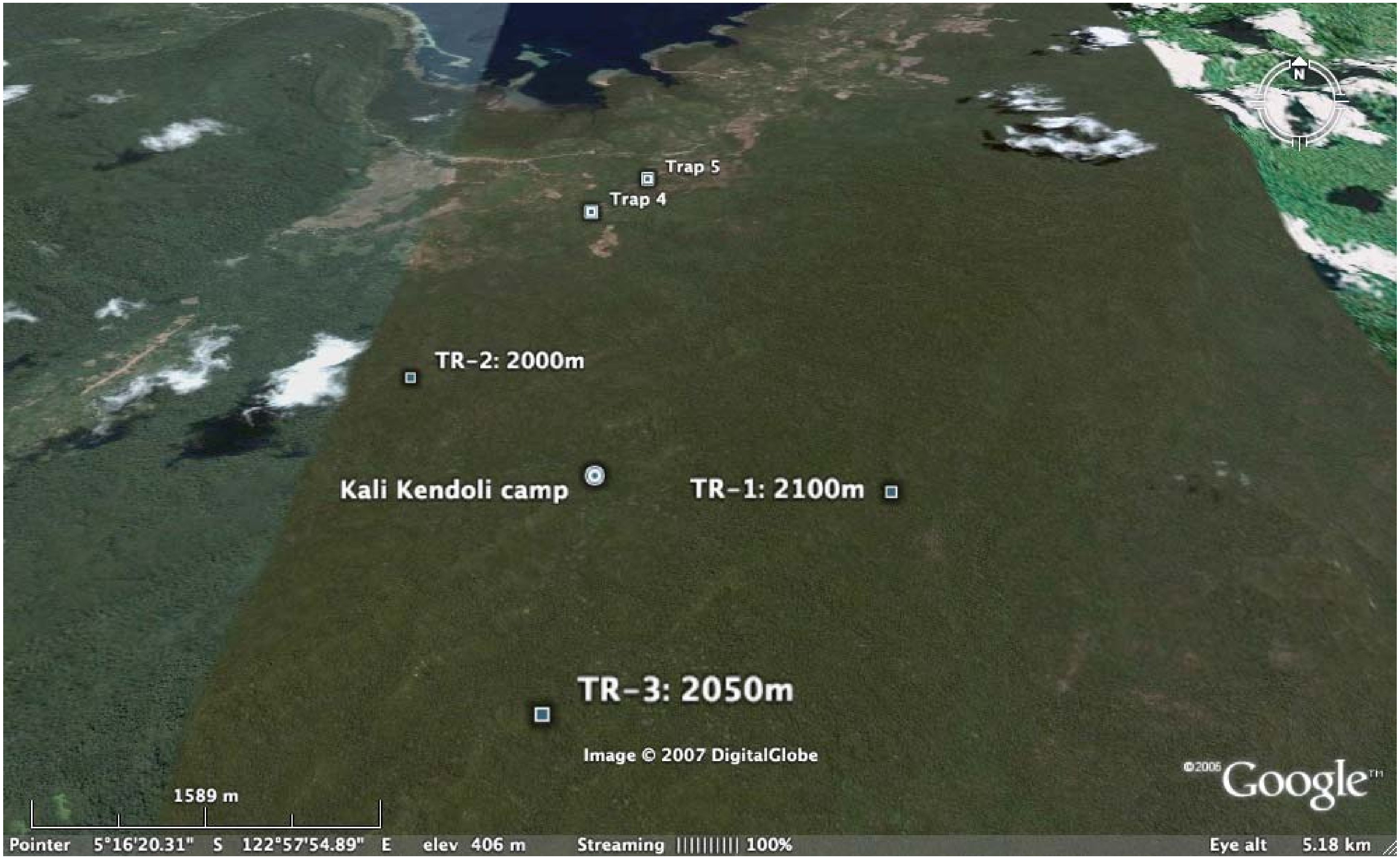
Trap 5
Trap 4
TR-2: 2000m
Kali Kendoli camp
TR-1: 2100m
TR-3: 2050m
Image © 2007 DigitalGlobe
©2006 Google™
N
1589 m
Pointer 5°16'20.31" S 122°57'54.89" E elev 406 m Streaming |||||||||| 100% Eye alt 5.18 km

**Figure 2.8**

# Chapter Three

## Morphological divergence and stasis in 9-kyr-old allopatric populations of Sulawesi booted macaques (Cercopithecidae: *Macaca ochreata*).

### I. Body size, adult allometry and sexual dimorphism

## Abstract

The macaques of Sulawesi island, Indonesia, are thought to represent the greatest spatial concentration of morphological diversity within the genus *Macaca.* Much diversification in the wild occurs via ecological selection, yet the Sulawesi macaques seem poorly-differentiated with respect to trophic morphology, and have experienced long-term isolation in a predator-poor environment. It is currently unclear, however, which traits account for most of the variability, and how quickly change has occurred in each aspect of Sulawesi macaques' morphology—body size, secondary sexual traits, limb proportions, facial shape, body color, and so on. This study quantifies trait-by-trait divergence and stasis in the only pair of Sulawesi macaque populations whose evolutionary history is well-known: the booted macaque, *Macaca ochreata sensu lato*. For the purposes of this dissertation, I focus upon size, proportions, and growth of the body, and certain male secondary-sexual traits; data on other traits such as facial shape and body color, along with more detailed ecological data, will be analyzed and included in future papers.

Within *M. ochreata*, one subspecific population (*M. o. brunnescens*) occurs only on a pair of land-bridge islands (Buton and Muna) whose area is small relative to the peninsular southeast Sulawesi "mainland." According to the island rule, *brunnescens* should have become smaller than *ochreata*. Nevertheless, it appears that (among adults) the size and sexual dimorphism of the body as a whole and of the canine teeth have remained stable during the ca. 9 kyr separation of these two populations. Since there are no differences between the predators and competitors present on the mainland and the land-bridge islands, it seems that mild differences in primary forest productivity alone are not sufficient to cause insular dwarfism in these medium-sized frugivores.

There is, however, evidence for reduced relative head breadth in *M. o. brunnescens* relative to the other macaques of southern Sulawesi. Whether the divergence is due to selection or drift is not currently known, though the latter seems likely for several reasons.

On the other hand, strong sexual dimorphism and strongly positive allometry in male maxillary canine teeth suggest a history of strong but convergent sexual selection within both populations of booted macaques. In combination with evidence that males (but not females) of both populations continue growing in body size after puberty, and grow as fast as food availability allows (see chapter four), a recent history of strong but convergent and possibly stabilizing selection is suggested for body size and especially for maxillary canine size. There is some support for an hypothesis of differential investment in weapons (and agonistic contest competition over mates) in older males, with younger males investing more in testes size (and sperm competition).

It appears that in these two isolated populations, strongly conservative (parallel) selection may be maintaining body size and canine size (and sexual dimorphism thereof) in stasis rather than permitting even stochastic divergence. On the other hand, the possible slight divergence in cranial proportions (head breadth) may have occurred by chance, suggesting that conservative selection does not affect head breadth. When results of chapter three are assessed together with those of chapter four (*vis-a-vis* limb proportions), it would appear that some body proportions are more subject to selective constraints than are others, suggesting that natural selection may as often prevent evolution as promote it.

It further appears that either mild resource limitation (or at least mild differences in forest structure) has not affected natural selection on body size in the insular population, or demographic factors (e.g. population growth rate or effective population size) have not yet permitted a detectable response to selection. This does not mean that the island rule does not apply to primates; rather, I hope this work will make some small contribution toward building an ecological understanding of how the island rule works, and thus how it might affect specific hominin populations.

## Introduction

### *3.1: Prologue to the empirical chapters*

*Overall background*—Over the past few decades paleoanthropologists have uncovered evidence of a great deal of cladogenetic diversity among extinct hominins—yet the human fossil record, like that of most vertebrates, gives us little information about intraspecific diversity and no data about divergence in soft tissues, body color, and so on. Living human populations, moreover, confront us with inter-populational diversity that must have arisen sometime between the appearance of modern human morphology in Africa some 150 kya (Clark et al. 2003; White et al. 2003), and the beginnings of recorded history. Yet we can see that not all hominin traits are equally evolutionarily labile—some seem to be more evolvable than others, though we do not yet know exactly why (Hlusko 2004; Kirschner and Gerhart 1998; Wagner and Altenberg 1996; West-Eberhard 1998).

The effects of phylogeny are more widely appreciated than ever in the biological and anthropological literature (Cheverud et al. 1986; Di Fiore and Rendall 1994; Harcourt et al. 1995). Much emphasis, however, has been placed upon controlling for phylogeny, which is critically important; still, phylogenetic effects can be interesting phenomena of themselves, worthy of direct study.

One obvious starting point is to ask to what extent divergence occurs in a law-like manner (i.e., to what extent its course is predictable). After establishing the regularities of pattern (and, ideally, its mechanistic basis), we can then ask to what extent human divergence and inter-population diversification followed the same pattern, and to what extent it is unique. Another clearly logical starting point is to focus primarily upon morphological features, whose genetic basis is not entirely obscure, and is becoming clearer lately due to advances in developmental biology, such as advances in understanding the regulation of expression of *bmp*, bone morphogenetic protein (e.g., Sears et al. 2006).

To the extent that evolutionary divergence (at least among mammals) is predictable, we can then ask what made human evolution unique as a process, since obviously the outcome was quite unique. Such an approach—which will lead to a more parsimonious interpretation of human evolution in some of its respects (those that are law-like) and an agnostic interpretation in other respects—is more likely to succeed than are the less parsimonious possibilities, e.g. post-hoc hypotheses that apply only to humans, hominins or some other monophyletic entity. For example, more comparative information about differential evolvability of traits on short time scales (this chapter and chapter five) could deepen our understanding of the early evolutionary divergence (cladogenesis) and subsequent inter-population diversification of our species, as well as the apparent divergence of certain isolated hominin populations that may have experienced rapid diversification, such as contemporary pygmoid populations, dwarfed populations on Flores and Palau, and *Homo erectus sensu stricto* (Berger et al. 2008; Brown et al. 2004; Jacob et al. 2006; Morwood et al. 2005; Richards 2006; Swisher et al. 1994; Walker and Hamilton 2008). Likewise, data on the effects of habitat differences upon growth and sexual dimorphism could help to interpret body size data from fossils by providing a set of expectations about within-species variability and potential error in estimation of species averages based upon small samples.

In short, I ask: are there more rules to evolution than are currently recognized? Upon what mechanistic phenomena are the rules based? To what extent did human evolution (divergence from other hominins, as well as subsequent interpopulation diversification) follow these identifiable rules? I believe that my suggested approach could play an important supplemental role in answering questions about human evolution, and about evolution in general. While convincing tests of the many adaptive hypotheses for bipedalism remain elusive, the chromatic diversity of many vertebrates (especially primates) offers hope of understanding why humans come in so many hues, for example.

*The Sulawesi macaques*—It is clear that the Sulawesi macaques have diverged from one another in color and form of the hair, facial shape, and perhaps in other traits (Albrecht 1978; Fooden 1969; Hamada et al. 1988; Hill 1974). What is unclear is the relative magnitude of change that has occurred in various different somatic traits, and the time scale on which those changes occurred; in fact, the phyletic interrelationships of the Sulawesi macaques are still unclear in many cases, with somewhat conflicting data from morphology, nuclear DNA and mitochondrial DNA, further complicated by Sulawesi's highly complex Neogene geological history (see below). I have therefore chosen to study the earliest stage of morphological divergence among Sulawesi macaques, represented by two reciprocally-monophyletic sister populations of Sulawesi booted macaques (*Macaca ochreta*) (Groves 1980) that are thought to have become separated from one another during the early Holocene (see below). The relatively short time scale makes questions of evolutionary rate more meaningful in a synchronic study, as there is less potential for averaging of rapid change and stasis (Hendry and Kinnison 1999), and also somewhat reduces potential complications such as massive geological changes, serially reticulate gene flow, and ambiguous molecular-phylogeny reconstructions, which are more likely to occur over longer time scales.

This is the first study to quantitatively examine whole-body morphology in adult Sulawesi booted macaques, and also the first to examine free-ranging juveniles; it builds upon previous whole-body studies of juvenile pet monkeys (Hamada et al. 1985; Hamada et al. 1988; Watanabe et al. 1985) and a studies of crania by Fooden (1969) and Albrecht (1978). This may also represent the first study to present growth data for Sulawesi booted macaques and possibly of any Sulawesi macaque, albeit based upon cross-sectional, ordinal age categories (see chapter four). Preliminary results for one of the populations, *M. o. ochreata*, were reported by Schillaci & Stallmann (2005), though the preliminary paper used a less-detailed age-ranking system for adults, and thus could not examine post-pubertal growth; body color, sexual swellings, and facial shape—the traits to be examined in chapter five—also were not included in the analysis. There likewise is a dearth of data comparing ecology and habitat usage in these two populations, except for a short-term study of time budgets in crop-raiding village monkeys (Kilner 2001), as well as two Indonesian master's theses that are all but impossible to obtain. Sulawesi macaques' apparently unspecialized frugivorous diets, and Sulawesi's relatively homogeneous predator and competitor communities, suggest that ecological selection may not have played a major role in diversification of the Sulawesi macaques (Albrecht

1978; Bynum 1999; Fooden 1969; Kinnaird et al. 1999; Matsumura 1991; O'Brien and Kinnaird 1997).

The point of this dissertation is to quantify divergence and stasis in various traits, in two isolated populations living as naturally as possible (within limits of methodology); to ask which traits are divergent, and which are static, and to what extent; and finally to ask what processes may have caused the observed patterns. While a study of a single pair of populations is hardly a basis for generalizations, it is my hope that the present study will contribute data relevant for (incrementally) advancing our understanding of the processes of evolutionary diversification and stasis on geologically short time scales.

I plan future work with other mammalian populations in insular southeast Asia, with a view to replication of the present rather limited study. I believe that a balance of replication across many populations and regions, with detailed comparisions (such as the present one) comprising a subset of those replications (the others being mostly studies of museum specimens), will be the most productive long-term approach. Ultimately the present study will form part of a large-scale effort that integrates morphology, ecology, and historical physical geography in an effort to understand evolutionary patterns, including the burgeoning hominin fossil record.

### *3.2: The questions to be asked in this chapter*

*Question one:* Have subtle differences in seasonality of rainfall, with concomitant differences in food abundance, led to divergence in body size (dwarfing) in the insular population? Since rainfall on Buton and Muna islands is more seasonal, on average, than that of peninsular southeast Sulawesi, primary productivity of the forest should be somewhat lower on Buton and Muna. The resource-limitation hypothesis of insular dwarfism predicts that populations trapped in resource-poor habitats should evolve smaller body sizes.

*Question two*: Have *ochreata* and *brunnescens* diverged in any relative body dimensions, and if so, which dimensions?

*Question three:* If stasis is observed between the two populations, is stasis enforced by on-going convergent selection (sexual or ecological, or both) within each population?

This chapter deals only with adult body size (and canine size), and adult (post-pubertal) ontogenetic allometry, mostly in males. The following chapter will address divergence and stasis in overall growth and relative (allometric) growth throughout the life cycle among Sulawesi macaque populations. The final chapter will address differences in evolutionary rate among multiple morphological traits.

### *3.3: Evolutionary divergence in body size and sexual dimorphism thereof*

*The island rule: validity and generality*—Foster (1964) noted that large mammals (such as artiodactyls) are likely to become smaller when isolated on islands (insular dwarfism), while small animals (such as rodents) are likely to increase in body size when so isolated. Later, Lomolino (1985; 2005) noted that the degree of dwarfism (as a proportion of the "normal," ancestral body size for a given genus or other taxon) is directly proportional to ancestral body size; the larger a given taxon is, the greater the proportional degree of dwarfism on islands. The island rule seems to be robust, as insular dwarfism occurs in birds as well as mammals (Clegg and Owens 2002), and seems to have affected even dinosaurs isolated on paleo-islands (Lomolino et al. 2006).

The pivot point of body mass, at which no insular change occurs, seems to be 1 kg; mammals over about 5 kg are expected to show at least some dwarfism on islands (Lomolino 1985; Lomolino 2005), and modest-sized primates are not immune from the mammalian trend (Bromham and Cardillo 2007). Since Sulawesi booted macaques have adult body masses of well over 1 kg, I will henceforth restrict my discussion to insular dwarfism and will not further consider insular gigantism (the latter is anyway rather a weak statistical trend, compared to insular dwarfism, and occurs mostly in rodents: Lomolino 2005).

There has been some controversy regarding the generality of the island rule, particularly among mammals. Meiri et al. (2004) have used data from carnivores, for example, to argue that the island rule is not widespread among mammals. I follow Lomolino (2005), however, in arguing that the data of Meiri et al. are in fact consistent with the island rule. Meiri et al. (2006) critique studies that have found support for the island rule, but in doing so they make a number of incorrect statistical assumptions that have to do with statistical significance, power, types of error and so on. Meiri et al. (2006) report that they obtained significant results "only with one-tailed tests," and that "a negative correlation between island : mainland size ratio and body mass was significant ($P = 0.047$, one-tailed) only when we use [sic] populations with $n \geq 10$ specimens from both islands and mainlands." (Meiri et al. 2006: 1572).

First of all, Meiri et al. apparently rely upon inferential statistical tests to provide a simple either-or decision rule about significance. While that interpretation is certainly the most common in the biological literature, its logical soundness is very questionable (Gigerenzer et al. 2004). Second, Meiri et al. do not balance the risk of type II statistical error (missing a truly significant difference due to a lack of power) with that of type I error (mistaken detection of a trend that is not real); conventional statistical tests minimize type I error but ignore type II, thus care must be taken in the interpretation of these tests. Third, Meiri et al. note that they obtained (arbitrarily) significant results only when they compared populations for which they had a reasonable amount of within-population data (at least ten specimens per population). That is entirely to be expected, since larger within-population sample sizes reduce the amount of noise in the data and the error of the data point in question. In other words, if one uses a single individual or a small handful of them to represent an entire species' mean, there will inevitably be more error for that data point and more noise in the data overall, possibly obscuring real trends.

Finally, Meiri et al. (2006) seem to pass over one of Lomolino's (2005) main points—that the island rule is a rather subtle trend that is obscured by much noise (see

Lomolino 2005: his fig. 1), but the pattern is nonetheless robust. In order to determine whether a subtle pattern is both subtle and real, or only illusory, one must absolutely minimize noise and error when looking for evidence of a robust pattern. Meiri et al.'s (2006) regressions, however, are simply plots of island body sizes vs. mainland body sizes among all mammals, not differences between ancestor-descendant sister populations. Meiri et al. (2006) defend this strategy by claiming that "if the island rule is as prevalent as claimed, we should expect at least some pattern in a plot spanning taxa from shrews to elephants." The most relevant issue, however, is not the range of size variability (which is also important), but noise around the regression line, which of course will be massively introduced by ignoring sister-population relationships. That noise will then increase the width of the regression slope's confidence interval—and Meiri et al. (2006) ultimately rejected the island rule based on the 95% confidence interval's overlap with one.

Another critical issue when using inter-specific regression models arises as well: What exactly is the regression measuring? When differences between ancestor-descendant populations are plotted, the regression shows the degree of evolutionary change in body size as a function of original body size (e.g., Lomolino 2005: his fig. 1). When one plots data points that represent static individual species values, the resulting regression has nothing to do with evolutionary change (cf. Gould 1975a).

Thus the main problem with Meiri et al.'s (2006) critique of the island rule is that they seem not to consider the possibility that subtle but nonetheless biologically significant patterns can be obscured by noise introduced by certain types of very broad analyses. One might say that statistical significance (with its disporportionate emphasis on minimizing type I error, and its frequent interpretation as a clear-cut decision rule) should not be allowed to trump possible biological significance, especially when there is so much noise in the data.

I argue, then, that the island rule is robust and very real, but subtle and rather noisy—as would be expected when examining body size, which can be affected by so many factors, whether evolutionary or environmental (see, e.g., chapter four). Most relevant for this chapter's analysis was the study by Bromham and Cardillo (2007), who found that within the order Primates (taking into account island-mainland sister population relationships), the island rule is subtle yet robust (as argued above). While Bromham and Cardillo's (2007) regressions are rather noisy, the credibility of their results is greatly strengthened by their finding that all insular primate populations whose mainland relatives weigh < 5 kg are larger than their mainland ancestors, and all those from populations of > 5 kg have become smaller on islands.

*The island rule and evolutionary ecology*—From the beginning, Foster (1964) pointed out that the island rule phenomenon must be caused by some ecological factor that tends to occur in insular settings. Foster (1964) suggested that food limitation (usually called "resource limitation" in the literature) could explain insular dwarfism in large taxa, since fewer resources may be present on islands compared to the mainland. Insular food limitation would also explain, for example, why a continental population of fossil dwarf rhinoceroses apparently switched to a browsing niche (Prothero and Sereno 1982); it would explain why the anoas of Sulawesi (*Bubalus* [*Anoa*] spp.) are the only forest-living, browsing buffalo in Asia and are also the smallest Asian buffalo (as

Sulawesi lacks primary savannas and has very limited wetlands); and it would explain why among carnivores, only those that are limited to terrestrial prey (i.e. those prey that can be found on the island itself) show the expected degree of dwarism for their body size (Lomolino 2005). On the other hand, the anoa relative *Bubalus mindorensis* (endemic to Mindoro island, Philippines) is similarly dwarfed relative to continental *Bubalus*, yet is reported to be a grazer. Still, the original vegetation of Mindoro is thought to have been dipterocarp forest—the current grasslands are probably secondary, thus grazing may be a habit adopted facultatively in the face of anthropogenic pressures. Whether there may have been natural grasslands in Wallacea during the dry spells of the Pleistocene is not currently known with certainty, though if they did exist they would have been more likely to exist in southern Sulawesi than in north-central Sulawesi or on Mindoro (Bird et al. 2005; Heaney 1991).

Foster (1964) also pointed out that release from predation could lead to dwarfism; the largest animals have the fewest predators, and thus are most likely to find themselves without predators on islands—at least on oceanic islands colonized by sweepstakes dispersal across water, and on land-bridge islands too resource-poor to support large predators' large home ranges. Release from predation could then remove one of the principal advantages of large body size. Predator release is probably a better explanation for insular gigantism in rodents, however, than it is for dwarfism in large animals, since it is easy to see how reduced predation could lead to larger body sizes through a relaxation of selection for faster maturation (and smaller size at maturity). For large animals, predation release could lead to smaller body sizes if there is non-predator-related selection for small size; on the other hand, it could lead to larger sizes on predator-free islands as well, due to life-history mechanisms (lower extrinsic mortality).

Aside from release from predation, release from interspecific competition could be a cause of the island rule. Again, however, as with predation release, it is easier to see how release from competition could possibly lead to insular gigantism in small species, while the relevance for dwarfing in larger taxa is more obscure (but see Prothero and Sereno 1982).

Most important, though, are lines of independent evidence that suggest a role for resource limitation in dwarfing: *viz.*, dwarfed populations that live in measurably resource-poor environments yet do not live on islands, and do not experience different predation regimes from non-dwarfed populations. Cavalli-Sforza (1986) has pointed out that similar instances of dwarfism occur in contemporary human populations that live in tropical forests, whether on islands (as, e.g., certain southeast Asian negrito populations) or on large continents (e.g., African pygmies), and proposed that tropical forests could be considered "ecological islands" that encourage dwarfing via the same mechanisms that lead to insular dwarfism. It is also true that accessible energy is extremely limited in tropical forests. Height in pygmies seems to have a simple genetic basis (Hasstedt 1986), and pygmies' amino acid profiles show signs of mild protein malnutrition (Pennetti et al. 1986), which is consistent with the difficulty of obtaining game (which is mostly arboreal) in tropical forests.

While Cavalli-Sforza (1986) interpreted pygmies' time budgets (45% of their time is spent collecting and processing food) to mean that pygmies cannot be food-limited, current optimal-foraging theory shows that maximal time allocation to foraging is not expected under even extreme food limitation; time allocation is always sensitive to net energy returns (Hill and Hurtado 1996: 319-320). Cavalli-Sforza's interpretation is further undermined by the amino acid research by Pennetti et al. (1986). Thus it seems possible that pygmies are food limited, they are food-limited because of their long-term tropical forest environment, and such an environment probably mimics the food-limited conditions of islands (tropical and non-tropical).

The rate of divergence in body size of continental dwarfs (those on "ecological islands") may be very slow, however (depending also upon the intensity of ecological selection), due to greater gene flow from outside populations, relative to island populations In the case of seafaring *H. sapiens* of the past 40 kyr, however, geographical insularity may make little difference in gene flow—indeed in spite of modern humans' mobility, there may be some evidence for insular dwarfism in humans of the past few kyr (Berger et al. 2008). Such a difference in gene flow would account for the relative rarity of continental dwarfism as opposed to insular dwarfism (in fossil rhinos, humans, and other taxa), if selection were weak relative to gene flow (Foster 1964). That possibility is strengthened by the observation of widespread dwarfism within truly isolated habitat "islands" such as mountaintops in the American Southwest (Marquet and Taper 1998). Among African groups, pygmies (along with San) have experienced very minimal gene flow from Arabs and other outside groups; thus they may better reflect *in situ* adaptation to their environment than do most other African groups (Cavalli-Sforza 1986).

Of course, the problem with the "tropical forests as continental islands" hypothesis is that it is based largely upon patterns occurring within one species, humans—there is very little comparative data on the correlates of insular dwarfism in non-humans, though there are occasional non-human examples such as the aforementioned pygmy rhinos. For example, gorillas are restricted entirely to tropical forest—one subspecies is further isolated on mountaintops—and yet gorillas are the largest of all primates.

Much stronger support for the food-limitation hypothesis of dwarfism comes from the deep sea (McClain et al. 2006). Deep-sea gastropods are thought to have migrated to their present habitat from shallower coastal waters during the past 30 myr. The benthic environment is extremely resource-poor, however, due to the lack of sunlight preventing direct primary production; and remineralization of food items as they fall through the water column toward the benthic level. Dwarfism is, accordingly, observed in deep-sea gastropods derived from relatively large-bodied coastal taxa, even though the benthic environment is characterized by very high predation; ancestrally smaller taxa show a tendency toward gigantism (McClain et al. 2006). Furthermore, as with mammals (Lomolino 2005), deep-sea gastropods' size shifts are proportionally greater in more extreme-sized species (McClain et al. 2006). Meanwhile, gastropods in shallow-water areas are noted for their lack of interspecific competition (McClain et al. 2006). This is striking, totally independent evidence in support of the resource-limitation hypothesis and against the predation-release and competition-release hypotheses.

Finally, there is evidence for repeated, convergent evolution of flightlessness in certain bird species after they colonized islands (Diamond 1991), and their flightless condition has been interpreted as an adaptation to low energy availability on the islands (McNab 1994). When the deep-sea evidence is considered together with flighlessness in birds, we have powerful independent evidence that dwarfism on islands does indeed result from food limitation. First, we have a similar evolutionary response (dwarfism) in a similarly resource-poor but non-insular environment (the deep sea). Second, there is a very different evolutionary response (flightlessness) in an insular environment that has similar energetic consequences, suggesting again that islands are resource-poor and that that condition leads to diverse evolutionary consequences. Of course, it is also possible that flightlessness could have resulted from relaxed selection in the absence of predators. The relaxed-selection hypothesis and the energy-saving hypothesis are not mutually exclusive, however; it is quite possible that selection for flight (possibly for escape from predators) and selection against flight (to save energy) oppose one another; when predators are absent and food is limited, the balance could be tipped toward flightlessness as an optimal phenotype. This question clearly needs further investigation, however.

Taken together, the deep-sea gastropod and insular bird evidence suggest that the resource limitation that leads to insular dwarfism may be an absolute limitation of resources, rather than, as assumed by Lomolino (2005), one caused by a greater density of conspecific competitors on islands (McClain et al. 2006). In fact it seems to me that any species capable of reasonably long-term existence on an island will have small home range size relative to the size of the island; the range sizes (packing of individuals within a species) should not respond to the geographic size or contours of the island, as any individual animal (or those individuals that determine group movement patterns, in gregarious species) will adjust its ranging behavior in response to immediately perceived food availability at a given time, relative to the additional energy expenditure needed to travel farther.

How would an insular environment lead to absolute food limitation? In some cases, insular climates may be more extreme in some way than mainland ones, thus limiting the diversity or overall productivity of the plant community of the island (Nakamura et al. 2007); in other cases, the number of different plant communities (savanna, wetland, lowland forest, montane forest, etc.) may be limited by the sheer size of the island as well as the climatic, topographic and hydrological homogeneity that results from its size. While care must be taken not to assume that current island conditions reflect long-term conditions (e.g., what is now forest may have been savanna during Pleistocene glacial periods), the present study is restricted to the Holocene period which is relatively climatically stable.

The missing puzzle piece seems to be direct measurement of environmental differences between insular (or resource-poor non-insular) environments and mainland environments, combined with quantitative measurement of size differences on a known time scale. For example, Anderson and Handley's (2002) study of sloths claimed to examine land-bridge islands of known and distinct ages (though their methods for doing so, in an earlier paper they cited, are given only as "in litt."), but included essentially no information on ecological differences among the islands and between the islands and the mainland. In the present study I will attempt to provide more detailed environmental information about southeast Sulawesi than is normally given in studies of insular body size, though it is mostly from the published literature and is still not as detailed as I would prefer.

*Size transitions in the Hominini*—The transition from *Australopithecus* to *Homo ergaster* was marked by a substantial increase in body size (McHenry and Coffing 2000: their table 1). The increase in body size was accompanied by reduced curvature of the proximal phalanges of the hands and feet, a change from a climbing-adapted, ape-like thorax to a barrel-shaped thorax, and a reduction in robusticity of the humerus, as well as changes in limb proportions, all of which probably indicate reduced climbing behavior (McHenry and Coffing 2000; McHenry 1994). On the other hand, it is also possible that changes in limb proportions seem to occcur together with changes in body size (longer arms with shorter bodies) because of allometric growth trends, as observed in some modern pygmy populations (Richards 2006).

It is possible that increasing specialization for terrestrial locomotion made larger body sizes possible, since large animals can incur large locomotor costs when engaging in vertical movement of the body, such as climbing, or explosive movements such as leaping. That possibility would accord quite parsimoniously with the mammalian trend of arboreality associated with smaller body size, which may be caused by the negative allometry of both muscular power and maximum aerobic capacity relative to body mass (Dooman and Vandenburgh 2000; Hill 1950; Marden 1994; Stallmann and Harcourt 2006; Taylor et al. 1972; Taylor et al. 1981; Watts et al. 2003). At any rate, it is clear that divergence in body size has adaptive consequences, and that changes in body size were significant components of the evolutionary diversification of hominins.

More recently, interest in rapid evolutionary change in body size among hominins has been piqued by the discovery of a terminal Pleistocene population of small-bodied hominins in Flores, Indonesia (Brown et al. 2004) and a similar Holocene population in

Palau, Micronesia (Berger et al. 2008). The Flores population has been assigned tentatively to a new species, "Homo floresiensis," while the Palau population has been postulated as a dwarfed population within *Homo sapiens*, but both taxonomic assignments are controversial due to the morphology of the populations, which (apparently) includes both primitive and uniquely derived traits. These recent discoveries have also motivated researchers to speculate about the possibility of insular dwarfism, or more broadly evolutionary dwarfism (as opposed to environment-related plasticity and individual abnormalities) occurring in hominins (e.g., Lahr and Foley 2004).

Most relevant for the present paper are the questions of (1) the time scale on which insular dwarfism normally occurs in primates, or more broadly, the evolutionary lability of body size as compared to other traits; and (2) the ecological circumstances that actually lead to insular dwarfism. While the Flores population has been dated fairly securely, no one has any idea how long the hominins in question lived on Flores nor whether they descended from *Homo erectus sensu stricto*, vs. some other, possibly earlier hominin population, as the Flores population is very small-brained and small-bodied for *Homo* (Brown et al. 2004; Morwood et al. 2005). The Flores hominins seem a particularly odd fit as supposedly insularly-dwarfed *Homo erectus* when one considers that the normal brain-to-body negative interspecific allometry for mammals would have to be reversed in order to accomodate the Flores hominins as dwarfed *Homo* (Jerison 1970).

On the other hand, leaving the brain aside, a highly detailed multivariate allometric study of the Flores cranium (LB1) shows that the cranium (exclusively of brain size) clusters closest to African and eastern European *H. ergaster*, with slightly more distant affinities to *H. erectus sensu stricto*, and to *Australopithecus*; it appears quite unlike later *Homo* (*H. neanderthalensis and H. sapiens*) when shape differences are examined without regard to size. Bivariate analyses show that the Flores hominins seem most divergent from *H. sapiens* in maxillary prognathism and occipital breadth (Gordon et al. 2008). While the comparative sample of Recent *H. sapiens* crania used in Gordon et al.'s study is extremely large and widespread, it is unclear whether it includes the Australomelanesian population studied by Jacob et al. Still, the multivariate allometric study of the Flores cranium by Gordon et al. is the most detailed to date, and its authors interpret its results as supporting the hypothesis that the Flores hominin is in fact a new species, albeit possibly a relict of very early *Homo* colonization of eastern Asia, not a short-term offshoot of *H. erectus sensu stricto*.

The analysis by Gordon et al. used an extremely broad comparative sample (encompassing normal human variability from virtually all major regions of the earth), as did similar analyses of the Flores specimens. One problem with such analyses, however, is that they fail to consider the many forms of dwarfism known in modern humans, some of which can affect facial or body traits in ways that seem phylogenetic. For example, Richards (2006) painstakingly demonstrates that most (and possibly all) of the postcranial characters identified by Morwood et al. are actually found in contemporary pygmies—for example, torsion of the humeral head. Richards (2006) also points out that Morwood et al.'s (Morwood et al. 2005) comparison of Flores' humeral head to that of *Hylobates* is incorrect, that the degree of torsion is within the modern human range (though extreme for non-pygmies) and that the specimen's humeral head is damaged anyway. Furthermore, the more primitive limb proportions (relatively longer arms than in *H.*

*sapiens*) claimed for Flores by Morwood et al. are actually found in modern pygmy populations, and are consistent with broad, intraspecific allometric patterns (Richards 2006)—a fact that calls into question the imputation of divergent ecological adaptation for Flores. The body shape of modern African pygmies, moreover, was once thought to be phyletically primitive or to reflect special climatic adaptations; now these shape differences are generally agreed to result from relatively premature truncation of growth, and the allometric consequences thereof (Shea and Bailey 1996).

Moving to the cranium itself, Richards (2006) points out that various types of dwarfism (whether in rare, abnormal individuals, and in pygmy populations) often result in differences in facial structure, which could possibly mimic phylogenetic differences. As Richards puts it quite concisely, abnormal dwarfism and pygmy dwarfism "are worthy of investigation before entertaining alternatives requiring deeper phylogenetic divisions." Richards (2006) argues that Brown et al. (2004) gave such short shrift to the more parsimonious non-phylogenetic hypotheses, that they did not bother to look up the currently correct name of a type of microcephalic dwarfism that they dismissed. Aside from that, Brown et al. did not touch upon the other three hundred or so genetic etiologies that can lead to primary microcephaly in humans (Richards 2006). Richards also points out that the brain-endocast research conducted by Falk (cited in Richards 2006), which allegedly supported specific status for the Flores hominin, also used outdated terminology, seemed completely uninformed by any up-to-date knowledge about either microcephaly or dwarfism, and was based on comparison with a single brain from a highly abnormal ten-year-old boy.

Another major problem is that, in using an extremely broad sample, Gordon et al. (2008) and similar studies perhaps exaggerate the degree of divergence of the Flores specimens, where a more regionally-restricted comparative sample might have been more appropriate. Such a narrower, deeper sub-regional sample can reveal various traits that normally occur at low but significant frequency in those sub-regions, but would not show up in a very broad comparative sample. In fact, even the prehistoric Holocene populations of *H. sapiens* found in the same cave with the more famous Flores hominins have not been described, as Richards (2006) points out, in spite of their obvious relevance for interpretation of their famous but small-brained cave-mate. Jacob et al. (2006) provide seemingly strong evidence that the allegedly primitive craniofacial traits of the Flores population that were identified by Brown et al. (2004)—for example, the lack of a chin—are actually regional Australomelanesian characters that persist in Flores people to this day, and that the one cranium recovered to date is probably from a microcephalic individual. Such a possibility suggests that perhaps both the Flores and Palau populations result from very rapid instraspecific dwarfing in the face of gene flow, not long-term isolation—but here again, more comparative data on the evolutionary lability of body size, facial shape and other traits would be extremely informative in evaluating the realism of the various hypotheses.

It seems, however, that most studies on the Flores hominins have considered only two alternative hypotheses about this population: microcephalic *H. sapiens*, or normal cousin of *H. erectus sensu lato*. The possibility that this one individual (only one complete cranium has thus far been recovered) could have been an abonormal microcephalic, yet also belonging to a previously unknown species of early *Homo* descended from *H. ergaster*, does not seem to have been seriously considered. Yet surely microcephaly must have occurred in non-human hominin populations. Since paleoanthropology must make the most of very small samples, a single individual sometimes is assumed to represent species-typical morphology. While Morwood et al.'s (2005) paper described postcranial and additional mandibular remains—and argued that the Flores morphology had now been confirmed to be representative of an entire population—in fact nothing can be said about the cranial morphology of the Flores hominin population as a whole. There is still only *one* more or less complete cranium, and its limbs, while representative of more than one individual, are not unlike those of some living pygmies (Richards 2006).

The Palau population, however, seems to suggest much more rapid dwarfing as well as other morphological changes such as divergence in facial structure. While full crania from the Palau population have yet to be recovered, preserved frontal bones from two individuals suggest that the population is markedly divergent in frontal-bone morphology from other modern human populations, despite having lived only a few thousand years ago, with at least some gene flow from large-bodied, gracile-faced mainland populations. While morphology of the glabella and supraorbital torus may fall (barely) within the range of living humans, the interorbital breadth exhibited by this population is extraordinary indeed, given its temporal context. The Palau dwarf population is replaced, moreover, by large-bodied and possibly more cognitively-advanced (inferred from the presence of grave goods) population of normal-sized modern humans within only about 300 years (Berger et al. 2008).

Berger et al. (2008) have nonetheless suggested that the Palau specimens represent a population of *H. sapiens* that was subject to rapid insular dwarfing (Foster 1964) or perhaps a founder effect (genetic drift); they maintain that the aforementioned primitive craniofacial features (apparently including the extraordinary interorbital breadth) could have been caused by "possible pleiotropic or epigenetic correlates of developmental programs of small body size." Clearly, additional information on the developmental correlates of primitive facial structure in combination with comparative data on the evolutionary lability of both facial structures and overall body size would be helpful in evaluating Berger et al.'s (2008) hypothesis, although the evidence provided by Richard (2006) does provide some support for it. For example, if tooth size is less evolutionarily labile than body size, this might explain the absence or abnormal rotation of third molars observed in the Palau hominin population (Berger et al. 2008; Lucas 2006), which would support the hypothesis of rapid insular dwarfing, though not necessarily the hypothesis that the Palau population is derived from modern humans.

These new data on insular hominin populations raise a few important questions. Was the Palau population derived relatively rapidly from mainland populations of *H. sapiens* with typically modern morphology—or were they more likely descended from some ancient, long-isolated population of earlier hominins? Did the Palau dwarfs evolve into large-bodied, gracile-faced people in only a few hundred years, as is implied by Berger et al. (2008) with their assessment of "temporal variation in body size," or were they replaced by modern immigrants from the mainland or from other islands? Is the former scenario of extremely rapid evolution indeed possible, within reason?

Hiernaux (1977, cited in Richards 2006) suggested that African pygmies' divergence in body size compared to other Africans who lived in similar rainforest environments could be due to the pygmies' having spent a longer time in rainforest habitat; likewise Anderson and Handley (Anderson and Handley Jr. 2002) suggest that insular dwarfism in sloths tends to gradually increase over a time scale of several thousand years, while others (Lister 1989; Millien 2006) have shown that other mammal species such as red deer are capable of dwarfing within a few generations. So, are primates (and hominins in particular) sloth-like or deer-like in their rate of body size evolution? Lomolino (2005) described continuous, monotonic differences in realized insular body size, dependent upon body mass of the ancestral population; could ancestral body size similarly affect the rate of approach to the realized insular size? Additionally, more comparative data on the relative contributions of environment-caused plasticity vs. evolutionary genetic divergence may provide a more solid baseline against which to evaluate hypotheses of divergence in body size and other morphological traits (e.g., Altmann and Alberts 2005; Harcourt 2007; Turner et al. 1997; this chapter).

More extensive comparative data will thus be helpful to interpret (in the broadest sense, not just the phylogenetic sense) these newly-discovered fossil populations; in particular, we need to know more about the evolutionary lability (change per generation) of various traits, such as body size, sexual dimorphism, brain size and facial shape, in a broad spectrum of mammal species. We also need to know much more about the ecological correlates of slow change, random change and no change in body size and in other traits. What are some specific ecological circumstances that might have led to dwarfism in certain fossil and contemporary hominin populations? What intensity of ecological selection is necessary to overcome the influence of gene flow, in cases where some gene flow exists? How important, for example, are differences in ecological selection regimes for divergence in, say, body size, as opposed to body color? Surely the ecological causes of dwarfism are at least as interesting as the place of any given population in the hominin family tree.

### *3.4: Divergence in allometric proportions and sexual dimorphism of body parts*

One normally expects an isometric, or linear, relationship between the size of any body part and overall body size. Body parts often vary in their scaling relative to overall body size, however. Some parts or traits are negatively allometric, proportionally larger in smaller individuals; others are positively allometric, proportionally larger in larger individuals. Allometries show a certain predictability or regularity among species, whether one compares the slopes of within-species regression models, or whether one actually plots species or genus averages in an interspecific regression analysis to find a single interspecific slope (Cheverud 1982; Huxley 1932). Due to these striking interspecific regularities, allometric patterns have usually been thought to reflect underlying developmental constraints that can bias the direction of evolution within a given lineage (Gould 1966).

It is important, however, to distinguish interspecific from intraspecific allometry, and to delineate the proper uses of each. Interspecific allometries (each data point representing the average adult in a given species or other taxon) suggest functional-morphological constraints, but cannot be used to infer evolutionary trajectories or mechanisms. To quote Gould (1975a: 277), interspecific allometry "does not express evolutionary variation within an evolving group. It can be used to predict blueprints for adaptation; it does not represent the path traveled by any organism toward that adaptation." In other words, interspecific allometric patterns represent the long-term outcome of evolution and work best as a starting point for suggesting new hypotheses.

For detailed information about evolutionary mechanisms, we must consider intraspecific allometry, of which there are two types. First, age-independent or static intraspecific allometries depict variation among individuals rather than among age groups; thus they are often thought to represent variation that is immediately available to selection. Second, ontogenetic allometries represent relative growth rates of one or more body parts, relative to overall body size (Gould 1966; Gould 1975a). The latter kind of allometry is useful for comparing the developmental trajectories of different populations or species.

Allometry may be caused by functional constraints. Functional constraints result from natural selection and depend upon the adaptive needs of an organism at a certain body size (Gould 1975b). While allometry has been very well-studied statistically, the underlying mechanisms and etiologies are still poorly-known.

*Allometry and selection*—In animals from beetles to mammals, male traits used in competitive male-male displays, and sometimes in fighting, tend to show especially high positive allometry (extinct giant deer: Gould 1973; 1974; invertebrates: Kelly 2005 and literature cited therein); penises also sometimes show positive allometry in mammals such as African mole rats, harp seals and bats (Kinahan et al. 2007; Lüpold et al. 2004;

Miller and Burton 2001). In few cases, however, is there strong evidence for both positive allometry and on-going sexual selection. In water striders (*Aquarius remigis*), Bertin and Fairbairn (2007) found low variability and negative allometry in genitalia, in spite of independent evidence of strong, on-going directional sexual selection. It should be noted, however, that the pattern of negative genital allometry is quite widespread among invertebrates (Kelly 2005) in spite of presumably widespread sexual selection upon invertebrates' genitalia; meanwhile positive allometry is the norm in mammalian genitalia (Kinahan et al. 2007; Lüpold et al. 2004; Miller and Burton 2001).

The evolutionary conservativeness or low evolvability of allometries may be intermediately caused by deep characteristics of the genotype-phenotype map (Blows et al. 2004), which could constrain the direction of evolution to some extent (Schluter 1996; Wagner and Altenberg 1996). Such a possibility sounds a note of caution regarding all hypotheses that are based upon presumptions of unconstrained natural selection—such as models of the evolution of animal behavior that are based purely upon game theory and other economic models, without taking into account the nature and structure of the relevant genetic variation in (putative) neurological structures, to say nothing of the possibility of widespread neutral divergence even in functional, adaptive traits (Nei 2007).

Petrie (1988; 1992) and Green (1992) propose that a larger display trait or weapon might tend to have a larger selective advantage for relatively larger animals, thus accounting for positive allometry in traits under sexual selection. While their purely adaptationist approach (assuming unconstrained selection) is reasonable as an hypothesis, there are surely factors other than differential reproductive success that influence patterns in the evolution of form; among them, differential phylogenetic intertia among traits, and the characteristics of genotype-phenotype maps, or the underlying genetic structure of phenotypic variation. Phylogenetic intertia, regardless of its underlying mechanism, may affect allometric patterns (Cheverud et al. 1986), and a complete account would consider phylogenetic inertia as an interesting phenomenon to be investigated, rather than as a mysterious confounding factor to be removed and ignored.

That said, however, one hypothesis of Petrie (1992: hypothesis 4) deserves special mention due to its congruence with a much larger and well-supported body of evolutionary theory (i.e., life history theory). Petrie suggests that positive intraspecific allometry of secondary sexual traits can be caused by progressive increase in trait size relative to body size throughout adulthood—a developmental trajectory that would be advantageous because, as an individual (especially a male) ages, the benefits of investing in growth (i.e., in future reproduction) decrease sharply, with strong selection expected for all-out investment in current reproduction (especially in mating effort). Such an hypothesis may fit Sulawesi macaques; they appear to employ an "age-graded" dominance hierarchy wherein many males live in one group, but sub-alpha males rarely mate (Reed et al. 1997; Thierry et al. 1994; Watanabe and Matsumura 1996), while males, especially in natural forest populations, tend to continue growing steadily throughout adulthood (see section 3.11).

*Size, shape and sexual dimorphism: maxillary canine teeth*—Males and females are largely the same genetically; ontogenetic divergence between the sexes occurs via differential expression (transcription) of numerous genes. These differences in gene expression are ultimately triggered by a small number of sex-specific genes, such as *sry*, the sex-determining locus on the Y chromosome.

Sexual dimorphism in traits that are thought to function in mating or intrasexual competitive displays, or in intrasexual fighting, tends to covary broadly with mating systems (Clutton-Brock 1980; Plavcan and Van Schaik 1992); thus conventional wisdom holds that sex differences in magnitude (or presence) of traits have been produced, and maintained, by sexual selection. Until recently there has been little strong within-species evidence to support that hypothesis, however, and at least one study of wild birds has challenged it, providing evidence for a lack of on-going sexual selection upon sexually-dimorphic display traits, in spite of high sexual dimorphism in the same traits (Westneat 2006). A detailed morphological-behavioral study of sifakas that incorporated data on male paternity also found evidence of neither sexual dimorphism nor on-going sexual selection on male canine dimensions, despite frequent contest competition between males (presumably over mating opportunities) (Lawler et al. 2005), and studies of strepsirhine primates have found no evidence for sexual dimorphism in spite of polygynous breeding systems (Kappeler 1996). Still, the strong and taxonomically widespread correlation between breeding system and sexual dimorphism is difficult to explain without reference to sexual selection. More detailed within-species work in a variety of taxa is still needed to sort out the details and mechanisms.

An allometric correlation between body size and the degree of sexual dimorphism, known as Rensch's rule (Rensch 1959), has long been noted (though even the correlation's consistent existence is disputed), and this interspecific allometric trend has been interpreted as showing that sexual dimorphism is at least partly a non-adaptive consequence of growth laws. Other authors, however, have proposed that selection could have led to the observed interspecific trend (e.g. Mitani et al. 1996). Interspecific allometries are notoriously poor means of inferring evolutionary mechanism, however (Gould 1975a); a selection experiment on *Drosophila* fruit flies found no evidence of increasing dimorphism with selection on body size (Reeve and Fairbairn 1996), though in any intraspecific study the range of variability is necessarily small.

Much of the variability within species in sexual dimorphism remains unexplained when only the operational sex ratio or some other indicator of male-male sexual competition is considered (Plavcan et al. 1995). There is some statistical evidence that food-related competition among females can increase the size of females' canines, thus lessening sexual dimorphism (Plavcan et al. 1995), though Greenfield (1998) has provided functional-morphological evidence that female primates' canines and sectorial premolars are not in fact weapons-grade, and may instead serve an incisal function. Rather than pointing only to correlated selection, however, such a function raises the possibility of "sexual bi-niche-ism" or some degree of ecological divergence between the sexes—a source of ecological selection that could further confound the presumed statistical effects of sexual selection upon interspecific variability in sexual dimorphism (Butler et al. 2007; Gordon 2006; Plavcan et al. 1995).

It seems nevertheless true that the hypothesis of sexual selection on males explains the available intra- and interspecific data on canine size variation better than any *single* alternative hypothesis (Greenfield and Washburn 1991). There is also a good deal of functional-morphological evidence that sexual selection on maxillary canine morphology in males has been more intense within some groups, such as cercopithecine primates (including the species examined in this chapter), than others. Evidence for extreme selection on male canine morphology in cercopithecines includes extreme sharpness of the distal edge of the maxillary canine; pronounced hypertrophy of the sectorial lower premolar, which hones the maxillary canine; and great height (or projection) relative to breadth of the maxillary canine, which facilitates both slashing and puncturing (Greenfield and Washburn 1991). Indeed, the sharpest maxillary canines measured by Greenfield and Washburn (1991: their table 2) belonged to *Macaca nemestrina*, which is the sister species to all Sulawesi macaques (they did not measure any Sulawesi macaque species), and which also exhibits extreme body-size sexual dimorphism.

In spite of evidence for pronounced differences in canine dimorphism, sharpness, height, and shape among higher taxonomic groups, however (such as families and subfamilies), there is also considerable evidence for phylogenetic inertia or evolutionary conservatism within these higher taxa, even in the face of substantial intra-taxon variability in the degree of polygyny or the operational sex ratio (Greenfield and Washburn 1991; Kappeler 1996). Such phylogenetic conservatism may reflect low evolvability of canines on short time-scales, if there is independent evidence of directional selection (Kappeler 1996; Lucas 2006), or may reflect similar levels of stabilizing sexual selection in the populations concerned (Brooks et al. 2005). Such a possibility opposes a common assumption (Arnqvist 1997; Manning and Chamberlain 1993; West-Eberhard 1983) that sexual selection is inherently directional rather than stabilizing, and is devoid of optima.

### *3.5: Population history of the Sulawesi booted macaque*

The remainder of this dissertation focuses upon a single pair of populations within Sulawesi booted macaques, *Macaca ochreata sensu lato*. These populations are *M. o. ochreata* from peninsular southeast Sulawesi (Lake Matano in the north to the Buton and Tiworo straits in the south), and *M. o. brunnescens* from Buton and Muna Islands (fig. 3.1). For the sake of brevity I will henceforth refer to these populations as simply *ochreata* and *brunnescens*, omitting the generic and specific epithets. It should be understood that these names, appearing by themselves, refer to the allopatric populations (subspecies) within *M. ochreata*. The name *M. ochreata*, when used here, thus refers collectively to both populations, *viz., M. ochreata sensu lato*. It is important to make this point clear since the two populations under discussion here are usually accorded specific rank in the literature on Sulawesi macaques.

*Evolutionary divergence of Sulawesian mammals as a whole*—Sulawesi is located in Wallacea, which is a transitional zone between Oriental and Meganesian (Greater Australian or Sahul Shelf) faunas. Wallace (1869) noted a sharp transition in the composition of the bird community in this region, and it is primarily upon the avifauna that Wallace's Line, which lies just west of Sulawesi, is based. Huxley later modified Wallace's line so that the Philippines are included in the "Wallacea" transitional zone (Huxley 1869), and modern biologists have accepted Huxley's version as more valid than Wallace's original. Less well-known is Lydekker's Line, which lies east of Sulawesi along the margin of the Sahul shelf (the continental shelf of Meganesia), and is based upon mammalian fauna.  Thus Sulawesi's mammalian fauna is dominated by Eutheria with only a few Metatheria (two phalangerid genera, *Ailurops* and *Phalanger*), and shows more affinities with the Sunda shelf than with the Philippines (Groves 2001).

Sulawesi's mammalian fauna is not particularly diverse, as compared to Borneo; for example, while there are tigers on Sumatra and clouded leopards are the largest felids on Borneo, there are no felids on Sulawesi.  Sulawesi's mammalian fauna is extremely endemic—"a world unto itself" in the words of Groves.  The distribution of snake genera is broadly similar to that of mammals—extremely endemic on Sulawesi, but more similar to Oriental than to Meganesian fauna (How and Kitchener 1997).

The low diversity but extremely high endemism of Sulawesian mammals presumably came about due to Sulawesi's position between the earth's two major faunal zones (dating to the ancient split of Gondwanaland and Laurasia), and most of all its long-term isolation.  While the islands of the Sunda Shelf (including Sumatra, Borneo and Java) were intermittently connected to each other and the Asian mainland throughout the Pleistocene, Sulawesi has been isolated for about 5 myr by the deep oceanic trenches that ring the island.  A predominant view, which is based largely upon fossil evidence for the timing of macaque dispersal from north Africa through Eurasia, has been that Sulawesi's mammals arrived one-by-one via sweepstakes dispersal across a water barrier, largely in the mid-Pleistocene (about 750 kya in the case of macaques, according to Delson (1980).

Groves (2001), however, points out that Sulawesi's mammals are not really as depauperate as is often supposed; he provides evidence that most Sulawesian mammals (those called by Groves "old endemics") arrived "dry-shod" about 5 mya, during

Sulawesi's last geologically-plausible connection to Sundaland. Such a possibility would explain the existence of a diverse and extremely endemic anuran fauna on Sulawesi, for example, since dispersal across salt water is extremely unlikely for anurans, for physiological reasons (Inger and Voris 2001). Aside from the large sample of morphology-based systematic evidence presented by Groves (2001), his "old endemics" hypothesis is strongly supported by recent molecular genetic studies on Sulawesi macaques (Evans et al. 1999); anoas (dwarf forest buffaloes), *Bubalus* spp. (Pitra et al. 1997; Schreiber et al. 1999); and grasshoppers, *Chitaura* spp. (Walton et al. 1997), all of which point to a probable Miocene age of colonization of Sulawesi by most, though not all, of its animals. Other systematists have argued on overall biogeographic evidence, however, that Sulawesi has never been connected to the Sahul shelf; the consensus of geologists also seems to be that no dry land has existed between Sulawesi and Borneo, at least in the middle to late Cenozoic (Hall 2001).

Perhaps the most likely scenario that could account for the existence of many vertebrate species on Sulawesi that would seem ill-suited for crossing water barriers might be the potentially very narrow gap that may have existed at one time between Borneo and central Sulawesi (Moss and Wilson 1998). While the strait is currently of substantial breadth, a relatively shallow, submerged shelf (the Paternoster Platform) extends from Borneo very nearly to Sulawesi, across the middle of the Makassar Strait—the distance between the 75 m isobaths is only about 40-50 km at this location (Katili 1978: his fig. 8; Voris 2000); the shelf would have been exposed, for example, as recently as 12 kya, ignoring tectonic uplift (Geyh ea '79, Fairbanks '89, Chappell & Polach '91). In theory, vegetation mats that became dislodged from eastern Borneo's eastward-facing river deltas—such as that of the Mahakam River, which currently empties just north of the Paternoster Platform—could have carried various vertebrates across a narrowed Makassar strait during times of low sea level (Froehlich et al. 1996). Empirical data collected by Heaney (1986), however, suggests that colonization events across even much narrower sea channels (5-25 km) is rare, with one to two colonizations per 500 kyr.

It is unclear just how much of the Sulawesian mammals' divergence could have occurred due to ecological selection in concert with genetic isolation. Certainly the northern and central parts of Sulawesi were less affected by the periodic dessication and expansion of grasslands that occurred throughout the Pleistocene on more southerly islands such as (eastern) Java, Flores and Timor (Bird et al. 2005; Heaney 1991). Likewise, montane forests (featuring trees such as family Fagaceae, and ferns) shifted to lower altitudes during the last glaciation, until about 12 kya (Flenley 1985).

Sulawesi's forests also differ from those of the Sunda Shelf islands such as Borneo, in that trees of family Dipterocarpaceae are nearly absent on Sulawesi while they dominate on the Sunda islands (Whitten et al. 1987). While dipterocarps are of very low importance as a food source for cercopithecine primates (M. Leighton and A. J. Marshall, unpub. data), the dipterocarps' absence probably does have a significant effect on forest structure, and might affect the economics of locomotion in the canopy as well as the distribution or abundance of the berry- and drupe- producing tree species that are typically favored by macaques as food sources. Unfortunately, most detailed ecological work in Sulawesi has been conducted in extreme northern Sulawesi (which has highly volcanic soils) and in southwestern Sulawesi with its highly fragmented forest on limestone outcrops; very little work has been conducted in Southeast Sulawesi (which has mostly non-volcanic soils).

*Diversification within Sulawesi*—Sulawesi is rather a large island, and over the course of a few million years, a good deal of diversification has occurred within the island. This diversity manifests itself in two ways, depending upon the taxon in question—first, divergence among the island's five major regions (the central area, plus northern, eastern, southwestern and southeastern peninsulas); second, divergence by altitude (Groves 2001). Altitudinal divergence is seen (possibly) in dwarf forest buffaloes or anoas (Bovidae), with lowland (*Bubalus* [*Anoa*] *depressicornis*) and mountain (*B.* (*A.*) *quarlesi*) forms; these two forms are distinguished by body size and horn morphology, and show both an ancient time depth as a clade, and ancient divergence from one another (Pitra et al. 1997; Schreiber et al. 1999). There are far more murid rodent species in central Sulawesi than in the other regions (Musser 1983-84; Musser 1987), possibly owing to the greater altitudes present in the central part of the island. In the Philippines, maximum diversity is observed in montane forest from 1,500-2,000 m (Heaney 2001); in southeastern Sulawesi such elevations are fairly rare except in the Mekongga mountain range. Certainly *Tarsius pumilus* (Tarsiidae) shows not only restricted distribution (montane forests in central Sulawesi), but apparent morphological adapatations for clinging to moss-covered montane forest trees (Musser et al. 1987). *Prosciurillus abstrusus* (Sciuridae) is one of only three mammalian species that are endemic to the southeastern peninsula of Sulawesi (the other two are *Macaca ochreata* and Rodentia: *Maxomys dollmani*) (Musser 1983-84; Musser 1987), and *P. abstrusus* is known only from the Mekongga mountains, the highest mountains on that peninsula.

Among mammals, peninsular diversification is probably strongest in macaques (Albrecht 1978; Fooden 1969) and squirrels (Groves 2001), although the babirusa (Suidae: *Babyrousa babyrussa*) of the northern peninsula (and, historically, on the southwest peninsula) may have diverged at the specific level at least. Diversification seems stronger on the island of Peleng (off the southern coast of Sulawesi's eastern-central peninsula), which has its own endemic species of phalanger (Phalangeridae: *Phalanger pelengensis*), for example, and a rat species that seems to show mild insular gigantism (Rodentia: *Rattus pelurus*) (Musser 1983-84). The strait separating Peleng from the Sulawesi mainland is deeper than that separating Buton and Muna island (see below) from the mainland; thus it seems likely that Peleng was connected to Sulawesi less frequently and for shorter periods (if at all) than were Buton and Muna, during the Pleistocene, especially considering the history of rapid uplift of the coast that faces Peleng (Sumosusastro et al. 1989). The consequent reduction in gene flow would account for Peleng's apparently greater divergence in mammals relative to Buton and Muna.

There is nonetheless a great deal of apparently parapatric, peninsular divergence among mammals on Sulawesi, including seven or eight populations of macaques that are usually assigned to either four or seven species. Similar divergence has been observed in toads (Evans et al. 2003b), squirrels (Groves 2001), and several invertebrate species (Holloway 1990). In recent decades biologists have generally assumed that any level of gene flow, however slight, will prevent divergence among populations (see chapter one);

thus Fooden's (1969) conjecture that Sulawesi was once a "paleo-archipelago" with the present-day lowlands submerged. Fooden's hypothesis has proven popular and has largely been adopted by today's biogeographers of Sulawesi, owing to widespread assumptions about the supposed implausibility of non-allopatric speciation (see chapter one).

The paleo-archipelago hypothesis seems well-supported where the southern half of the southwestern peninsula (south of the Tempe Depression) is concerned; indeed this peninsula had its own unique Pliocene fauna (the Walanae fauna, ca. 4.6-3.0 mya) which is not known from the rest of Sulawesi; this fauna included a now-extinct giant pig (*Celebochoerus*), dwarfed elephant-like stegodonts (*Stegodon*), giant tortoises, and an early form of babirusa (Groves 2001). The Tempe Depression is to this day one of the lowest points on Sulawesi, and it seems likely that it was at least partially flooded as recently as the mid-Holocene (Gremmen 1990), and certainly on-going uplift would have made flooding of this area even more likely—and probably of longer duration—in the Plio-Pleistocene.

While Fooden (1969) cites sources that support a history of uplift of the eastern peninsula and of the Buton-Muna platelet, it simply does not follow that all of Sulawesi has been subject to equal amounts of uplift in the Plio-Pleistocene; Sulawesi was formed from the collisions of a number of distinct platelets and mircocontinents; the western arm is of southeast Asian provenance, while the eastern and southeastern arms migrated over from the Sahul area near Australia; they collided during the Miocene and Pliocene and today are joined by a strike-slip fault (the Palu fault) (Hall 2001). Buton, meanwhile (which forms much of the habitat of *M. o. brunnescens*), is a microcontinent of itself, originally submerged, and is likewise of Sahul origins; its central mountains were formed via sandwiching between the Tukang Besi platform and peninsular southeast Sulawesi (Fortuin et al. 1990). Thus Fooden (1969) is correct that much of Sulawesi was once underwater; the uplift occurred over a longer time scale than he envisioned, however, with most of Sulawesi dry land by 5 mya, excepting the Tempe Depression (again, accounting for the unique Walanae fauna of that time) (Hall 2001: his fig. 10).

The overall reconstruction of the "paleo-archipelago" is highly conjectural, especially where the best-differentiated macaque populations are concerned. The morphologically least-differentiated pair of Sulawesi macaque populations, *Macaca ochreata ochreata* and *M. o. brunnescens* (the subjects of this dissertation) (Groves 1980) are also the only ones currently allopatric (albeit having been so only a very short time: see below). Meanwhile, the contact zone of *M. o. ochreata* and *M. tonkeana* is very narrow and characterized by very limited morphological introgression (limited to introgression of a pelage trait), suggesting some degree of pre-mating isolation—yet there is palynological evidence that the shore of Lake Matano (which lies in the *ochreata-tonkeana* contact zone) has been dry land for at least several hundred thousand years (Hope 2001). There is also no good geological evidence for any historical geological discontinuity in this contact area, at least after the end of the Miocene; there are several existing strike-slip faults in central and southeast Sulawesi, but their positions and orientations do not match the *ochreata-tonkeana* contact zone nor any other faunal contact zone.

On the other hand, the area in Sulawesi with the best evidence (current elevation, paleofauna, palynology) for long-term, recurrent isolation—the southern peninsula south of the Tempe Depression, home to *M. maura*—shows far less-effective isolation between the macaque populations. Until recent habitat destruction made it impossible, *M. maura* and *M. tonkeana* seem to have shown continuous morphological intergradation across the former geographic barrier, forming a broad secondary hybrid zone (Froehlich and Supriatna 1996).

Still, Fooden's (1969) paleo-archipelago hypothesis is strengthened by the fact that ecological selection (rather than sexual selection or genetic drift) normally opposes the homogenizing effects of gene flow, yet macaques tend to be ecological generalists, and there is as yet no evidence for differentiation of diet nor of trophic morphology among the Sulawesi macaques (Albrecht 1978; Fooden 1969; Matsumura 1991; O'Brien and Kinnaird 1997). Aside from that, there seems to be genetic, morphological and geological evidence pointing to an ancient (perhaps Miocene) colonization of Sulawesi by mammals (Sulawesi has, after all, a large number of endemic *genera* of mammals), which raises the possibility of substantial plate uplift that was implausible on Fooden's (1969) Late Pleistocene time scale. There is evidence that divergence in mtDNA sequences has occurred in parallel in both macaques and toads (Evans et al. 2003b), though data on invertebrates such as grasshoppers do not seem entirely consistent with that pattern (Walton et al. 1997), and at any rate divergence in mtDNA does not necessarily indicate range fragmentation (Irwin 2002).

Such rather indirect evidence does not, however, justify the widespread *assumption* that all diversification on Sulawesi was allopatric (see chapter one)—for example, the statement by Evans et al. (2003a) that Sulawesi macaques "underwent an explosive diversification as a result of range fragmentation. Today, barriers to dispersal have receded...." The evidence for such barriers is weak and indirect.

It seems just as plausible that reduced gene flow was important in peninsular diversification of Sulawesian mammals (especially given the weak ecological differentiation of the island), but that isolation by distance, not habitat fragmentation, encouraged diversification in many cases. On the other hand, Evans et al. (2003) note a lack of inter-population structuring in autosomal DNA within Sulawesi macaque species, which rather supports the historical fragmentation or isolation model, as opposed to isolation by distance—in other words, the genetic data suggest that dispersal distance of male Sulawesi macaques may be large. Given the history of desiccation and grassland expansion in much of the Pleistocene (Bird et al. 2005; Brandon-Jones 1996; Heaney 1991; Hope 2001), refugial isolation via altitudinal shifts in forest zonation could have played a role in diversification, though it is difficult to see how lowland rainforest refugia could have existed in all the peninsulas of Sulawesi, especially the relatively drier southern peninsulas.

As noted by Walton et al. (1997), however, the geological and climatic history of Sulawesi is quite complex, and it is unlikely that any single, simple hypothesis (such as the paleo-archipelago) will satisfactorily explain divergence on the island. This is why I have chosen to study in detail the divergence of two macaque sister populations, *Macaca ochreata ochreata* and *M. o. brunnescens*, whose geological and genetic history is comparatively simple and well-understood (see below), and whose divergence from one another seems to have begun relatively recently.

Of course, dessication in the drier southern peninsulas, particularly during the glacial maxima of the Pleistocene (Bird et al. 2005; Heaney 1991; Hope 2001), could conceivably have led (separately) to morphological divergence of *M. maura* (southwest Sulawesi) and *M. ochreata* (southeast) from *M. tonkeana* (central). From 30-15 kya, Lake Matano (in the present-day *ochreata-tonkeana* contact zone, the northern limit of *ochreata*'s distribution) was dominated by plants adapted to colder, drier conditions, such as Fagaceae (e.g. *Castanopsis* and *Lithocarpus*), with grasses and sedges (Poaceae) also more common than today (Hope 2001). It is likely, then, that during the Pleistocene, the more southerly and probably drier portions of *M. ochreata*'s range were even more divergent from today's tropical lowland forests (Bird et al. 2005; Heaney 1991).

Even today, rainfall becomes gradually more seasonal as one moves southward on the two southerly peninsulas (Fontanel and Chantefort 1978b), and any effects on the distribution and structure of forests could have been more exaggerated during the aforementioned periods of the Pleistocene, possibly leading to divergence by ecological selection (see chapter one). In fact, the more southerly position of Buton and Muna islands (*brunnescens*' range) compared to the midpoint of the southeastern peninsula (*ochreata*'s range) suggests that *brunnescens* may have experienced a more seasonal climate, on average, than *ochreata*—though climate will have stabilized by the time the two populations were isolated from one another, leaving only the effects (if any) of mild differences in seasonality of rainfall. For example, on southern Buton island, *Castanopsis* (Fagaceae) can be found in large stands on hilltops in lowland tropical forest (pers. obs.), suggesting a possibly drier or more seasonal climate overall, and macaques there appear to be capable of eating its nuts. Buton seems to be poor, however, in certain tree species such as breadfruit (*Artocarpus*, Moraceae), that are exploited by *ochreata* on peninsular southeast Sulawesi. Breadfruit trees could have been introduced by human cultivation on the peninsula, however, since their fruit (*nangka*) is popular among local people. In peninsular southeast Sulawesi, it is not unusual to find enormous strangler figs (*Ficus*) growing atop hills over 300m above sea level, while on Buton the distribution and abundance of figs and of certain other trees whose fruit is consumed by monkeys (such as *Dillennia*, Dilleniaceae) seems more restricted. Many berry- and drupe-producing tree species are found only near creeks in Buton (especially southern Buton), suggesting possible effects of the more seasonal rainfall there (all pers. obs.). Still, these are only casual observations and a quantitative comparison is yet to be conducted.

The trouble with scenarios of divergence by ecological selection is that there seems to be no morphological evidence (at least not craniofacial evidence) for correlations between morphology and environment or diet in Sulawesi macaques (Albrecht 1978: 94-95; Fooden 1969: 39). Hill (1974: 768) speculated that ecological selection might have led to morphological divergence of the macaques of southern Sulawesi, which he assigned to a separate genus and subgenus (*Macaca, Gymnopyga*) from northern Sulawesi macaques (*Cynopithecus niger*). His description of *M. maura*'s habitat, however (limestone outcrops) may be marginal habitat for this species (due to deforestation of all low-lying areas for agriculture), and certainly does not apply to the lowland forest habitat of *M. ochreata*. Likewise Hill's inference that *M. maura* is naturally more terrestrial than *M. nigra* is probably wrong; there simply is little continuity in the forest canopy in these limestone areas of southwest Sulawesi.

*Isolation of booted macaque populations: biological evidence—M. o. ochreata* is found from the Lake Matano area at the northern end of Sulawesi's southeastern peninsula, southward to the narrow, shallow water barrier formed by the Buton and Tiworo Straits. South of these shallow straits, on the islands of Buton and Muna, we find *M. o. brunnescens*. These populations are morphologically the least-differentiated of all Sulawesi macaque populations (Groves 1980; Juliandi 2007; B. Suryobroto, pers. comm.). The morphological, mitochondrial DNA, microsatellite, and blood protein evidence indicate that *ochreata* and *brunnescens* are sister populations, a clade to the exclusion of all other Sulawesi macaques; they also appear to be reciprocally monophyletic (each having a distinct ancestor) (Evans et al. 1999; Evans et al. 2003a; Groves 1980; Harihara et al. 1995; Juliandi 2007).

There is a great deal of ambiguity in the mtDNA data (Evans et al. 1999; Evans et al. 2003a), and reconstructions vary depending upon which statistical method is used, while paraphyly seems rampant even within species—the mtDNA of *M. tonkeana* seems paraphyletic with respect to the other species, for example (Evans et al. 2003). On the basis of the same mitochondrial DNA evidence, Evans et al. (1999) once postulated that the Sulawesi macaques were diphyletic, with the northern and southern Sulawesi macaques most closely related to distinct subspecies of *M. nemestrina*. *M. nemestrina*'s mtDNA was also paraphyletic, with most of its populations somehow nested within the southern Sulawesi clade, and another *M. nemestrina* population as sister to all Sulawesi macaques. Aside from that, some aspects of proposed mtDNA-based phylogenies are evolutionarily or biogeographically implausible—for example, the proposal that different populations of *M. nemestrina* within Borneo gave rise to southern vs. northern Sulawesi macaques (Evans et al. 1999) is evolutionarily implausible, since *M. nemestrina* as a whole and Sulawesi macaques are sister species, sharing a common ancestor >> 1 mya. MtDNA-based phylogenies have also resulted in some biogeographically implausible scenarios (Evans et al. 2003a; Harihara et al. 1996). Further attempts to elucidate Sulawesi macaque phylogeny using only mtDNA have produced tortuous diagrams (Evans et al. 2003a). All this leads one to suspect that mtDNA should not be used as the primary, let alone the only, source of phylogenetic data, as the phylogenies produced either are not replicated by independent methods (nuclear DNA, proteins, morphology) or are unlikely on theoretical grounds.

It seems likely that there are inherent problems with reconstructing phylogenies on the basis of mtDNA alone. One problem is that mtDNA segregates as one locus and thus it offers no replication; another problem is that the usual assumption of strictly maternal inheritance may be wrong (Ankel-Simons and Cummins 1996). In fact, however, any single-locus study can be problematic, as many authors have claimed paraphyly of multiple macaque species, including Sulawesi macaques, based solely upon mtDNA, or the Y chromosome, or single autosomal loci (Brandon-Jones et al. 2004; Morales and Melnick 1998). Both mtDNA and Y-chromosome data have yielded multiple polytomies, multiple equally-parsimonious phylogenetic trees, and irreconcilable phylogenies based on independent data (Tosi et al. 2000).

Older studies of protein variation, though a possible source of corroboration, can be somewhat diffiicult to interpret. In an analysis of the primary structure of hemoglobin beta chains, Takenaka et al. (1987) found that *ochreata* and *brunnescens* differed from one another by at least two nucleotides; an equal amount of polymorphism was observed, however, within *M. nigra* of northern Sulawesi. *Brunnescens* clustered with most of the other Sulawesi species; *ochreata* had diverged to become like *M. hecki* (Takenaka et al. 1987). Takenaka et al. (1987) considered parallel evolution unlikely and instead raised the possibility of ancestral polymorphism throughout Sulawesi, followed by differential loss of various alleles, presumably via genetic drift.

At any rate, the fact that Takenaka et al.'s (1987) sample of *ochreata* (N = 18) and *brunnescens* (N = 17) are well-differentiated in terms of hemoglobin at least bolsters the case that the two have not mixed (for example, via anthropogenic introductions or hydrological phenomena) in several thousand years. While the molecular data can be difficult to interpret, the status of *M. ochreata* as a clade to the exclusion of other Sulawesi macaques is bolstered greatly by morphological data (Groves 1980; Juliandi 2007). In fact, the difficulty of constructing a clear-cut phylogeny with molecular data alone may be related to the relatively rapid diversification of macaques on Sulawesi—morphology may have diverged much faster than neutral DNA markers.

*Isolation of booted macaque populations: geological evidence*—Since this study is concerned with evolutionary rates and the time scales of divergence and stasis in various traits, it is critically important first to review the geological evidence, to establish the duration and continuity of the separation of the populations. My aim is to constrain the number of possible permutations of population history, and thus the range of hypotheses and scenarios that could complicate interpretation of my observations; and to provide an accurate time scale for the observed degree of divergence and stasis.

The time since isolation of the peninsular (*ochreata*) and Buton-Muna (*brunnescens*) populations has been affected simultaneously by two major variables that are, unfortunately, wholly independent of one another: first, eustatic changes in sea level due to glacial melting since the last glacial maximum (ca. 17-18 kya); second, tectonic uplift. I first deal with changes in sea level, ignoring uplift; then, I attempt to factor in the latter as accurately as possible.

Geyh et al. (1979) obtained Pleistocene-Holocene sea-level estimates by $^{14}$C-dating peat (which tends to form at shorelines) and *in situ* mangrove roots in the Straits of Malacca, in southeast Asia near Singapore, producing a diagram that estimates sea level as a function of time, though their curve extended only to about 12 kya. A more recent study in the Caribbean (Barbados) by Fairbanks (1989), reconstructed ice volumes (and thereby, sea levels) using oxygen isotopes, by making use of the fact that 18O levels are much lower in glacial ice than they are in liquid seawater. Fairbanks replicated Geyh et al.'s results, resulting in a very similar curve (e.g., Geyh et al: -50m at 10 kya; Fairbanks: -50m at 9.5 kya). The similar curves produced at the two locations, using two very different methods, suggest that the results are repeatable and were little affected by local tectonic processes such as uplift. Finally, Chappell and Polach (1991) replicated Fairbanks' results with a similar study closer to Sulawesi (Papua New Guinea), and also corrected for local differences in uplift relative to Barbados, again producing a curve nearly identical to that of Fairbanks (-50m at 9.5 kya).

Gross reconstructions of sea levels that show isobaths connecting various land masses show Buton and Muna connected to peninsular southeast Sulawesi at the -50m isobath but not at -75m (Voris 2000). I was interested in obtaining more precise local depths, however, along possible dispersal routes, and detailed bathymetric maps seem unavailable for the relevant straits (the Buton and Tiworo straits, and the narrows between Buton and Muna). I therefore consulted nautical charts which include numerous sonar soundings taken in these straits (U. S. Defense Mapping Agency 1995).

The charts indicate some currently very shallow and narrow areas between peninsular southeast Sulawesi and Muna island, most notably the area between Tobea Besar island, off Amolengo Cape (surrounded by a shallow atoll) and Muna, with an area of -32m; and Laea Bay to the west, with linear north-south routes of maximum -41m (fig. 3.2). Direct routes between the peninsular mainland and northern Buton island (via Peropa Cape) appear rather deep, with maximum depths of -80 to -95m in the shallowest areas. Animals could have dispersed to Muna island, however (both Muna and Buton are within the current range of *brunnescens*), and then dispersed further to Buton via the relatively shallow narrows that separate the two islands. In the southern part of the narrows at ca. 5° 26' S latitude, there is a very narrow and shallow area with a depth of 32m to 34m (fig. 3.3). Farther north in the narrows (4° 46' S), there is another area with a linear west-east route of maximum depth 43m (not shown in figures). Of course, sea depths can vary on very short time scales depending upon fluctuations in sedimentation and other factors, but I have no reason to suspect that such fluctuations would have led to a directional trend during the Holocene, especially since there seem to be no major drainages in these areas.

Tectonic uplift constitutes the other significant factor that must be taken into account. The southern part of Buton island, for example, has Quaternary algal and coral reefs at altitudes of up to 700m (Wiryosujono and Hainim 1978), though uplift seems to have been much more mild in northern Buton (Elnusa Geosciences Inc. 2005). Muna island has Quaternary reefs at up to 425m above sea level, suggesting a rate of uplift lower than that of southern Buton (van Bemmelen 1949, cited in Fooden 1969: 63). More recently, however, Fortuin et al. (1990) have shown that the fastest uplift occurred in southeastern Buton, with slower uplift in southwest Buton (the latter faces the narrows with Muna island). Fortuin et al. (1990: 120) have provided an estimated rate of uplift for southwest Buton, based on a radiometrically-dated terrace: ca. 80 cm/kyr. This would of course result in about 8m of uplift over 10 kyr.

I will assume that the seafloor in the narrows between Buton and Muna, and in the Tiworo strait between Muna and peninsular southeast Sulawesi, was subject to the same rate of uplift as southwest Buton (a conservative assumption since southern Buton's rate of uplift is relatively rapid: Elnusa Geosciences Inc. 2005); this would mean the sea floor could have been about 8m deeper than at present, at the beginning of the Holocene. Adding the minimum depths (32m) to the maximum uplift (8m) we then have 40m. Both Fairbanks (1989) and Chappell and Polach (1991) give a date of 9 kya for this sea depth. Thus I think it is reasonable to conclude that *ochreata*'s range was most likely to have been last connected to *brunnescens*' range about nine thousand years ago, though there is at present no way of placing confidence intervals around that estimate. Since evidence from other islands in Southeast Asia indicates that overwater colonization events are very rare (Heaney 1986), it is unlikely that booted macaques crossed the straits after they were flooded at about 9 kya.

### *3.6: Holocene-Recent bioclimatology of southeastern Sulawesi*

*Climatic differences*—Hot, dry winds originating in the vast deserts of Australia (directly to the south of Sulawesi) have a marked influence upon the climate of southern Wallacea (Wallace 1869). Thus a marked dry season is present in Timor (closer to Australia than Sulawesi), and seasonality of rainfall decreases gradually from Timor northward to central Sulawesi. A south-to-north gradient of decreasing rainfall seasonality can thus be observed in the southern peninsulas of Sulawesi, with the northern half of *ochreata*'s range having an ever-wet climate (see fig. 3.4). In this section, my arguments will rest largely upon the work of Fontanel and Chantefort (1978a; 1978b), who collected long-term rainfall and climatic data from dozens of government-operated climatic and rain-gauge stations throughout Sulawesi, including several in southeast Sulawesi (see dots on fig. 3.4, and figs. 3.6a-3.6c), and combined these data with knowledge of topography and meteorological principles to produce an extremely thorough and rigorous series of climatic maps (fig. 3.4-3.5, and other maps not reproduced here).

The range of *brunnescens*, and the southern extreme of *ochreata*'s range, has rainfall described by Fontanel and Chantefort (1978b) as "moderately seasonal," i.e. a dry season lasting 3 to 4 months (see also Whitmore 1984b: his fig. 4.1, p. 55, and references cited in its caption). If we assume that the climate today is similar to that throughout most of the Holocene, then we can see that during the past 9 kyr or so, *brunnescens* has experienced, on average, a more seasonal climate than has *ochreata*, while *ochreata*'s climate has been more seasonal on average than that of *M. tonkeana*, their neighbor to the north (figs. 3.4, 3.6a-3.6c) (Fontanel and Chantefort 1978a; Fontanel and Chantefort 1978b). A look at the 20-year data of Schmidt and Ferguson (1951: 72) largely confirms the pattern postulated by Fontanel and Chantefort, except that Schmidt and Ferguson's data show little difference between the southeastern extreme of *ochreata*'s range and the range of *brunnescens*.

The south-to-north gradations in rainfall seasonality are shown in fig. 3.4. Fig. 3.5 shows that there is also a south-to-north gradient in total annual rainfall, although the gradient is slightly less clear; at any rate seasonality is more important for limiting plant diversity and productivity than is total rainfall (see below). Fig. 3.6a shows that in an average year, for a period of three months, rainfall in Bau-Bau in southern Buton Island (the southern part of *brunnescens*' range) falls at or below Fontanel and Chantefort's criterion of a bioclimatically consequential dry season, *viz.*, $P < 2T$ (where $P$ = precipitation in mm, $T$ = temperature in degrees C). Rainfall in Kendari (in the southern part of *ochreata*'s range) barely reaches this criterion for one month in an average year (fig. 3.6b). Meanwhile, rainfall in Kolonodale (a town in central Sulawesi, just to the north of the northern limit of *ochreata*'s range) is seasonally variable but never approaches the dry-season criterion that is thought to be potentially vegetation-limiting (fig. 3.6c).

The ranges of *ochreata* and *brunnescens* probably differ in average altitude (and thus average temperature), with that of *ochreata* being greater. While Sulawesi macaques have been observed in sub-montane forests between 1,000-2,000m asl (Fooden 1969), they seem to occur rarely above 1,000m (Whitten et al. 1987), and anyway such low-density, high-altitude primate populations may be sink populations that exert little evolutionary influence (Marshall, in press). Therefore the most relevant environmental difference between *ochreata*'s and *brunnescens*' ranges seems to be seasonality of rainfall rather than temperature or altitude.

*Consequences for vegetation and habitat*—The difference between a moderately seasonal rainfall and an ever-wet climate is sufficient to cause some differences in the structure and composition of forests, and the primary productivity thereof. I will therefore argue here that, during their ca. 9 kyr of peripatric separation, *brunnescens* experienced greater resource limitation than ochreata. I will thus ask whether this subtle difference in resource availability, forest composition and forest structure is sufficient to cause insular dwarfism to evolve in *brunnescens*.

In tropical lowland forests (the habitat of Sulawesi macaques), average temperature differences are minimal; most differences in vegetation communities are related to seasonality of rainfall, not total rainfall (Fontanel and Chantefort 1978b: 65; Gentry 1988; Richards 1952: 142; Whitmore 1984b: 159). According to Fontanel and Chantefort (1978b: 87), a dry season of more than two months is sufficient to affect forest structure: "the deciduous species gain importance and the forest becomes of a mesophilous type called the monsoon forest." Significantly, almost all of *ochreata*'s range (except the extreme south of the southeastern peninsula) features aseasonal to slightly seasonal rainfall, while the entirety of *brunnescens*' range features a dry season of 3 to 4 months (fig. 3.4, 3.6).

Opinions differ among botanists regarding how dry a forest must be before it is considered a monsoon forest; some limit the term to obviously distinctive habitats such as woodlands and partly wooded savannas. Whitmore (1984b), however, describes a number of subtly different forest types that can be found in southeast Asia—types differentiated by seasonality of rainfall and by altitude (we are concerned here with the former only). Most significant is his distinction between tropical lowland evergreen rainforest and tropical semi-evergreen rainforest. The latter occurs wherever "water-stress is absent or only brief and intermittent" from 0 to 1,200m asl (Whitmore 1984b: 157), while the former occurs "where there is regular annual water-stress of at least a few weeks' duration" (Whitmore 1984b: 159). A vegetation map by Whitmore (1984a) further confirms that rainfall seasonality in *brunnescens*' range (and the southern extreme of *ocrheata*'s range) has affected forest composition in that area (fig. 3.7).

Tropical semi-evergreen forests have very abundant woody climbers—a description borne out by a patch of enormous, multi-branched woody lianas that I found on one transect in southern Buton, but that I have never seen in peninsular southeast Sulawesi. Most trees in semi-evergreen forests are evergreen, but up to one-third of larger trees can be deciduous (Whitmore 1984b: 159); furthermore, semi-evergreen forest is more easily destroyed by burning and converted into *alang-alang* grass (*Imperata cylindrica*), due to the longer dry seasons; both of these descriptions are quite well borne out by my field observations. Alang-alang grasslands are of vast extent only in the extreme south of peninsular southeast Sulawesi; despite the likelihood of centuries of settlement in the Konaweha River valley by people of the indigenous Tolaki ethnic group, *alang-alang* patches there are still of very modest size. Fontanel and Chantefort (1978b) refer to the presence of deciduous Leguminosae and teak trees (*Tectona grandis*) in semi-evergreen forests (though they use the term "monsoon forest"); natural stands of teak are apparently gone due to the species' economic popularity, but it is still grown in enormous manmade tree farms on Muna Island, probably owing to its originally natural occurrence there, and the suitable climate.

*Bioclimate, diversity and primary productivity*—Within the Amazon (which is better-studied than southeast Asia), aseasonal forest areas have far more tree species than seasonal areas; the latter are comparable to subtropical forests (those much farther from the equator, and thus affected by seasonal shifts in insolation) in species-level tree diversity. The diversity of lianas does not seem particularly affected by rainfall seasonality, however, and soil quality can have independent effects upon tree diversity (Gentry 1988: his fig. 5, p. 11). Epiphytes also increase greatly in diversity as rainfall increases, although it is not entirely clear whether rainfall seasonality or total rainfall is the more important limiting factor (Gentry 1988); in any case, *brunnescens*' range has lower total rainfall as well as more seasonal rainfall compared to the range of *ochreata* (see figs. 3.4, 3.5).

There is some evidence that primary productivity (at least in the Neotropics—there are fewer data available for Asia) reaches a peak at about 2,500mm of rainfall per year, then declines when total rainfall rises above that level, possibly because of continual cloudiness reducing the potential for photosynthesis (Kay et al. 1997). A look at fig. 3.5 will show that virtually all of *brunnescens*' range, but less than half of *ochreata*'s range, receives 1,500-2,000mm of rainfall per year. Kay et al. (1997) show that primate species diversity generally follows the trend of primary productivity (primate diversity is reduced as rainfall falls below 2,000-2,500mm), and argue that this trend is caused by either absolutely less fruit production in drier forests, or lower diversity of fruit-producing trees. It should be noted that low fruit diversity could have consequences even within species, since the tree species missing from drier forests may be critical keystone or fallback species that could otherwise have been relied upon in periods of scarcity.

The forests of the southern extreme of southeastern Sulawesi (*brunnescens*' range, and the southern extreme of *ochreata*'s range) generally receive between 1,500 and 2,000 mm of rainfall per year (fig. 3.5), and thus would fall on the borderline between Gentry's (1995) "dry forest" and "moist semievergreen forest." In the Neotropics, moist semievergreen forests have 100-150 tree species (DBH > 2.5 cm) per 0.1 hectare, while "wet evergreen forests" have 150-200 species in the same space; "pluvial" forests have 200-250 species (Gentry 1995). It is thus apparent that differences in rainfall of the type seen throughout southeastern Sulawesi can have a substantial effect on tree diversity, and thus upon the dietary options of frugivores.

Fruit production in tropical forests—particularly in southeast Asia where mast-fruiting tree species are common—tends to be synchronous, with long periods of little fruit production. The more seasonally dry the forest, moreover, the greater the synchrony in fruiting (Van Schaik et al. 1993). That fact alone puts a premium on tree species diversity: the more tree species there are, the greater the chance that at least one species will be producing fruit during an otherwise scarce period. It can be appreciated, then, that either reduced absolute fruit production in seasonally dry (semi-evergreen) forests or reduced tree diversity therein, could lead to significant resource limitation for frugivores, relative to ever-wet habitats. Animals in more seasonal forests are forced to rely periodically upon lower-quality backup foods, creating a circannual selective filter that can have significant evolutionary consequences (Marshall and Wrangham 2007).

In periods of fruit scarcity, it is sometimes possible for macaque populations to rely upon trees and other plants that tend to be reproductively asynchronous, such as strangler figs (Moraceae: *Ficus* spp.). Kinnaird et al. (1996) observe that figs may play such a critical buffering role at their research site in extreme northern Sulawesi, Tangkoko-Dua Saudara Nature Reserve. It should be noted, however, that although Kinnaird et al. (1996) characterize their research site as seasonal, and rainfall does vary greatly between seasons, the level of rainfall (relative to monthly temperature) never comes near Fontanel and Chantefort's (1978b) criterion of a bioclimatic dry season, $P < 2T$. This can be seen by examining fig. 3.6d, showing Manado rainfall, where rainfall never falls below the $P < 2T$ criterion (shown on the graph as a horizontal dotted line); compare fig. 3.7a, showing rainfall in Bau-Bau (southern Buton island, southern extreme of brunnescens' range), which shows the existence of true dry seasons.

My field observations suggest that there are probably fewer strangler figs in the southern part of *ochreata*'s range relative to the Manado-Tangkoko area; and there are almost certainly fewer on Buton island, where I very rarely encountered strangler figs, especially in southern Buton. This is not entirely surprising since the Manado-Tangkoko area has an entirely different type of soil than does southeastern Sulawesi, the former being highly volcanic. During the dry season, moreover, the otherwise largely arboreal *brunnescens* in Buton seemed to come to the ground more often, perhaps abandoning a fruitless canopy in favor of whatever food might be available on the ground.

Therefore I hold that it is very likely that, throughout its peripheral isolation during the Holocene, *brunnescens* experienced resource limitation (at least seasonally), relative to *ochreata*. If resource limitation is an important cause of insular dwarfism, then given that Buton and Muna islands (the range of *brunnescens*) are land-bridge islands that do not differ from the mainland in either predator or competitor communities, that approximately 9 kyr have passed probably without any gene flow, and that adult booted macaques weigh >> 1 kg (males: ca. 10 kg; females: 6.4 kg—see Results, below), we should expect to see insular dwarfism in *brunnescens*.

## Methods

### *3.7: Populations and research localities*

Please see chapter two.

### *3.8: Field morphometry*

Please see chapter two.

### *3.9: Statistical analyses*

All statistical analyses were conducted with JMP statistical software, version 7 (SAS Institute). Although I report p-values, two important points should be borne in mind. First, p-values are the probability of obtaining the observed data if the "null" hypothesis of no difference between groups (or no difference between a regression slope and zero) is true. A p-value is not a probability of an hypothesis—not even the null hypothesis (Gigerenzer et al. 2004). Aside from that, null hypotheses are in fact very unlikely to be true; as sample sizes increase, the probability of a significant difference approaches one. P-values are thus reported only as a rough heuristic tool for evaluating the likelihood that the pattern observed is due to chance.

Second, I do not perform Bonferroni or other corrections for multiple inferential tests, for reasons that have been summarized by Preneger (1998). Briefly stated, for the purposes of this paper I interpret p-values as exact probabilities in Fisher's sense, not as representing an "alpha" or "rejection region," because the purpose here is scientific interpretation rather than, for example, industrial quality control (Gigerenzer et al. 2004).

I conducted univariate allometric regressions using reduced major-axis or model two linear regressions on transformed data, in order to explore the relationship between overall body size and shape, or proportional size of various component body parts. Reduced major-axis regression, unlike ordinary least-squares regression, does not assume that the x-axis variable is measured with zero error; it also does not assume that the x-axis variable is an experimental, truly independent (i.e., manipulated) variable. Therefore reduced major-axis regression is highly appropriate for allometric regression (Kermack and Haldane 1950; Zar 1968). I used the "Fit Orthogonal" command in JMP's "Fit Y by X" dialog, and chose the principle-components (i.e., empirical) estimation technique for relative error in each variable.

Data were transformed with base-10 logarithms or (in the case of body mass) base-10 logarithm of the cube root, in order to linearize the data and normalize it, thus meeting the assumptions of the regression and ANOVA models. I first tried using log trunk length (log crown-rump length or log CRL) as the standard of comparison (on the X-axis) for univariate allometry, and I also tried using log body mass. Log CRL seemed a reasonable standard of comparison, since it is a one-dimensional (linear) measure, as are the traits to which it is being compared. Log CRL sometimes produced regressions, however, that included extreme outliers and contained a notable amount of model error. This may have occurred because CRL takes account of variation in only one body dimension, leaving others free to vary. CRL in still important in one sense, however, since it is more temporally stable than body mass.

When I regressed log CRL vs. log body mass with the latter on the Y-axis, it seemed as though body mass were positively allometric with respect to CRL—but this pattern occurs only because body mass is proportional to volume, which scales geometrically as the third power of linear measures such as CRL. When I used a log-cube-root transformation of body mass (log [$\text{mass}^{1/3}$]), the mass-CRL regression (among adult males, N = 13, one outlier removed) became perfectly isometric, with slope = 1.00, and narrow CIs straddling that slope estimate (0.77, 1.29); the correlation is also strong at r = 0.88. This helps validate log cube-root body mass as a general and valid measure of overall body size. I excluded one outlier (no. 20, large circle on graph), from the regression; judging by the condition of his teeth (most were missing or stumps) he was clearly the oldest animal of the 82 that I captured, and was abnormally thin for his body length—"*tinggal tulang*," my assistant said ("only bones are left of him").

Thus, while log (mass$^{1/3}$) is on the same scale of measurement as linear traits of interest, making it appropriate for direct comparison with those traits, it is a simple transformation of a measurement (mass) that takes multiple aspects of size into account (length, girth, height, fatness, muscle mass). An example of log (mass$^{1/3}$), compared to log CRL, is that the former captures more information about an animal than does body length or CRL, though the two certainly are strongly correlated. When log (mass$^{1/3}$) was used on the x-axis of the regressions, model error (dispersal about the regression line) was generally reduced and correlations increased in some cases. Log-cube-root mass is also simpler and much easier to interpret than, for example, the first principle component (another popular measure of overall body size), which may be biased depending upon which body parts are measured and included in the analysis (M. Grote, pers. comm.); for example, the first principle component may include allometric components of shape (T. D. Weaver, pers. comm.). The disadvantage of log cube-root mass (compared to crown-rump length or CRL) is that mass is a more ephemeral or temporally variable measure, and can fluctuate seasonally, while log CRL is more stable. Therefore for most traits, I report results of both kinds of regression—log (mass$^{1/3}$) and log CRL as allometric size standards.

I report 95% confidence intervals or CIs (the upper and lower bounds of these intervals are referred to as confidence limits or CLs) for the slopes of these regressions. A 95% CI is the range within which the true slope (or other mean value) of the population is likely to fall, with a probability of 95%—thus CIs are more easily interpreted than the standard error of the mean, which is really just an expected standard deviation of the mean, and whose practical meaning can be unclear.

Any regression whose slope CI overlaps zero is neither graphed nor reported. If a regression's slope CI overlaps substantially with one, it is considered to indicate isometry (a simple linear relationship between the trait of interest and overall body size). If the slope's lower CL is above 1, positive allometry (proportionally larger trait for larger animals) is indicated. If the slope's CI (upper and lower CL) falls entirely between zero and one, negative allometry (proportionally smaller trait for larger animals) is indicated. In cases of positive allometry, the lower CL of the slope is worthy of particular scrutiny when comparing traits in their respective degrees of positive allometry.

In some cases, I needed to check for a subspecific difference in a trait of intertest while controlling for a third variable (such as body mass). For that purpose I simply used GLMs (general linear models) with a mixture of categorical or nominal data (subspecies) and continuous data, controlling for body size.

I strove not to exclude outliers unless there was some biological (as opposed to purely statistical) reason why a certain animal could be considered pathological or abnormal. When an outlier is excluded, I state this clearly and give the rationale for doing so. Before analyzing the canine-height data, I prepared a corrected version of the main data spreadsheet with chipped or apically worn canines excluded, based upon examination of field notes that I made in the margins of my data forms. I used left-side canines for my analyses as there were slightly more of these that were intact. I averaged testes length values since testes show marked asymmetry, and anyway the total physiological investment in testes tissue is the issue of interest; I assumed that testes length correlates well with volume or mass.

### *3.10: The sample and the definition of adulthood*

In this chapter, my aim is a static comparison of functional adults between subspecies, *ochreata* vs. *brunnescens*. Functional adulthood—the attainment of reproductive and somatic maturity—thus is more important than chronological age (or dental age, as a proxy of the same) for the purposes of the present chapter. The following chapter will deal with questions of growth and relative growth throughout the lifespan. In the present chapter, therefore, I consider only adult animals, and I define adulthood with respect to somatic reproductive maturity (not dental age). Thus, for the present chapter, an adult male is one whose testes have descended, and an adult female is a female with full coverage of pink sexual skin in the buttock area.

## **Results**

### *3.11: Growth and life history patterns among adults*

Data on wear of the lower molars indicate that males continue to increase in size beyond the age of puberty (lower molar wear score vs. body mass: Kendall's tau = 0.320, p = 0.059). Therefore, in this sample, adult allometry among males constitutes ontogenetic allometry, not truly static allometry. Likewise, I included in the upper canine height sample all males whose permanent upper canines have erupted; continuing eruption of the upper canine crown reflects continuing growth of the canine root. By contrast, the lack of any correlation of body mass with molar wear among adult females indicates that females stop growing at puberty. Aside from that, there were no females in the sample that had reached puberty and were still nulliparous—all postpubertal females had elongated nipples, indicating suckling. Thus females quickly ceased growth and began reproduction at puberty. For the most part I consider males, since (1) the male sample size is larger, and (2) ontogenetic increase in body size among adult males creates enough variability for allometric trends to be examined among adults.

### *3.12: Body size, insularity and habitat differences:* ochreata *vs.* brunnescens

*Question one:* Have subtle differences in seasonality of rainfall, with concomitant differences in food abundance, led to divergence in body size (dwarfing) in the insular population? The ranges of *brunnescens* and *ochreata* probably differ in resource limitation, but not in predators nor in competitors (Whitten et al. 1987).

<u>Hypothesis 3.1:</u> Resource limitation (seasonally reduced abundance or diversity of fruit) should lead to dwarfism in evolutionarily isolated populations.

- Prediction 3.1.1: *Brunnescens* should be smaller than *ochreata* in overall body size.

Contrary to Prediction 3.1.1, there were no differences in body mass between adult male *ochreata* and *brunnescens* populations (fig. 3.8a). While sample sizes were very small (*ochreata*: N = 10; *brunnescens*: N = 14), there was little difference in mean and median body mass (*ochreata*: mean = 10.03 kg, median = 9.95 kg; *brunnescens*: mean = 9.69 kg, median = 9.70 kg). Mean and median body length (crown-rump length, CRL) differed by < 1 cm (*ochreata*: mean = 50.82 cm, median = 51.55 cm; *brunnescens*: mean = 51.43 cm, median = 51.00 cm) (fig. 3.9b). Notably, the slight observed difference in CRL between the subspecific samples was opposite to the direction predicted, with *brunnescens* very slightly larger.

While the male samples were small, the adult female *brunnescens* sample was smaller still (N = 7 for mass, N = 6 for CRL). As with males, there seemed to be a trend toward larger body size in *brunnescens* (figs. 3.9a, b), especially in terms of body length (CRL) (fig. 3.9b). Nonparametric tests detected no difference, possibly due to the small sample.

Since I wished to compare overall body size between the populations without regard to sex, I used a general linear model (GLM) to compare adult *ochreata* and *brunnescens* while controlling for sex. The GLM provided a somewhat more robust comparison as it allowed an increase in sample size. In this case I used log cube-root mass in order to normalize the distribution of the data and model errors. A parametric model such as a GLM allows one to use all the data without losing information (nonparametric tests generally reduce data to ranks) and have more power than nonparametric tests—therefore I employed a GLM in spite of the modest samples. I did not find any difference in size between adult *ochreata* and *brunnescens*, whether in body length (log CRL) (chi-square = 1.241, p = 0.265), or in log ($\text{mass}^{1/3}$) (chi-square = 0.012, p = 0.913).

Finally, I used another GLM to compare body sizes between the subspecies while controlling for both sex and age, pooling all age classes. This method enabled me to increase the sample size to N = 82 (for mass; N = 81 for CRL), thus increasing power and reducing the likelihood of type II error. When all age classes were included in the subspecific comparison, the greater body size in *brunnescens* became moderate for mass, and highly statistically significant for body length (log $[\text{mass}]^{1/3}$: chi-square = 3.361, p = 0.067; log CRL: chi-square = 10.702, p = 0.001). The direction of the difference is, again, opposite to that predicted under insular dwarfism via resource limitation (expected: *ochreata* > *brunnescens*; observed: *brunnescens* > *ochreata*), and the greater difference among juveniles as compared to adults suggests that the overall difference arises due to faster early growth in the *brunnescens* sample, with the populations converging in body size sometime after they reach adulthood (see chapter four). Such a pattern is almost certainly due to environmental causes (Altmann and Alberts 2005)—in this case it is likely due to crop-raiding by the *brunnescens* population.

The subspecies also do not differ in the allometry of body bulkiness (mass vs. body length), forearm girth or thigh girth (regressions performed but not shown here).

### *3.13: Subspecific divergence in head breadth*

*Question two*: Have *ochreata* and *brunnescens* diverged in any relative body dimensions, and if so, which dimensions?

I do not present specific hypotheses and predictions for this question, because I have no *a priori* reason to expect a particular direction of divergence in any particular trait.

I measured head breadth in three ways: bizygomatic breadth, bicanine breadth, and via photography. Results from the last of these methods will be examined in a future paper; the former two will be examined here. Unfortunately, I was able to obtain bizygomatic measures for only three adult male *ochreata* (due to a lack of spreading calipers in 2002), though I obtained the measure for all adult male *brunnescens*. I have a full set of bicanine measures for both subspecies, however. Bicanine breadth correlates with bizygomatic breadth in this sample (Pearson $r = 0.88$, $p < 0.0001$; Kendall's tau = 0.66, $p < 0.0001$). The partial correlation of log bicanine breadth with log bizygomatic breadth, controlling for log CRL, is 0.60. I therefore used bicanine breadth as a measure of overall head breadth.

The results of a GLM comparing log bicanine breadth between subspecies (reproductive adults only), controlling for body size and sex, suggested that relative head breadth is smaller in *brunnescens* than in o*chreata* (controlling for log CRL: chi-square = 4.802, $p = 0.028$, $N = 41$; controlling for log [$\text{mass}^{1/3}$]: chi-square = 3.533, $p = 0.060$, $N =$

42). As has often been the case in this study, the results are stronger when log CRL rather than log ($mass^{1/3}$) is used as the standard of size comparison.

A reduced major axis regression of log bicanine breadth on log ($mass^{1/3}$) showed a strong relationship, with $r = 0.87$ (fig. 3.10a). There was a slight tendency toward positive allometry but the relationship is essentially isometric, since the 95% CI overlapped with one. Females appear smaller than males to a degree not explained by allometry. The subspecific pattern is not very strong, however. Among males, eight *ochreata* cluster above the regression line while only two are beneath it; male *brunnescens* show no perceptible pattern. In females, the scatterplot does not suggest any subspecific difference except for one outlier *brunnescens*.

When I regressed log bicanine breadth on log CRL for adult males (pooling subspecies) (fig. 3.10b), error about the regression line was greater than in most of the allometric regressions ($r = 0.76$), but the subspecific pattern was more clearly apparent. Among males, *ochreata* tend to cluster above the regression line and *brunnescens* below it, though there are several exceptions. Among females, the largest in relative head breadth are almost all *ochreata*. Again, females cluster well below the male regression line, suggesting that the sex difference is not necessarily a byproduct of difference in body size.

On the whole, the hypothesis that *ochreata* and *brunnescens* have diverged in head breadth receives tentative support.

### *3.14: Convergent selection within populations?*

*Question three:* If stasis is observed between the two populations, is stasis enforced by on-going convergent selection (sexual or ecological) within each population?

*Body size sexual dimorphism and secondary sexual traits*— To compare overall body size between sexes, I performed GLMs of body size vs. sex. I pooled subspecies here, since no difference was found among adults from different subspecies (section 3.10). I found substantial adult sex differences in both log ($\text{mass}^{1/3}$) (Van der Waerden Z = -4.83, $p < 0.0001$, N = 42; fig. 3.11a) and log CRL (Van der Waerden Z = -4.02, $p < 0.0001$, N = 41; fig. 3.11b).

Mean adult female mass is 6.41 kg (n = 18; CI = 6.13, 6.68), while mean adult male mass is 9.83 kg (N = 24; CI = 9.03, 10.63), resulting in a body mass sexual dimorphism ratio of 1.53. Mean adult female CRL is 46.2 cm (N = 17, CI = [45.4, 47.1]), while mean adult male CRL is 51.2 cm (N = 24; CI = [49.7, 52.7]), resulting in a body length sexual dimorphism ratio of 1.11. Thus while the sexes are significantly different in both dimensions, the difference in length is quite small (about 10%) compared to the difference in mass (about 50%) showing that the difference in body size has much more to do with musculoskeletal bulkiness than with body length. This fact also points to the limitations of studies that rely upon linear measurements of museum specimens (e.g. skull length), and the importance of including mass data on museum tags.

Males were also far more variable than females in body mass, as mentioned above, which probably results in part from the fact that males continue their growth—

especially in body mass—long after reaching sexual maturity (descent of testes; see section 3.11). The greater variability of males can be seen in the raw mass x sex scatterplot (fig. 3.11a), and in the difference in standard deviations (SD) for mass: male SD = 1.90, female SD = 0.55, giving a variance-dimorphism ratio of 3.45. On the other hand, the greater variance in male than female mass could result from males' higher mean mass; however, the coefficient of variation of mass (which controls for differences in mean mass) is also higher in males (CV = 19.33) than in females (CV = 8.52). This sex difference in variability of mass undoubtedly results from males' continued growth after puberty (see section 3.11).

Hypothesis 3.2: Male upper canines (which males use in slashing attacks) and testes are under strong but conservative (non-divergent) sexual selection in both subspecies.

- Prediction 3.2.1: Adult male upper canine height will show stronger positive allometry than will lower canine height (both sexes) and adult female upper canine height.

Morphological traits that are thought to be subject to strong sexual selection typically show strongly positive allometry (i.e., rapid growth relative to overall body size) in a wide range of species, from invertebrates to mammals (Gould 1973; Kelly 2005; Kinahan et al. 2007; Lüpold et al. 2004; Miller and Burton 2001; see section 3.4).

The allometry of left upper canine height in males indeed appears more strongly positive than that of the somatic traits examined above, with a slope of 3.619 (CI = [2.537, 5.161]) when regressed on log ($\text{mass}^{1/3}$) (fig. 3.12a), and a slope of 3.731 and a *lower* CL of 2.172 (upper CL = 6.410) when regressed on log CRL (fig. 3.12b). The regression on mass shows a tighter, more linear relationship (r = 0.82) than does the regression on CRL (r = 0.70). A non-parametric analysis also showed a correlation of log upper canine height with log CRL (Kendall's tau = 0.504, p = 0.002) and with log ($\text{mass}^{1/3}$) (Kendall's tau = 0.495, p = 0.002). When age (molar wear score) was controlled, a partial correlation of r = 0.69 of log upper canine height with log CRL remained; age (molar wear score) did not correlate with upper canine height when log CRL was controlled. The scatterplot shows no subspecific difference, confirmed by a GLM analysis (below). I excluded a young but sexually-mature male (no. 62) whose upper canines appeared to have been impacted. His gums had swollen more than those of other young males whose upper canines were still erupting, and he was quite large for a male with incompletely erupted upper canines—hence I considered him a biologically abnormal (pathological) outlier and removed him from the regression.

In females, there is, again, simply no statistically significant relationship between body size and upper canine height, at least in terms of allometry among adults; there was likewise no correlation between log cube-root mass and log canine height in females (Kendall's tau = -0.081, p = 0.650). It is apparent, however, that females cluster well below the male regression lines for canine height (fig. 3.12), suggesting that females' smaller upper canines are not merely a correlated effect of their smaller body size. There seems to be no subspecific difference among females, moreover, in how far they are from the male regression line. A GLM of upper left canine height in adults of both sexes, with body size (log [mass$^{1/3}$] or log CRL), subspecies and sex as independent variables, confirmed a highly significant sex difference in upper canine height independent of body length (chi-square = 28.868, $p < 0.0001$), and of body mass (chi-square = 15.141, $p < 0.0001$), but no effect of subspecies.

We can also compare the degree of sexual dimorphism (male/female) in the raw upper canine data with that of raw body mass or CRL, to confirm that dimorphism is in fact greater than one would expect due to allometric effects of body size. Mean male upper canine height is 22.75 mm (CI = [20.43, 25.06]; N = 21), while the mean for females is 11.07 (CI = [10.38, 11.76]; N = 16), giving a dimorphism ratio of 2.06—greater than the mass dimorphism ratio of 1.56 (fig. 3.13; cf. fig. 3.11; see also table 3.1). The degree of dimorphism in variance is also quite large, but is about the same as the variance dimorphism for body mass, as would be expected since canine height correlates with body mass, which in males increases post-pubertally and is thus highly variable (see section 3.11).

In adult males, lower left canine height shows no allometric pattern whatsoever, with a slope not significantly different from zero (scatterplot not shown).

- <u>Prediction 3.2.2:</u> Adult male upper canine height will show less variation within sexes (i.e., lower CV; subspecies pooled) and greater sexual dimorphism compared to other traits measured with comparable precision (lower canine height and bicanine breadth).

In a variety of animals, traits thought to be under sexual selection show not only positive allometry, but also relatively large variability (Kinahan et al. 2007; Lüpold et al. 2004; Miller and Burton 2001), though the causal link with sexual selection has been questioned in a study of invertebrates (Bertin and Fairbairn 2007). The coefficient of variation (CV), or the standard deviation as a percentage of the mean, is one means of comparing variability among distinct morphological traits.

In accord with my expectation of stabilizing sexual selection, I predicted lower variability in upper canine height than in comparable traits (i.e. other hard traits of a similar magnitude that permitted precise measurement with calipers, such as lower canine height and bicanine breadth). In fact, however, male upper canine height seems to be more variable than any other trait, male or female (table 3.1)—a result that is in line with previous morphometric studies of traits thought to be under sexual selection in mammals (Kinahan et al. 2007), but which seems—along with the pattern of strongly positive allometry in upper canines—to indicate directional but not stabilizing sexual selection. The selection would seem to be in the same direction and magnitude in both *ochreata* and *brunnescens*, however, or opposed by the same constraints.

Within sexes, there is a clear trend in variation—upper canines are far more variable and also more sexually dimorphic in terms of both variance and mean, than comparably-measured traits (table 3.1). There is, however, higher sexual dimorphism in certain other traits (such as head breadth) than might be expected based on sexual dimorphism in body mass and body length. Aside from that, females show the same within-sex trend of greater variability in the upper canines compared to the other traits (table 3.1).

- Prediction 3.2.3: Scrotal circumference and mean testis length will show positive allometry.

Log scrotal circumference seems to show moderately postive allometry (larger males have proportionally larger scrotums) with respect to log ($\text{mass}^{1/3}$), with a slope of 2.04 (CI = 1.50, 2.76; fig. 3.14).

Testes length is more difficult to measure than scrotal circumference; as expected, there is more dispersion and error in the data than there is in the scrotal circumference data. As usual, there is more dispersion in the brunnescens data, and in the case of this regression, the slope of the brunnescens-only regression was not significantly different from zero. The overall (both subspecies) regression was significant, however, and also had a slope significantly > 1 (2.73; CI = 1.38, 5.41; fig. 3.15), again suggesting moderately positive allometry, as the lower CL is similar to that of scrotal circumference.

The degree of positive allometry in testes size is not as great as that of male upper canine height, however, even though both of these are epigamic characters that are emplaced at puberty and must grow quickly (subadult males' testes are still very small just before they descend; they can be palpated in the lower abdomen). This suggests that perhaps upper canines are under stronger sexual selection than testes. Indeed, it is common for sexually-selected weaponry to show the strongest positive allometry of any body part, even in invertebrates (Kelly 2005). Although it is expected for any sexually-selected trait to show positive allometry, the fact that the positive allometry of testes is markedly less than that of maxillary canines, suggests that the ontogenetic increase in size of testes in sexually-mature males is less than that of maxillary canines. That pattern would support an hypothesis of relatively greater investment in weapons (and agonistic contest competition, or display, for mates) by older males, with relatively greater investment in testes (and sperm competition) by younger males (Petrie 1992; Stockley and Purvis 1993).

Certainly there has been no divergence between the subspecies in upper canine height (see above). For testes, the evidence is equivocal. GLM models show highly significant subspecific differences in log average testicular length (controlling for log $[\text{mass}]^{1/3}$: chi-square = 18.52, p = 0.004; controlling for log CRL: chi-square = 9.66, p = 0.002), as does the allometric scatterplot (fig. 3.15). GLMs of scrotal circumference, however, show no subspecific difference whatsoever. Since testes length was very difficult to measure precisely, and the two measures' results should replicate one another if there were a real difference, I suspect that there has been no subspecific divergence in testes size.

*Limb circumferences*—A regression of log thigh circumference on log cube-root mass showed that there is no subspecific difference in girth of the thighs relative to body size. Overall slope for males was 1.800 (CI = 1.409, 2.299). The LCL was still > 1 at 99.9% confidence level. When regressions were performed separately for males of each subspecies, the slope for *brunnescens* only fell below one, probably due to dispersion in the *brunnescens* data. For females, slope was estimated at 2.605 (95% CI = [1.233, 5.507]), though the slope fell below one when confidence level was increased to 99%, probably owing to the small sample for females. I therefore conclude that, for both males and females, girth of the thighs seems to show slightly positive allometry, growing slightly faster than overall body mass.

I excluded one male outlier (no. 59: large square in this graph) that, when included, changed the slope only imperceptibly (1.828) and affected mostly the intercept and the breadth of the CI, though the lower 95% CL was still 1.199. This was the relatively old alpha male of the primary-forest group (site B-1), which had skinny thighs in spite of a quite respectably high body mass; regarding his thighs, I wrote in my field notes, "Looks big, but mostly fluffy fur." The largest males tend to be well-coiffed, probably due to extensive allogrooming, yet in this case the coiffure hid singularly unimpressive thighs. I do not have any evidence that this male's thighs were pathological or biologically abnormal, however. When the outlier is included, the overall (both subspecies) regression (but not the *brunnescens*-only regression) remains statistically significant (> 0) and significantly > 1 as well, though the lower bound of the CI is closer to 1; the intercept is affected slightly.

I next examined forearm girth relative to body size. Again, it is apparent that the two subspecies do not differ in their body proportions, based upon the very similar slopes with largely overlapping CIs. As with thigh circumference, we see mildly positive allometry in the overall regression for males (slope = 1.516, CI = 1.161, 1.981), with a stronger relationship in the male *ochreata* regression, and more data dispersion (and lower correlation) in the male *brunnescens* regression. The latter regression was still significantly > 0, but the lower CL fell below one, as in the thigh regression. Females also showed slightly positive allometry (slope = 1.890, CI = [1.310, 2.727]) in forearm circumference.

The pattern of positive allometry rather than isometry for girths of thighs and forearms may require an explanation. For example, larger monkeys that are largely arboreal and canopy-living (as seems to be true in this species: pers. obs.) may require proportionally larger thighs to accomodate more muscle for leaping, since power and muscle mass are negatively allometric to body size (see chapter four, section on limb proportions). On the other hand, the forearm should not show such a trend, yet the 95% CIs of thigh and forearm slopes overlap substantially. Aside from that, since the circumference measures included fur, the fluffiness factor may have introduced some error, potentially exaggerating the degree of positive allometry: the largest and presumably dominant male of the *ochreata* group, whose fur was thick, fluffy and beautifully groomed, had a rather large measured forearm girth even considering his very large body size.

## Discussion

### *3.15: Body size and secondary sexual traits: stasis and an absence of insular effects*

In isolated populations, some divergence is expected via genetic drift alone (Lynch 1988). Therefore, the lack of change (other than probably environmentally-induced) observed between *ochreata* and *brunnescens* in body size, secondary sexual traits such as canine teeth and testes, and sexual dimorphism thereof, could be caused by stabilizing selection within these populations (T. D. Weaver, pers. comm.). While the small adult sample sizes make it difficult to make robust inferences about histories of selection (stabilizing or otherwise), the relatively short time scale of separation in this case (ca. 9 kyr) reduces the likelihood that the apparent lack of divergence masks ancient histories of selection that have since become obscured by subsequent events (Lemos et al. 2001a). Of course, the possibility of some admixture between ochreata and brunnescens during the Pleistocene, perhaps via rafting, cannot be ruled out; the genetic evidence suggests that admixture is unlikely, however (see section 3.5, above).

Furthermore, while the subspecific samples are confounded by habitat-diet differences (all but four of the adult *brunnescens* sampled were from a crop-raiding group, while the *ochreata* were primarily wild-feeding), the hypothesis of evolutionary divergence (insular dwarfism) makes a prediction of difference in size (*ochreata* > *brunnescens*) that is clearly opposite to the trend expected under environmental influence of habitat or diet (*brunnescens* > *ochreata*). Therefore I think it is reasonable to conclude, at least provisionally, that there is no evolved difference between *ochreata* and *brunnescens* in body size, and certainly there is no difference between adults (within sexes) that approaches statistical significance. On the other hand, there is the possibility that a real evolutionary difference exists but was obscured by environmental factors—again, due to the opposite direction of their expected effects. That possibility seems unlikely, however, as I demonstrate in the following chapter (chapter four) that there definitely are environmental effects upon body size—but these effects are seen only in immature individuals, whereas the present chapter (chapter three) compares only adults between populations.

Some morphometric data collected on free-ranging adult monkeys suggest that *M. tonkeana* has diverged from the other macaques of southern Sulawesi (*M. ochreata sensu lato* and *M. maura*) with respect to a somewhat larger (or at least longer) body and a wider head (Froehlich and Supriatna 1996). Fooden's (1969) data on cranial length (his fig. 16) and body length (p. 111—but maximum value is from an abnormal individual) also seems to support a somewhat larger body size for *M. tonkeana*, and possibly *M. hecki*, relative to other Sulawesi macaques. While it is currently unclear whether *M. tonkeana* or *M. maura* is the sister species to *M. ochreata sensu lato* (*M. maura* is similar in size to *M. ochreata sensu lato*), it is at least known that *M. tonkeana* has been separated from *M. ochreata sensu lato* for a far longer time than the *ochreata* and *brunnescens* populations have been isolated from one another. The apparent divergence of *M. tonkeana*'s body size suggests that body size divergence can occur within the Sulawesi macaques, which perhaps strengthens the case for stabilizing (or convergent) selection on body size in *ochreata* and *brunnescens*.

Aside from evolutionary stasis in body size and size sexual dimorphism on the short time scale (ca. 9 kyr) of *ochreata-brunnescens* separation, there is evidence that body size (Hamada et al. 1985) and size sexual dimorphism (Froehlich and Supriatna 1996) have remained stable throughout Sulawesi (in the other Sulawesi macaques), though the data of Hamada et al. is from pet animals. Data collected on wild *M. tonkeana* by Froehlich and Supriatna (1996) (N = 7 males, 8 females) show a sexual dimorphism ratio in crown-rump length of 1.13, whereas for booted macaques (subpecies pooled) the ratio is 1.11. Since *M. tonkeana* must have separated from *M. ochreata* much longer ago than the *ochreata-brunnescens* split, long-term stability of size sexual dimorphism is suggested.

*Insular effects on body size*—What makes the overall body size results most interesting is the absence of insular dwarfism, even though Buton and Muna collectively have a small land area. Aside from that, Sulawesi macaques as a whole show no reduction in body size—even though bovids (anoas, *Bubalus* [*Anoa*] spp.) have become markedly dwarfed on Sulawesi. Anoas form a very old lineage according to molecular evidence, but then, there is some evidence that the Sulawesi macaques may be very old as well. Certainly dwarfism occurred in the elephant-like stegodonts in extreme southwestern Sulawesi (which was then almost certainly a separate island, larger in size than Buton plus Muna islands) during the Pliocene. There is enough data on the Walanae fauna of Pliocene southwest Sulawesi (including the stegodonts) to note some temporal trends—but no trend in body size has been observed, only an increase in hypsodonty (crown height) of the molars.

The anoa and stegodont dwarfism are undoubtedly due to ecological factors associated somehow with insularity. Foster (1964) pointed out that reduction or elimination of predators (due to depauperate fauna on islands) is more likely for large-bodied animals like artiodactyls than it is for smaller animals, since relatively few predators are large enough to eat the former. Foster (1964) further suggested that the lack of predators on islands could lead to greater competition for food among large animals. Prothero and Sereno (1982) use allometric and paleoecological data on Miocene dwarf rhinos from a continental plain to argue that dwarfism (insular or otherwise) may be associated with ecotones and with browsing in large animals, and the isolation on islands tends to be associated with browsing as an ecological strategy. If a lack of predators is particularly important as a cause of insular dwarfism in large animals (Foster 1964), then one would expect that macaques would have become smaller in Sulawesi relative to their Sunda shelf relatives, but there seems to be no evidence that any size reduction has occurred.

At any rate, there does seem to be an association between dwarfism and island-living in large (> 1 kg) animal taxa, and more data on ecology, paleoecology, and morphological data from insular fossil mammals are needed to solve the mystery of insular effects on body size. At the least, the fact that Buton island has essentially the same vegetation (with mild differences in rainfall seasonality), potential macaque competitors, and potential macaque predators as peninsular southeast Sulawesi—and macaques (and apparently anoas, suids, and other mammalian taxa) have not experienced dwarfing—suggests that either (1) ecological differences that are relevant to the species in question are necessary for insular dwarfism to occur, or (2) body size changes may occur too gradually to be detected on short time scales (Anderson and Handley Jr. 2002), or both.

Anderson and Handley (2002) found gradual dwarfing in three-toed sloths, as a linear function of time; the trend was detectable on a Holocene time scale, but then, sloths' generation time is likely shorter than that of macaques. It could be the case that body size is somehow constrained to diverge slowly, that other traits are inherently capable of evolving faster. The available evidence from a broad spectrum of mammalian taxa suggests, however, that that explanation is unlikely to be true—under the right conditions, body sizes can change drastically in just a few thousand years, or even less (Lister 1989; Millien 2006). Rather than inherent differences in possible evolutionary rate (or phylogenetic inertia) among traits, some ecological factor (or lack thereof, in the present case) is more likely at work.

Island area is one factor that has been proposed to affect the degree of dwarfing (though probably via some unknown ecological mechanism) (Heaney 1978). The present data can be counted as evidence against that hypothesis, since it shows that dwarfing in macaques has occurred neither on Sulawesi as a whole (relative to closely-related Sunda Shelf macaque species), nor on Buton—which has a much smaller land area than does Sulawesi. Anoas, moreover, have undergone dwarfing on Sulawesi, but not on Buton (relative to Sulawesi)—again suggesting that island size is not a determining factor in size divergence, and replicating the results of Anderson and Handley (2002) on that question.

Of course, a more specific ecological hypothesis is that some ecological factor correlated with island area or with insularity in general—such as a lack of predators or competitors on islands, or resource limitation on islands—is responsible for insular dwarfism in relatively large animals (> 1 kg). The present study provides evidence against the hypothesis that *moderate* resource limitation (here, in the form of increased seasonality of rainfall and likely seasonal limitation of primary productivity) leads predictably to insular dwarfism. While the present study does not include replication in other pairs of insularly-isolated sister species, it does at least offer some degree of ecological detail, rather than leaving resource limitation on the conjectural level. It would be preferable, though, to have yet more detailed data on differences in forest productivity on large spatial scales throughout southeast Sulawesi, as well as replication from other mammalian taxa on either side of the Buton-Tiworo strait, or other straits of similar age and with similar environmental gradients. Of course, severe resource limitation could still have led to insular dwarfism in this case, had it occurred during the Holocene.

It would be preferable, of course, to have an integrated theory of dwarfism (insular and continental) rather than a separate theory for each geographic circumstance. Perhaps ecological factors really are the underlying cause of dwarfing in both cases, but dwarfing tends to show up more often on islands because (1) islands, especially small islands, tend to have a limited range of available habitats or biomes, especially in climatically extreme periods; or (2) islands share certain other ecological features in common, at least within broadly similar latitudes; or, (3) ecological selection "for" dwarfism is widespread in continental areas, but actual divergence (long-term response to selection) is impeded by gene flow except when ecological selection is particularly strong (Foster 1964). It could be the case that large animals tend to be grazers on continents, but after dispersal to islands are "trapped" in a small land area where grasslands may nearly disappear during warmer periods, and must resort to browsing, forcing a decrease in body size due to consequent food limitation. On the other hand, conditions of ecological competition with other large ungulates could lead to the occasional case of continental dwarfism via niche separation (Prothero and Sereno 1982).

While many broad-scale, multi-taxa comparative papers have been written on insular body size effects, intensive ecological comparisons of a smaller number of species—focusing on the exceptions to the pattern—still seem to be missing.

We are still far from knowing what combination of island area, time, gene flow, and ecological selection might lead to insular dwarfism and gigantism, though a more complete theory would help us make sense of body-size changes among hominin populations on Flores, Palau, and various dwarfed continental populations of modern humans.

### *3.16: Subspecific divergence in head breadth*

Where both the GLM results and the allometric models are concerned, the strength of the subspecific difference in head breadth seems to depend upon whether trunk length or body mass is used as the standard of comparison. It is difficult to say whether log CRL or log cube-root mass should be considered, *a priori*, the more valid body-size standard for allometry. Body mass is far more ephemeral than CRL, and CRL as a simple linear body dimension, is perhaps expected to covary well with other linear dimensions. That would not explain the tighter relationship of bicanine breadth with mass than with CRL, however, and body mass also includes more information about overall body size than does CRL. Whether that information is extraneous (and possibly confounding) or relevant is unclear to me.

Macaques from the southern part of Sulawesi (*M. maura*, *M. o. ochreata*, and especially *M. tonkeana*) tend to have relatively wide heads; therefore it would likely be *brunnescens*, not *ochreata*, that had diverged from the ancestral type (*M. nigra*, in the northern tip of Sulawesi, also have relatively narrow heads, surely derived independently) (see Fooden 1969: 36-37). Fooden (1969: 36-37) presents some evidence that *brunnescens* has proportionally narrower heads than other southern Sulawesi macaques (I had not read that part of Fooden's book until after I obtained and analyzed the data), but his *brunnescens* sample was very small, and he was forced to use head length as the standard of comparison (rather than overall body size) because museum skulls were his source of data.

Data from my study may contradict the results obtained by Albrecht (1978), however. Albrecht's data on bicanine breadth indicated that female *ochreata* and *brunnescens* both have equally narrow heads relative to those of other macaques, while his male *ochreata* have slightly narrower bicanine breadths than male *brunnescens* (Albrecht 1978: his fig. 15). Albrecht does not report any statistical comparisons of univariate measurements for individual species and subspecies; he is mainly concerned to contrast Sulawesi macaques as a group with non-Sulawesi macaques. Thus the lack of subspecific difference in bicanine breadth reported by Albrecht may have to do with the larger taxonomic scale, and lower resolution, of his study. Albrecht (1978: 58) does report that *brunnescens* has relatively narrow bizygomatic and biauricular breadths, but not bicanine breadths; it is not clear from the context, however, nor from his scatterplots (his fig. 13), whether he is comparing *brunnescens* to *ochreata* or to the other Sulawesi macaques as a group.

Thus my study offers some support, with a somewhat larger sample and statistical control for body size, for Fooden's (1969) proposition that *brunnescens*' heads have become narrower than those of other southern Sulawesi macaques. While the observed difference is small, its potential significance is strengthened by the fact that Fooden

(1969) and I each observed it with different samples (museum skulls vs. living specimens) and different but related measurements (bizygomatic vs. bicanine breadths). I think that the difference in relative head breadth between these two populations, though slight, is probably due to evolutionary divergence. Certainly, more marked, long-term divergence in head breadth in other, more distantly-related Sulawesi populations (e.g. *M. tonkeana*: see Fooden 1969) suggests that head breadth is an evolutionarily labile trait in these species, which somewhat increases the plausibility of an hypothesis of evolutionary divergence.

Since the difference in head breadth between subspecies is so slight, and there are no known effects of head breadth upon ecological performance in these primates, there is a distinct possibility that divergence in head breadth was caused by genetic drift—perhaps due to a small effective population size for *brunnescens*, owing to peripatric isolation in a small range (relative to the range of *ochreata*). My observations suggest that the extreme scarcity of water in many areas of Muna Island and the seasonal conditions on both Muna and Buton Islands—with macaques and their preferred food trees perhaps tending to cluster near large year-round creeks—may further reduce population density within the already small range of *brunnescens*, though at present data are inadequate for a formal test of that hypothesis.

Divergence in cranial shape by genetic drift has been suggested to have occured among some New World primates (Marroig and Cheverud 2004) and between Neandertals and modern humans (Weaver et al. 2007). When one compares taxa that have been separated for many thousands of generations, however, it is possible that rapid adaptive change via natural selection did occur in the past, yet is undetected by rate tests (the type of test used to distinguish drift from selection) due to long-term stasis bracketing the rapid, intense episode of selection (Lemos et al. 2001b). The present study may provide a bit of additional evidence for the divergence-by-drift hypothesis for cranial characters (though I do not provide a formal rate test here), since I compare two populations separated for only about 9 kyr—thus there is less potential for a confounding effect of long-term stasis.

### *3.17: Male secondary sexual traits: strong selection without divergence?*

The strongly positive allometry of male maxillary canines, combined with their high degree of variance (CV), could be evidence that the upper canines are under strong, directional sexual selection. Such selection may be stronger, in fact, than the selection maintaining relatively large testes in *M. ochreata*. That possibility would make sense in light of the apparent social system of *M. ochreata*, which seems to be largely "age-graded," and the growth pattern in which males (especially in wild-feeding subpopulations) continue growing gradually long after puberty (see chapter four). In such a social system, the oldest and largest male monopolizes most mating opportunities, although young, immigrant males can challenge him. In this type of breeding system, which Watanabe and Matsumura (1996) describe as intermediate between one-male and multi-male systems, direct agonistic contest competition (or, more usually, the risk or threat thereof) will be more important than sperm competition.

Still, the relatively large testes of *M. ochreata* suggest that younger, smaller males must be able to compete for fertilizations (Harcourt et al. 1981; Harcourt et al. 1995; Stockley and Purvis 1993). In fact, when foraging during the day, forest-living *M. ochreata* tend to split up into foraging subgroups or to move through the canopy in a sort of lazy procession; on one occasion I estimated group spread (in the canopy)as 100-200m. The alpha male's view across the canopy must be heavily obscured by layers of leaves, as it was difficult for people on the ground to observe monkeys' behavior in the canopy. On one occasion, I observed a female about 100m from the other members of her group; on another occasion I saw a lone adult female on a hilltop, with no other group members visible or audible in the vicinity. Mating, meanwhile, takes only about two seconds (pers. obs.). I did also observe lone males, but no more often than I observed lone females.

The spatial behavior of Sulawesi macaques in primary rainforest contrasts somewhat with the high group cohesion during movements and relative terrestriality seen in oft-studied Sulawesi macaques that live in areas with volcanic soil (*M. nigra*), or on limestone outcrops next to a road (*M. maura*) (Matsumura 1991; Reed et al. 1997), or near a road in heavily disturbed forest (*M. ochreata*: pers. obs. at site O-1). Limestone and volcanic habitats, however, are probably historically marginal for Sulawesi macaques—Sulawesi macaques have likely been relegated to these marginal habitats due to increasing human population density in the recent past. I also have come to suspect that the "fission-fusion social organization" that has been alleged to be an adaptation of chimpanzees (*Pan troglodytes*), spider monkeys (*Ateles* sp.) and a few other mammals (including, allegedly, human hunter-gatherers), is simply a common pattern of spatial behavior in forest-living primates and is quite facultative, rather than being a genetic adaptation or some sort of ecological specialization, let alone a hominid homology.

The observations on primary-forest-living (and roadside) booted macaques, combined with data on relative testes size (this chapter), suggest that subordinate male Sulawesi booted macaques must engage in at least some sneaky mating, even if the relatively old alpha male dominates most "public" matings. Still, the relative rarity of multiple fully-swollen females may allow the dominant male to monopolize most matings even in a natural, forested environment, though behavioral data on that question is lacking.

Thus I suggest that perhaps male mating competition may occur via a mixture of agonistic competition and sperm competition, with the former generally exerting stronger selection. The loud call of Sulawesi macaques, which according to behavioral studies of other Sulawesi species is usually uttered by the alpha male (Kinnaird and O'Brien 1999; Watanabe and Matsumura 1996), may be a way of intimidating other males into staying away from females when the alpha male cannot directly observe the other males. The loud call has previously been interpreted as a signal by the alpha male of his readiness to intervene in agonistic conflicts between other group members (Kinnaird and O'Brien 1999), although these two functions are psychologically related (both involve intimidation) and need not be mutually exclusive. The observation that males are more responsive than females to the loud call (Muroyama and Thierry 1998), and that it is given mainly by the alpha male (Kinnaird and O'Brien 1999; Watanabe and Matsumura 1996), bolsters the case that the call may function in sexual intimidation.

Nevertheless, reproductive skew must not ultimately be extreme, as younger males who survive to full maturity are likely to have their eventual turn at dominance and a burst of reproduction. On the other hand, I trapped an extremely old male *ochreata* with an all-white coat, a very thin build with reduced fat and muscle, and only stumps remaining of his canines with several other teeth missing. Thus it seems that male *M. ochreata* probably reach their reproductive peak in late adulthood, then rapidly decline in their old age. Such a life history of largely delayed reproduction in males is probably especially marked in natural, wild-feeding populations (see chapter four). All this is based on morphological inference, however, and detailed behavioral data (especially for *M. ochreata*) are still lacking.

*Tables*

| | CV-M | RMA-M | N | CV-F | N | SD |
|---|---|---|---|---|---|---|
| Upper canine height | **22.4** | **3.6** | 21 | 11.8 | 16 | **2.1** |
| Lower canine height | 7.3 | -- | 19 | 7.5 | 17 | 1.6 |
| Bicanine breadth | 9.2 | 1.4 | 23 | 4.9 | 18 | 1.3 |

**Table 3.1.** Indications of possible sexual selection on male upper canine height. Coefficients of variation (CV-M, males; CV-F, females) sexual dimorphism (SD), and allometric coefficient (RMA-M, males only) of three traits. RMA-M are estimated slopes of reduced major-axis regressions of log-transformed variables on log cube-root body mass (for lower canine height, no significant non-zero slope). No subspecific differences were found, within sexes. The traits selected were hard, precisely-measurable features of similar magnitude, therefore measurement error should be small and comparable among these three traits, and there should be no magnitude-related bias in the CVs. Only left-side measurements are reported in this table. Male no. 62 was excluded from upper canine data only (included for other measures), due to his impacted upper canines. The higher CVs for males relative to females in upper canine height and bicanine breadth may reflect the continued growth of males beyond puberty—on the other hand, CVs for lower canine height are similar between males and females. Note that SD of lower canine height is similar to SD in body mass (1.5; see text).

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*Figures*

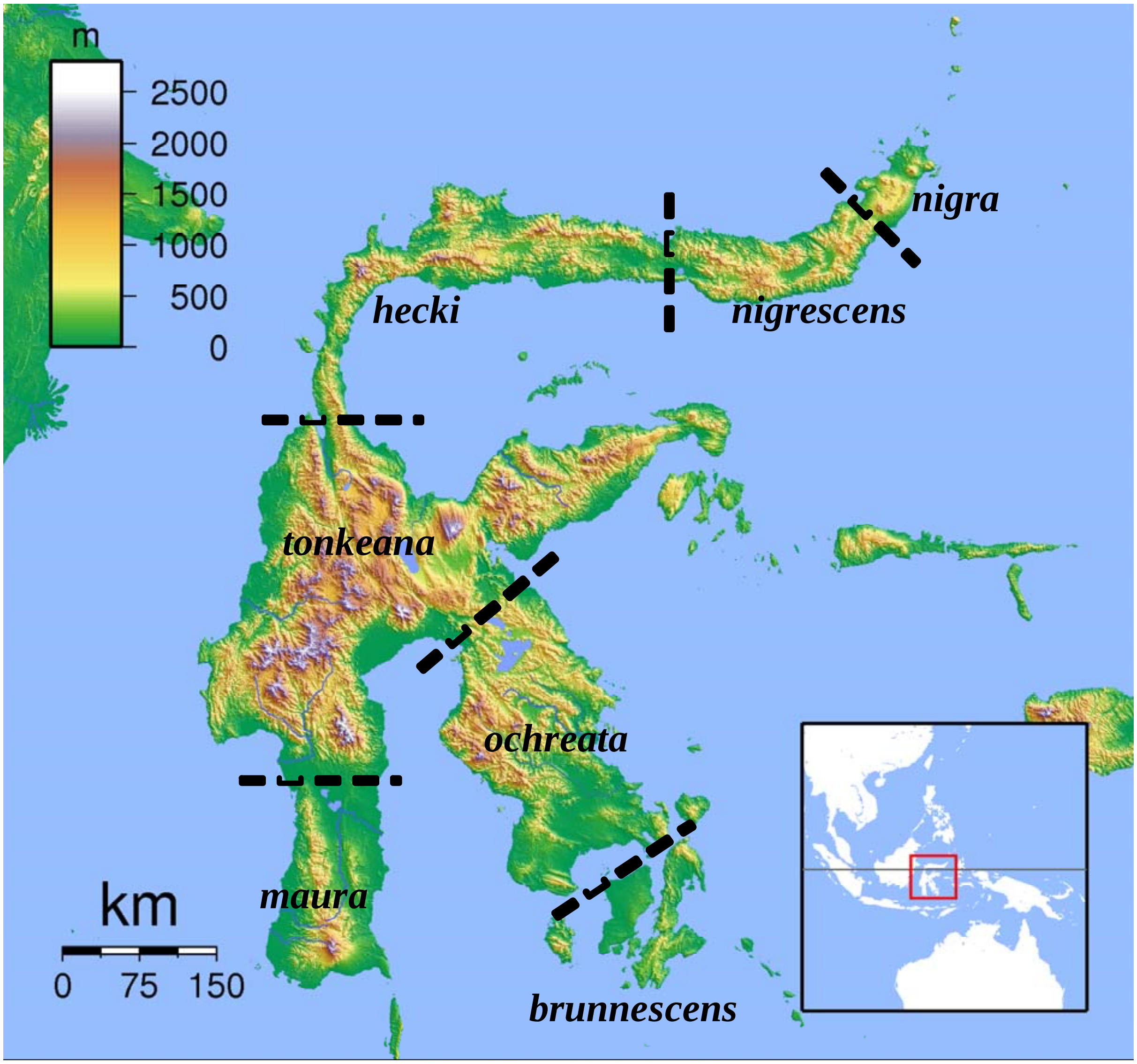

**Figure 3.1.** A map of Sulawesi showing general topography and macaque population ranges (modified from a figure obtained from Wikipedia).

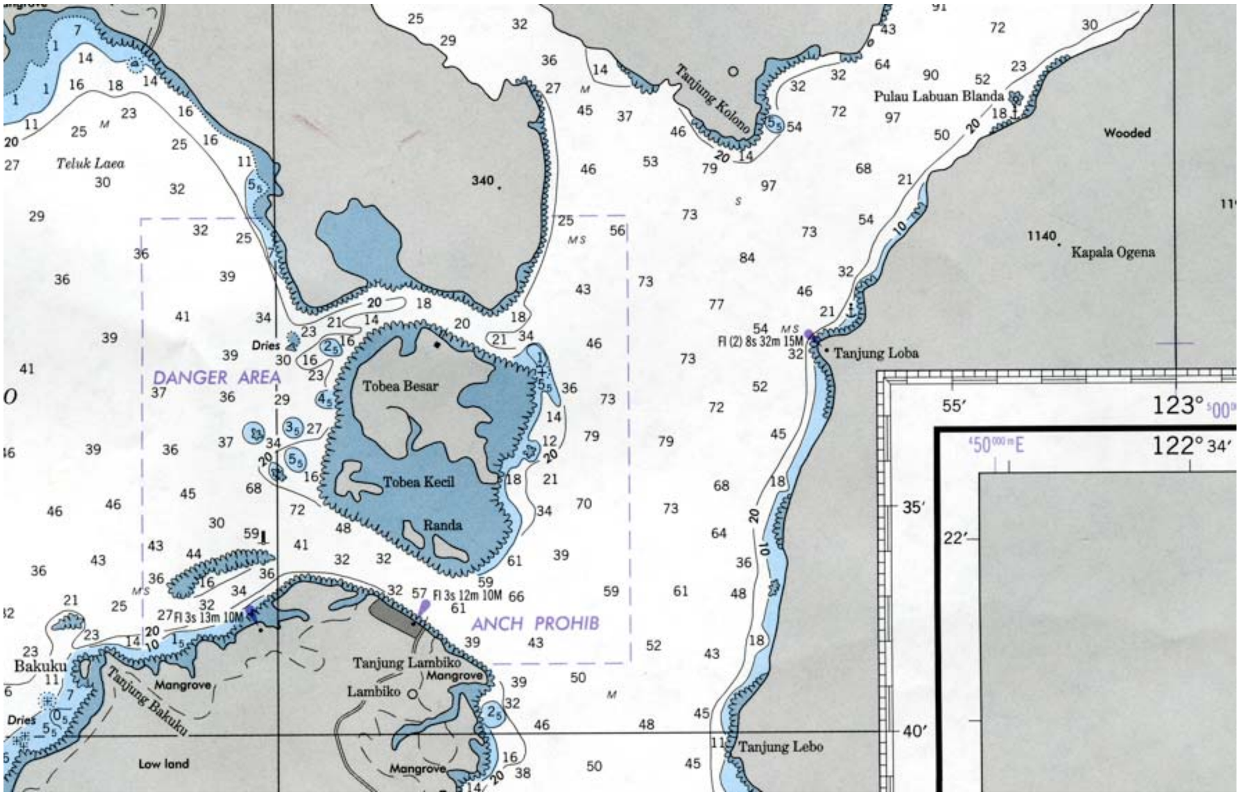

**Figure 3.2.** Detail from a nautical chart from U. S. Defense Mapping Agency (chart no. 73261) (U. S. Defense Mapping Agency 1995), based on Indonesian government data to 1980, showing depth soundings between peninsular southeast Sulawesi (top) and Muna Island (bottom left). Buton Island is at right. Depth soundings are in meters and are corrected for sound velocity.

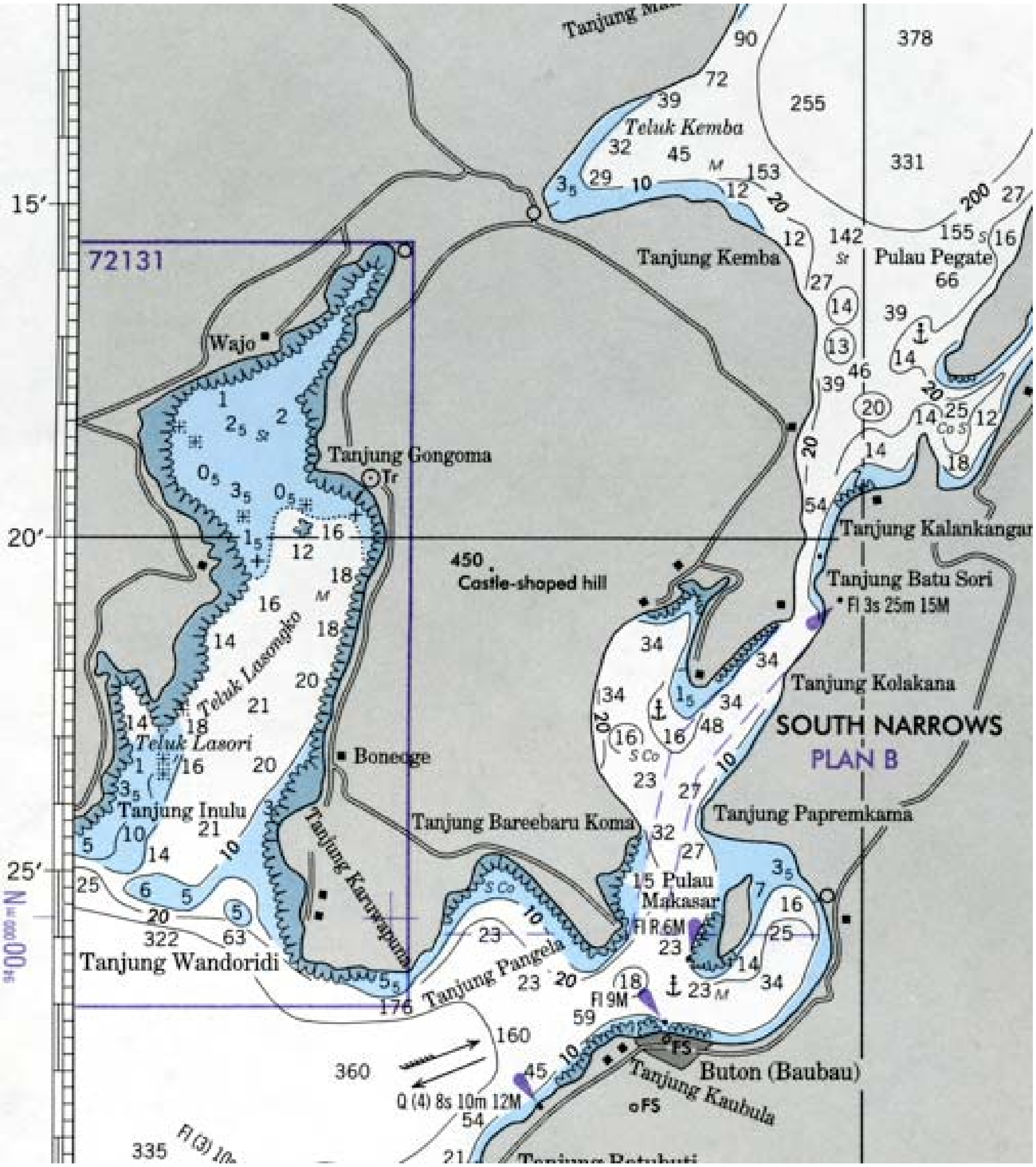

**Figure 3.3.** Another detail from the same nautical chart, showing the southern narrows between Muna (left) and Buton (right) Islands.

**Figure 3.4.** Duration of dry season in Sulawesi, in months, from Fontanel and Chantefort (1978a; 1978b). Note the south-to-north trend of decreasing seasonality in southeastern Sulawesi, indicating that *brunnescens* (restricted to Buton and Muna Islands: the two largest islands off the southern margin of southeastern Sulawesi) has experienced greater rainfall seasonality on average than has *ochreata*, since the time of their isolation (ca. 9 kya). Note also the dots on the map, which indicate positions of the raingauge stations from which data were obtained.

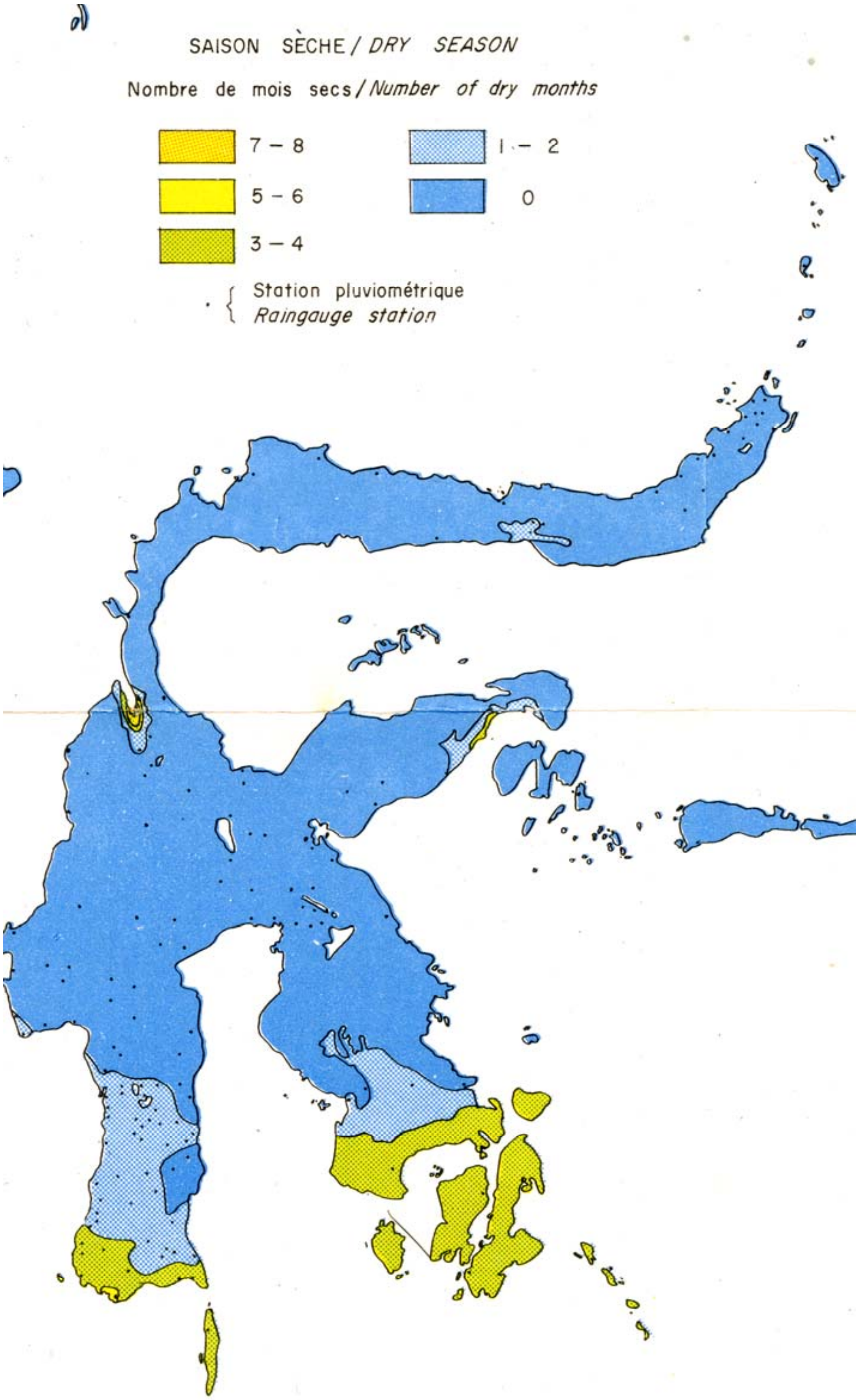
a)
SAISON SÈCHE / DRY SEASON
Nombre de mois secs / Number of dry months
7 – 8
5 – 6
3 – 4
1 – 2
0
Station pluviométrique
Raingauge station

**Figure 3.4**

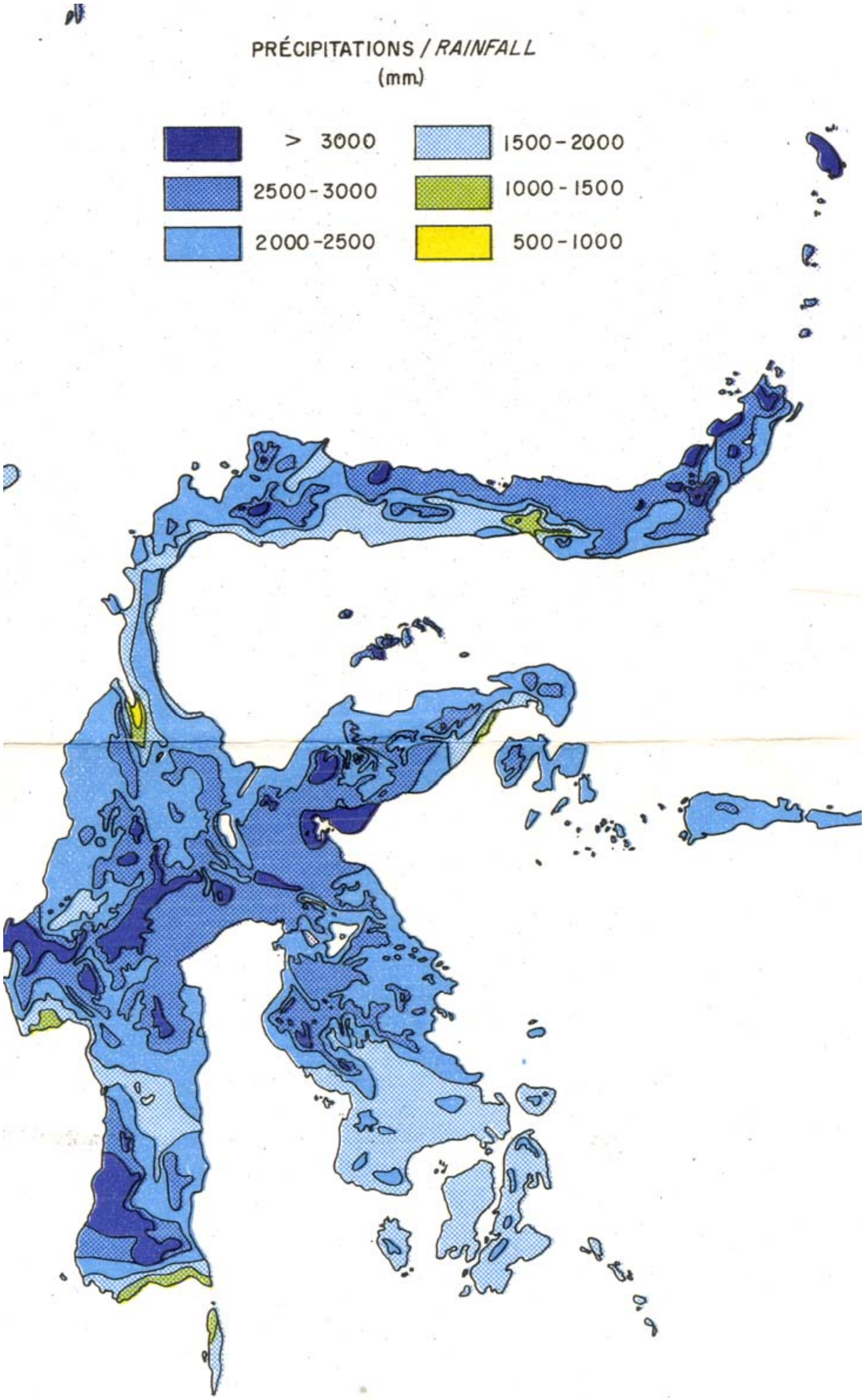

**Figure 3.5.** Total annual rainfall, from Fontanel and Chantefort (1978a; 1978b).

**Figure 3.6.** Rainfall and mean annual temperature data from Indonesian climatological stations, obtained by Fontanel and Chantefort (1978a; 1978b). There are fewer climatological stations (with both temperature and rainfall data) than there are raingauge stations (which only collect rainfall data: dots on Fig. 3.5). On the graphs, the cross-hatched area (if any) indicates the months during which rainfall levels fall below Fontanel and Chantefort's (1978a) bioclimatological criterion for a true dry season, *viz.*, $P < 2T$, where $P$ = precipitation (for a given month) in mm, $T$ = average annual temperature in degrees C. Data are from (a) Bau-Bau, southern Buton Island, near the southern extent of *brunnescens*' range; (b) Kendari, southeast Sulawesi, in the southern part of *ochreata*'s range; (c) Kolonodale, west-central Sulawesi, to the north of the northern limit of *ochreata*'s range; (d) Manado, in extreme northern Sulawesi in *M. nigra*'s range.

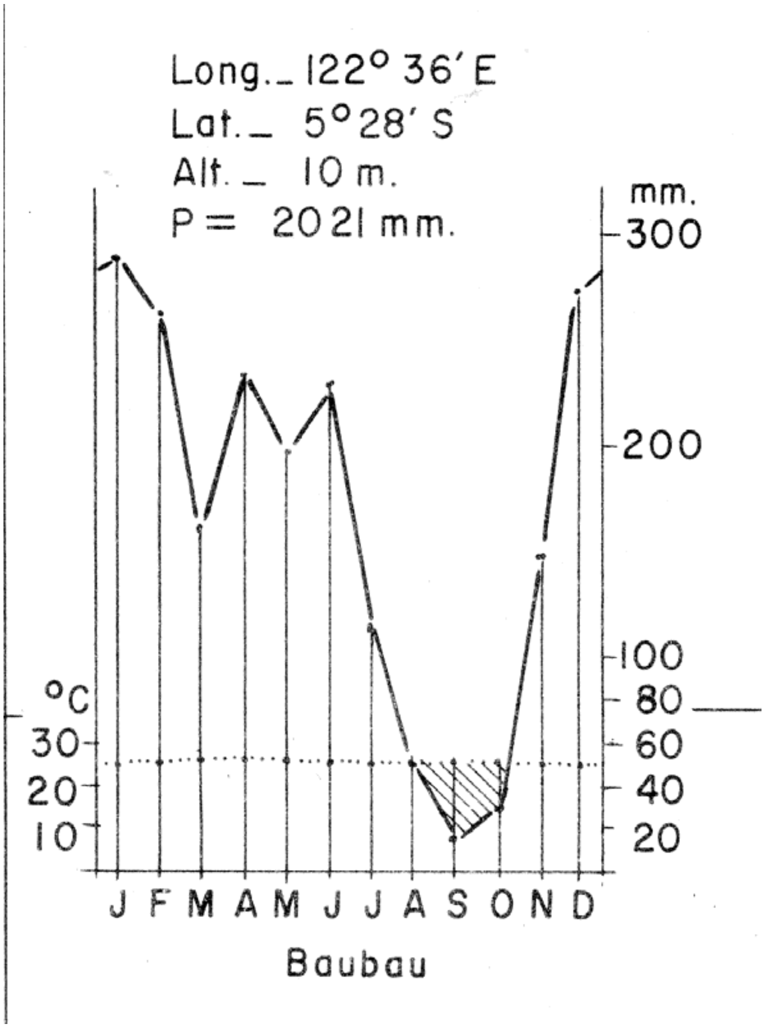
Long._ 122° 36′ E
Lat._ 5° 28′ S
Alt._ 10 m.
P = 2021 mm.
mm.
300
200
100
80
60
40
20
°C
30
20
10
J F M A M J J A S O N D
Baubau

**Figure 3.6a**

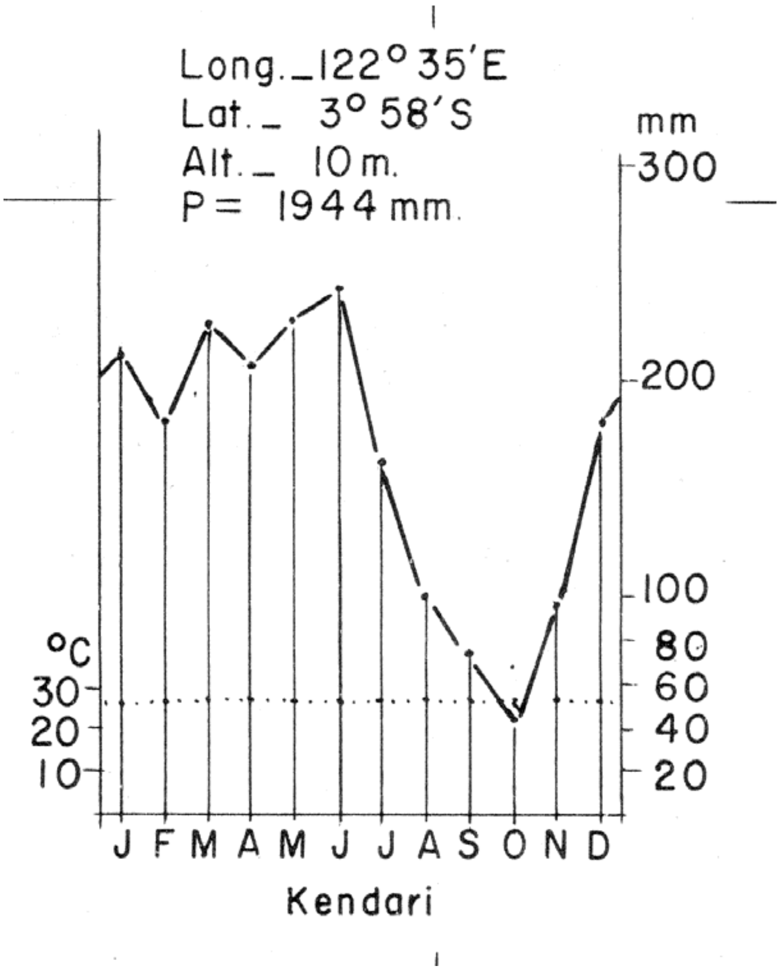
Long._122° 35'E
Lat._ 3° 58'S
Alt._ 10 m.
P= 1944 mm.
mm
300
200
100
80
60
40
20
°C
30
20
10
J F M A M J J A S O N D
Kendari

Figure 3.6b

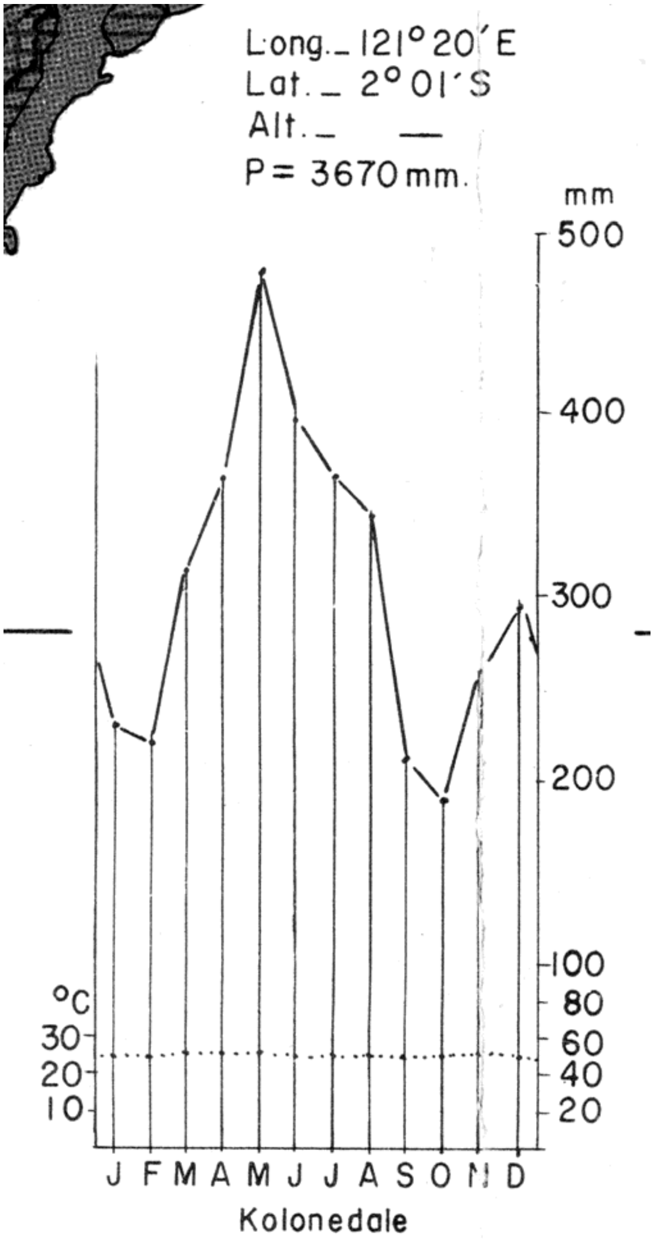
Long. _ 121° 20′ E
Lat. _ 2° 01′ S
Alt. _ —
P = 3670 mm.
mm
500
400
300
200
100
80
60
40
20
°C
30
20
10
J F M A M J J A S O N D
Kolonedale

**Figure 3.6c**

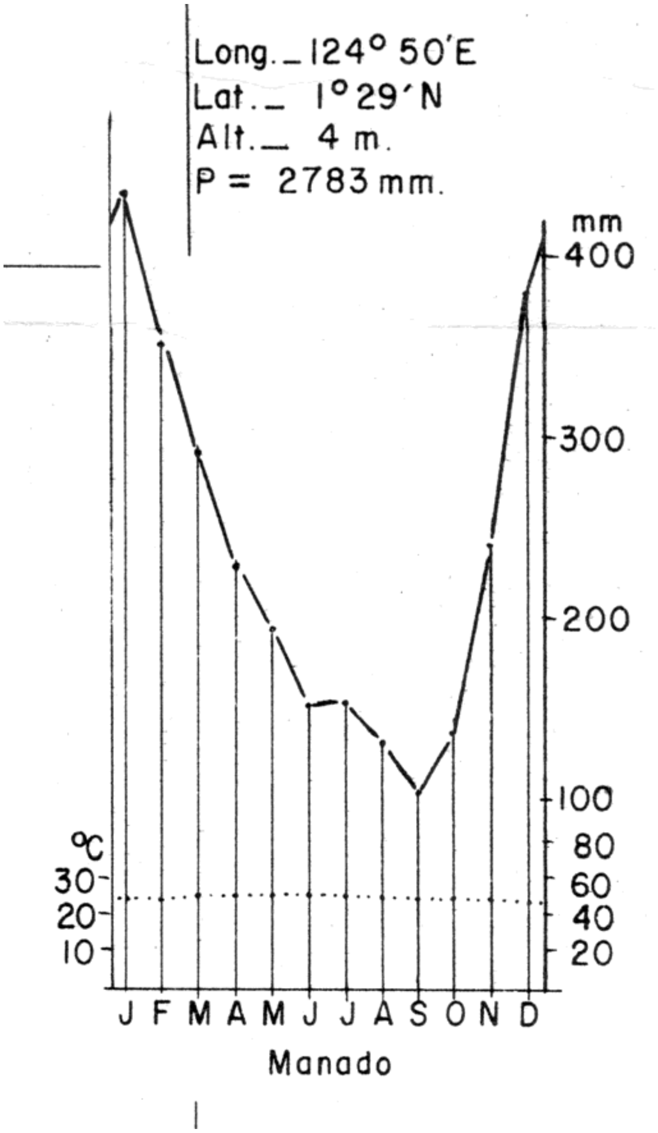
Long. _ 124° 50'E
Lat. _ 1° 29'N
Alt. _ 4 m.
P = 2783 mm.
mm
400
300
200
100
80
60
40
20
°C
30
20
10
J
F
M
A
M
J
J
A
S
O
N
D
Manado

Figure 3.6d

**Figure 3.7.** Forest types in Sulawesi, according to the classification of Whitmore (1984a). Color codes are as follows: brown = lowland monsoon rain forest; pink = limestone monsoon rain forest; light green = tropical lowland evergreen and semi-evergreen rain forest; dark green = tropical montane rain forest. The salient point to note here is that all of *brunnescens*' range is classified as monsoon forest while most of *ochreata*'s range (except the southern portion of the southeastern peninsula) is described as evergreen or semi-evergreen. In fact semi-evergreen would probably be a more accurate description of the "monsoon" areas, but the map supports the proposition that the dry seasons described in Fig. 3.6 have probably affected forest composition and structure in such a way as to differentiate most of *ochreata*'s range from that of *brunnescens*.


Menado
2
1
3
S t r a i t
Gulf of Tomini
Palu
BANGGAI
ISLANDS
4
5
SULAWESI
SULA ISLA
6
Gulf of Bone
Kendari
7
8
MUNA
BUTUNG
Ujung
Pandang

Figure 3.7

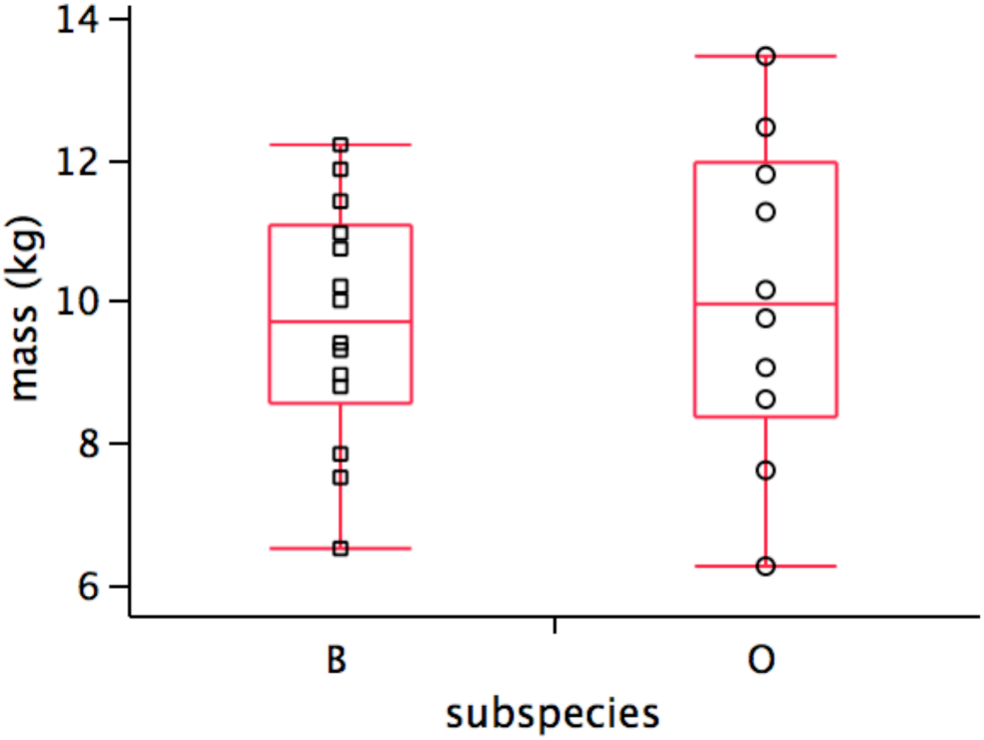

**Figure 3.8a.** Comparison of body mass in males, *ochreata* (O) vs. *brunnescens* (B). Raw data shown (kg). Circles = male *ochreata*; squares = male *brunnescens*. The central horizontal lines in the box plots are the medians.

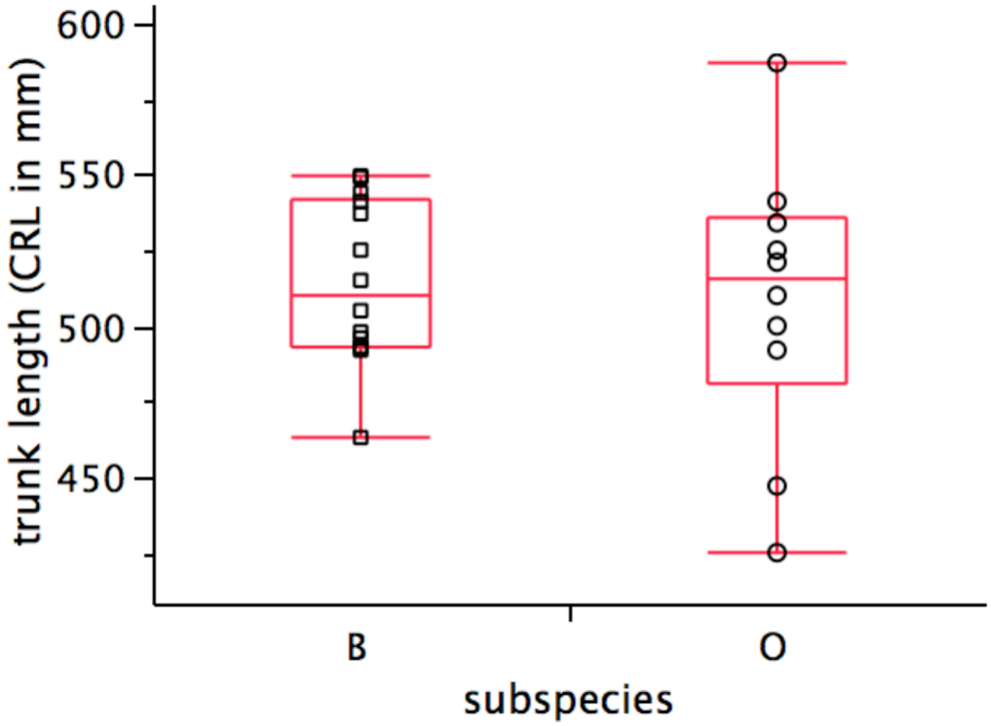

**Figure 3.8b.** Comparison of trunk length (crown-rump length, CRL, in mm) in males, *ochreata* (O) vs. *brunnescens* (B). Raw data shown (mm).

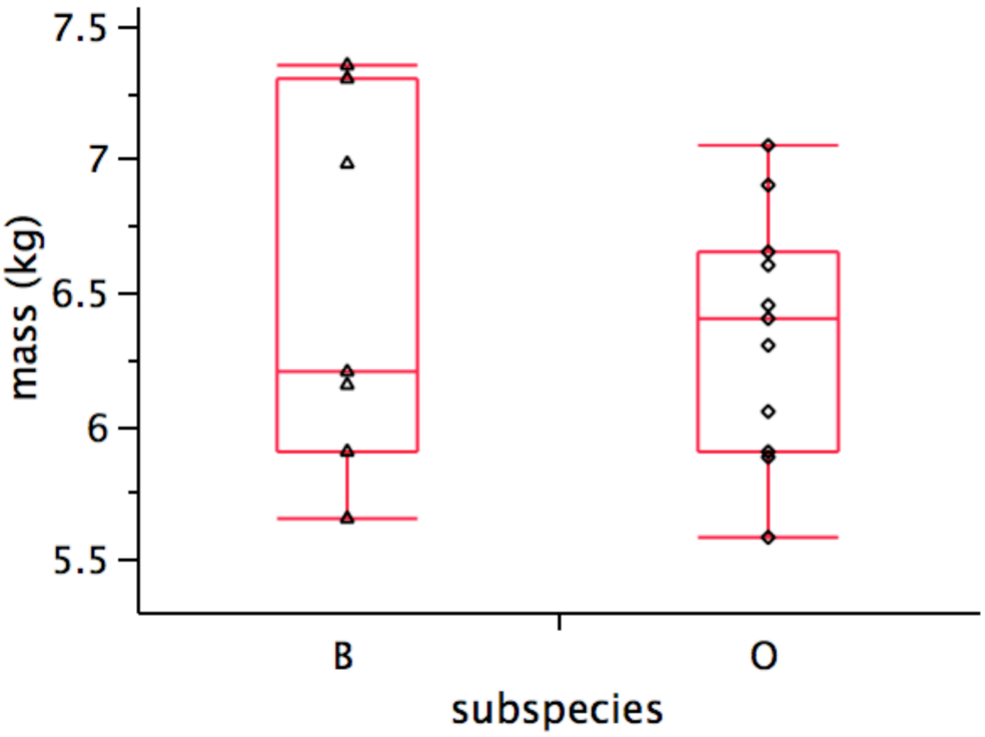

**Figure 3.9a.** Comparison of body mass in females, *ochreata* (O) vs. *brunnescens* (B). Raw data shown (kg). Diamonds = female *ochreata*; triangles = female *brunnescens*.

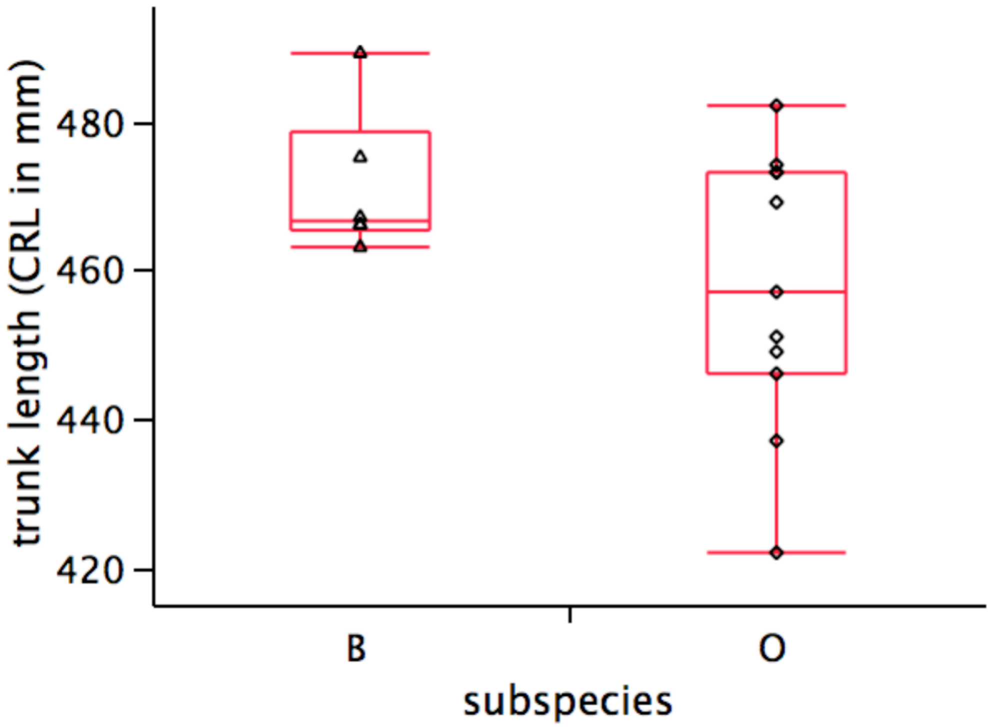

**Figure 3.9b.** Comparison of trunk length (crown-rump length, CRL) in females, *ochreata* (O) vs. *brunnescens* (B). Raw data shown (mm).

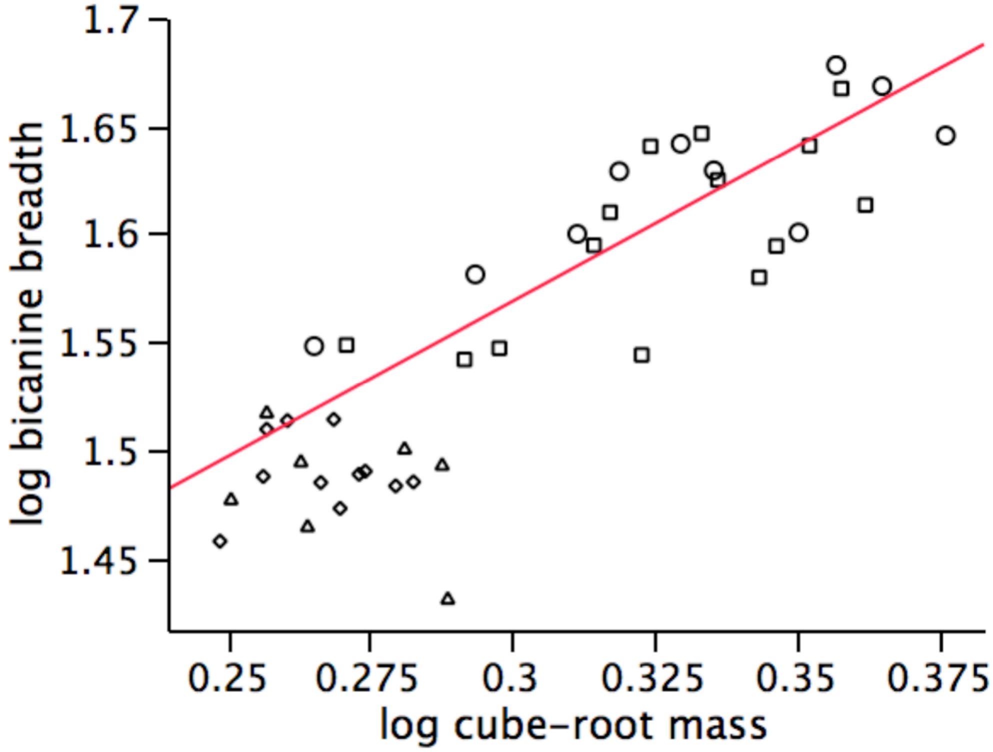

**Figure 3.10a.** Univariate allometry of log bicanine breadth in adult males, with respect to log ($mass^{1/3}$). Females' data points are shown (at lower left) but not included in the regression analysis. Symbols as in Figs. 3.8-3.9.

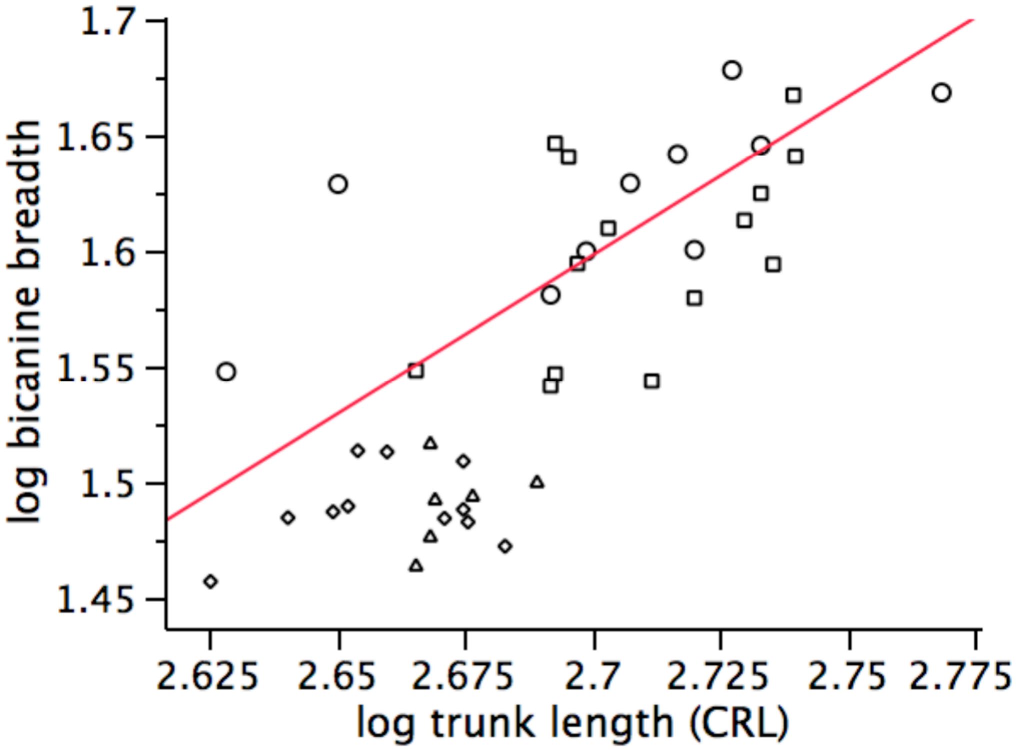

**Figure 3.10b.** Univariate allometry of log bicanine breadth in adult males, with respect to log trunk length (crown-rump length, CRL).

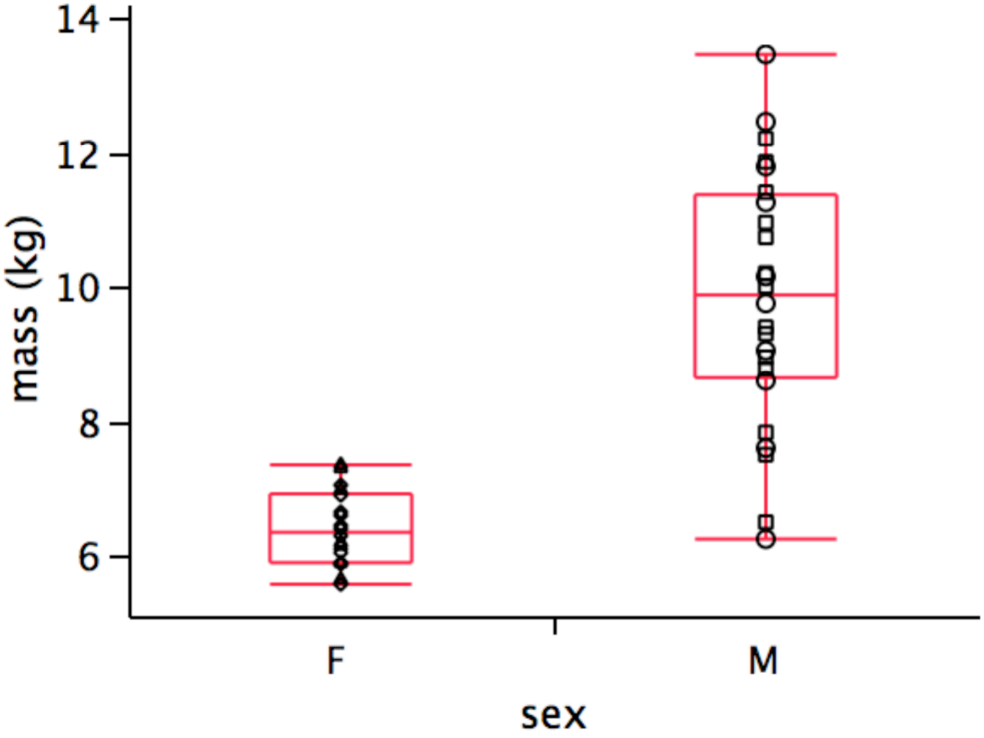

**Figure 3.11a.** Adult sex differences in mean and variance of body mass. Raw data shown (kg). The sex difference in both mean and variance is much larger for body mass than for body length. Symbols as in Figs. 3.8-3.9.

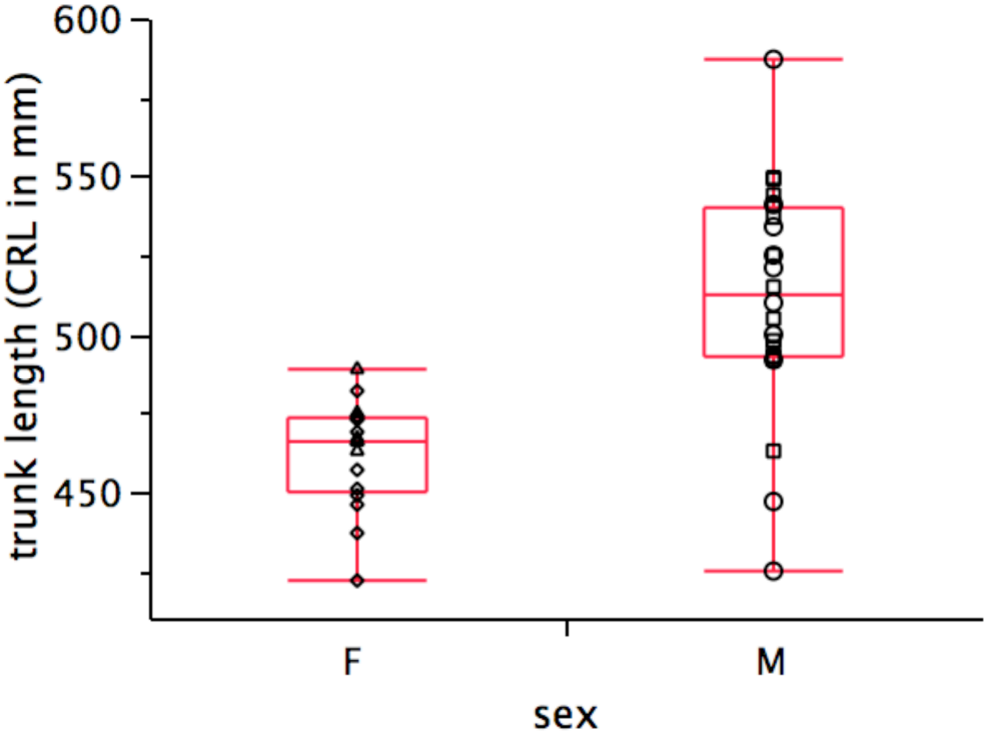

**Figure 3.11b.** Adult sex differences in mean and variance of trunk length (crown-rump length, CRL). Raw data shown (mm).

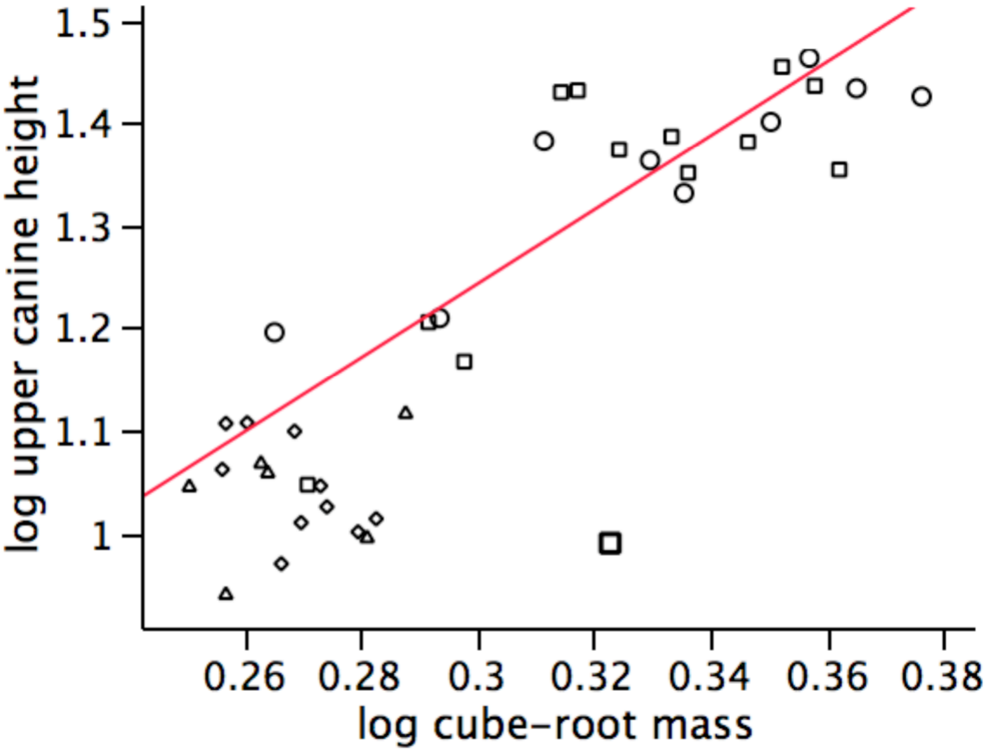

**Figure 3.12a.** Univariate allometry of upper left canine height in adult males, with respect to log (mass$^{1/3}$). Chipped or apically worn canines were removed from the sample; one young adult male removed from analysis because his upper canines were incompletely erupted and possibly impacted. Females shown (at lower left) but not included in the regression analysis. Symbols as in Fig. 3.8-3.9.

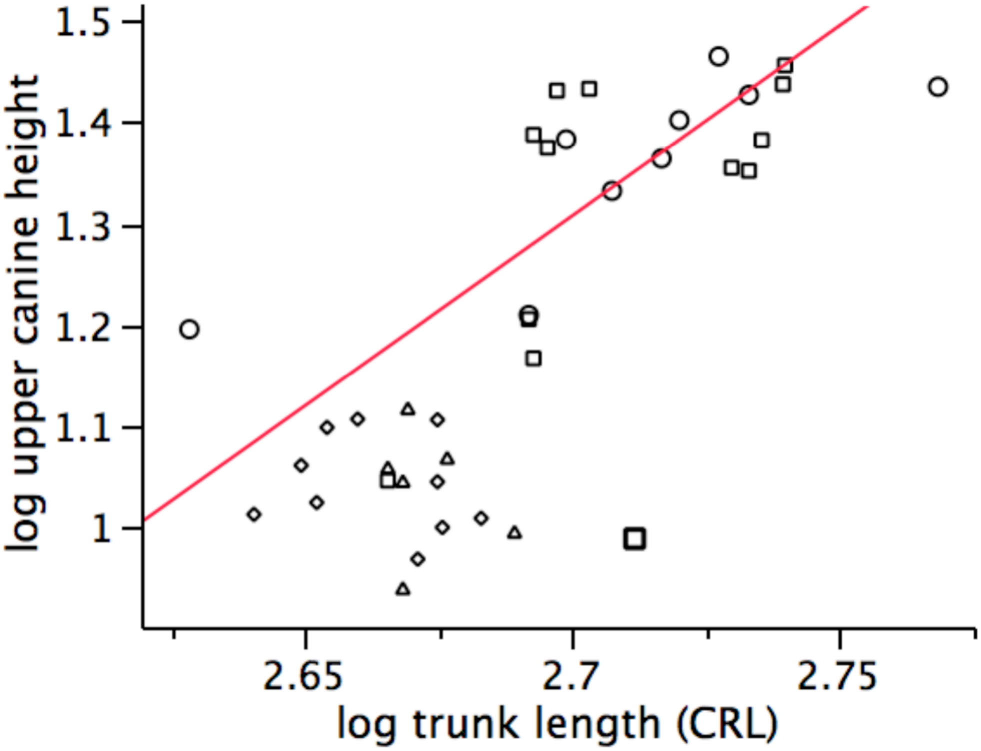

**Figure 3.12b.** Univariate allometry of upper left canine height in adult males, with respect to log trunk length (crown-rump length, CRL).

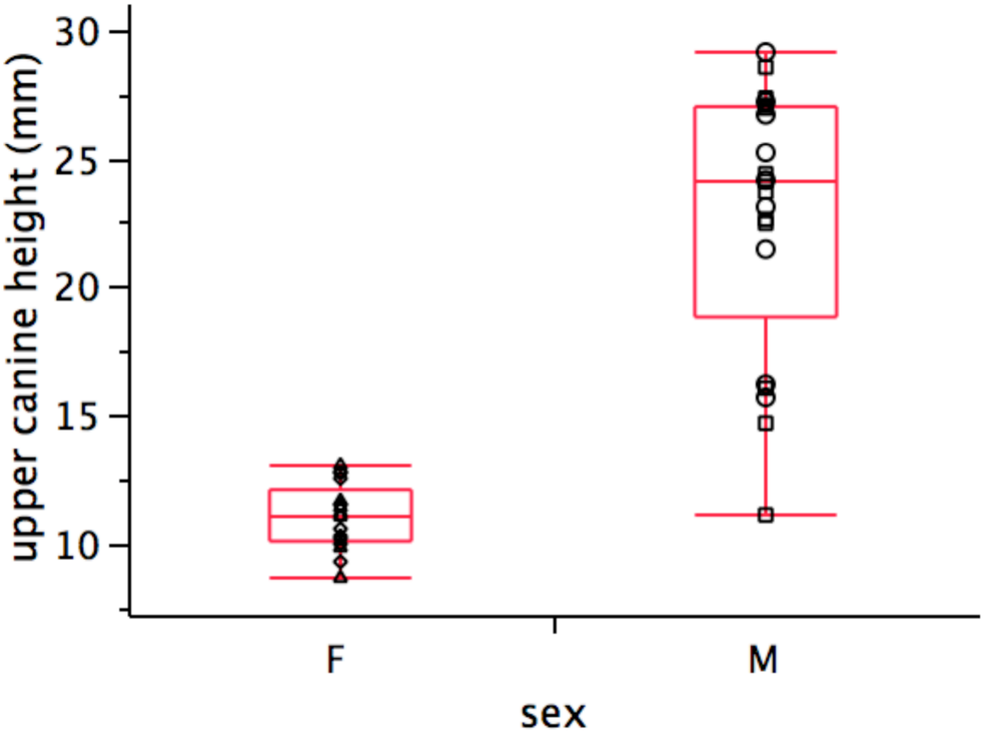

**Figure 3.13.** Sexual dimorphism in upper left canine height. Raw data shown (mm). Note the sexual dimorphism in variance as well as in mean. Upper canine height is the most sexually dimorphic trait and, within males, the most positively allometric trait.

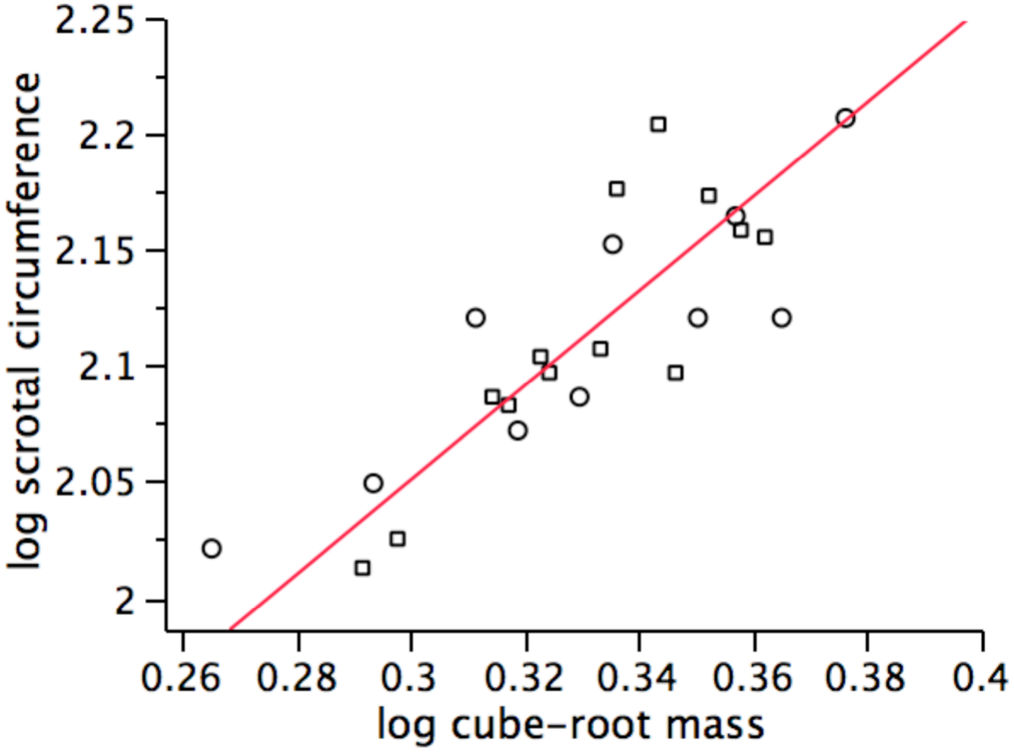

**Figure 3.14.** Univariate allometry of log scrotal circumference with respect to log ($mass^{1/3}$).

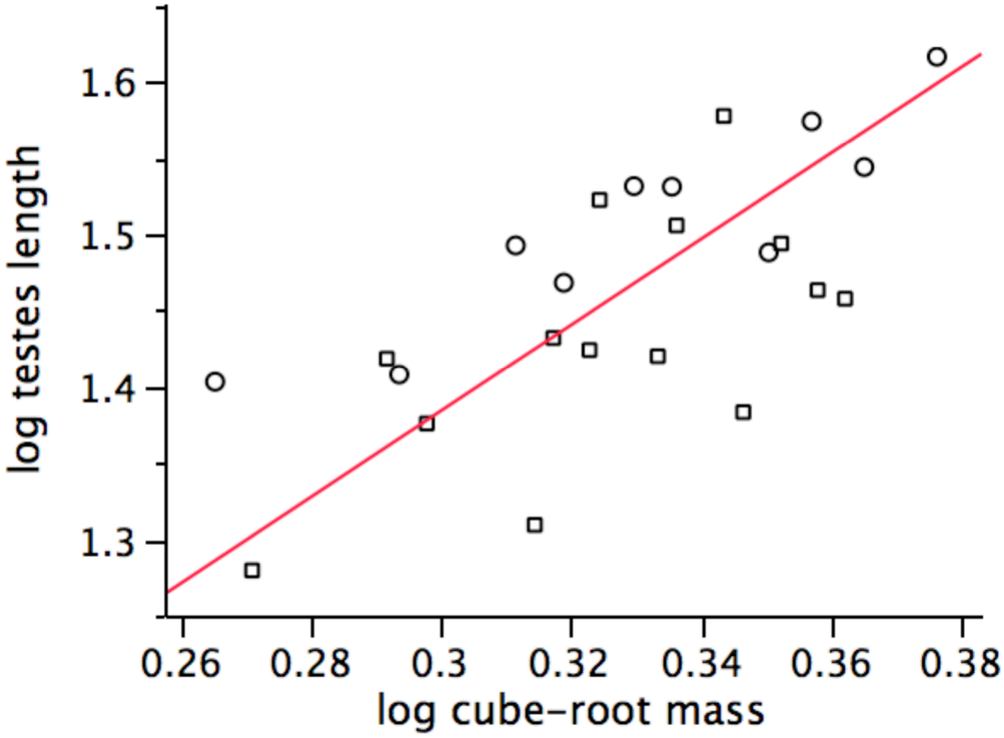

**Figure 3.15.** Univariate allometry of log mean testes length with respect to log ($\text{mass}^{1/3}$). The slope of the *brunnescens*-only regression was not significantly different from zero, hence that regression is not shown. Here there is more dispersion in the data than there is in the scrotal circumference data, probably because testes dimensions are very difficult to measure precisely with calipers, while scrotal circumference is somewhat easier.

# Chapter Four

## Morphological divergence and stasis in 9-kyr-old allopatric populations of Sulawesi booted macaques (Cercopithecidae: *Macaca ochreata*).

## II. Growth and growth allometry: effects of environment and evolution

### Abstract

Various morphological traits may differ in their rate (or qualitative propensity) to respond to natural selection or to environmental factors such as differences in nutrition and activity level. The study of such differential evolutionary and environmental lability among traits is worthwhile in order to learn more about the details of how evolutionary diversification actually works; and on a more practical level, to aid in interpreting the morphological clues left behind by small numbers of individuals from fossil populations. The present chapter poses three questions: (1) Are there evolved differences in whole-body growth rate, or in relative growth of the trunk, between *ochreata* and *brunnescens*? (2) Is relative growth rate of limb segments subject to environmentally-caused variability, and is it sexually monomorphic? (3) Do any body segments grow faster than others, and if so, why? I attempt to answer these questions by using data from macaques living in three different environmental conditions (forest-living, wild-feeding macaques; orchard-raiding macaques; and pet macaques) in two allopatric subspecies, *Macaca ochreata ochreata* and *M. o. brunnescens*.

Results of this study suggest that growth and relative growth in all the traits considered here (body size, relative length of the trunk, relative growth and proportions of the limb segments) are evolutionarily conservative, that is, they have not diverged since the split of *ochreata* and *brunnescens* at ca. 9 kya. Juveniles from different environments (regardless of subspecies) differ from one another in body size, probably due to differences in growth rates. Juveniles from different environments show greater differences in trunk length than in mass, and there is some evidence that this difference is due to faster growth of the trunk relative to body mass in juveniles from food-enriched or activity-limited environments, compared to juveniles from a more natural forested environment. Body sizes converge by adulthood, however, regardless of environment.

Growth of the limb segments, by contrast, seems to be highly canalized with no detectable differences between individuals from different environments, even during the juvenile period, and evolutionarily conservative, with no divergence between populations. The femur grows relatively faster than the other limb segments, a fact that is consistent with a history of on-going, parallel ecological selection in both *ochreata* and *brunnescens* for leaping ability when moving through the forest canopy. Behavioral data on primary-forest-living macaques is presented which corroborates the arboreal leaping behavior of both subspecies.

## Introduction

### *4.1: The questions to be asked in this chapter*

*Question one*: Are there evolved differences in whole-body growth rate, or in relative growth of the trunk (CRL, crown-rump length) relative to body mass, between *ochreata* and *brunnescens*?

*Question two*: Is relative growth of limb segments stable among populations in different environments (is it canalized, i.e., under strong genetic control)? Is it stable among species (evolutionarily conservative)? Is it stable between sexes (sexually monomorphic)?

*Question three:* Do any body segments grow faster than the others, and if so, why? Is this difference stable between different environments (canalized) and subspecies (evolutionarily conservative)?

### *4.2: General background*

Allometric modeling is a convenient way of investigating a number of biological questions. It is essentially an attempt to control for the evolutionary effects of body size (whether adaptive or simply geometric) when examining evolutionary divergence in growth and adult variation of various body segments. Allometric modeling does include a number of potentially problematic assumptions, however—for example, the assumption that logarithmic or other tranformations of raw data will not distort true, underlying relationships in the data. Such assumptions are not always warranted (Godfrey and Sutherland 1995), though at least the allometric "full model" (as used in this chapter) that does not force all regressions through the origin, removes one such problematic assumption—the assumption that timing of growth onset does not differ between the groups being compared (Albrecht 1987). Thus it also pays to consider age-based (as opposed to size-based) ontogeny of traits when interpreting ontogenetic intraspecific allometries.

Morphological divergence of populations with respect to specific traits must occur via divergence of the ontogenetic trajectories of those traits (Alberch et al. 1979; Reeve and Fairbairn 1996). Sexual dimorphism in overall body size may result from sexual differences in the duration of growth (time hypermorphosis or bimaturism), or in the rate of growth (rate hypermorphosis), or some combination of both. There are of course notable differences among species, and among higher taxa, in body size within sexes as well as in the degree of sexual dimorphism. Both body size and size dimorphism can, however, show significant environment-related plasticity within species, particularly in the timing and rate of growth that ultimately leads to adult dimorphism (Altmann and Alberts 2005; Turner et al. 1997).

Many authors have used manifest body size and inferred sexual dimorphism in small, geographically- and temporally-circumscribed populations of hominins to make inferences about ecological niches and especially about mating systems, on the assumption that the observed size and dimorphism represent evolved, species-typical morphology (reviewed in Larsen 2003). The size and sharpness of males' maxillary canines was greatly reduced even in the earliest hominins, compared to most non-hominin catarrhines; some authors have nonetheless pressed on with reconstructions of highly polygynous mating systems in, e.g., *Australopithecus afarensis*, based solely upon reconstructions of body size sexual dimorphism (Gordon et al. 2008; McHenry 1992; McHenry 1994; Reno et al. 2003). Comparative primate data, however, indicate that sexual dimorphism in canine height is a better predictor of breeding system than is sexual dimorphism in body size, yet reconstructions of hominin breeding systems generally ignore canines in favor of body size (Plavcan and Van Schaik 1997). There is likewise neither archeological nor osteological evidence that *Australopithecus* used extrasomatic weapons to substitute for large canine teeth. Larsen (2003), moreover, has questioned the precision of the sex-identification techniques used on fragmented fossils. Furthermore, the degree of sexual dimorphism inferred from the fossils seems to depend upon the method used by the researcher (Gordon et al. 2008; Reno et al. 2003).

Clearly, however, regardless of the methods used, to determine the degree of sexual dimorphism and its behavioral implications, we need to contextualize claims about fossil hominin mating systems and sexual dimorphism with comparative data on the environmental influences upon growth trajectories, in order to determine the degree of sexual dimorphism and its behavioral implications.

The reader is asked to note that, in the discussion of the literature that follows, I attempt to follow the taxonomy of Wilson and Reeder (2005), though any mistakes in the application of their taxonomy are my own.

### *4.3: Environment and growth in free-ranging primates*

Given that growth in non-human primates is a very large literature, the available data on postcranial growth in wild populations is surprisingly limited. Most allometric and ontogenetic studies of mammals have used skulls only—skulls from museum collections in most cases, with little information available about the environment in which the animal lived. Generally, skull length is used as the overall body-size standard for allometric comparison to sizes of body parts. Data on postcranial growth in more-or-less wild (i.e. free-ranging) populations of primates are available for vervet monkeys, *Chlorocebus pygerythrus* (Bolter and Zihlman 2003; Turner et al. 1997); hamadryas baboons, *Papio hamadryas* (Jolly and Phillips-Conroy 2003; Sigg et al. 1982); olive baboons, *Papio anubis* (Strum 1991); yellow baboons, *Papio cynocephalus* (Altmann and Alberts 2005); toque macaques, *Macaca sinica* (Cheverud et al. 1992), and Sulawesi booted macaques, *Macaca ochreata* (Schillaci and Stallmann 2005; this chapter). Of these, the studies by Strum (1991), Altmann & Alberts (2005), and this chapter include data subsets from completely wild subpopulations as well as free-ranging but crop-raiding subpopulations, and thus allow some inferences about the possible effects of ecological or nutritional differences among populations upon growth, body size, sexual dimorphism and allometries of various traits. (The study by Turner et al. (1997) apparently includes data from crop-raiding populations but, while their sample size is large, there is little specific information about the degree of crop-raiding vs. wild-feeding at each study site, rendering their interpretations somewhat conjectural.)

While morphological data on large, wild primates is very difficult to obtain (and is usually entirely cross-sectional in character, with strictly ordinal ages estimated from dental data), its distinctive value lies in the possibility of (1) measuring natural, as opposed to food-enhanced, growth trajectories, realized adult sizes, and sexual or populational differences thereof; (2) comparing natural growth to food-enhanced growth, the latter being possibly interpreted as an upper bound upon growth trajectories under ideal but atypical ecological conditions, and as an indication of the potential degree and direction of environmentally-caused spatiotemporal variability around species-level means; (3) comparing environment-induced plasticity vs. canalization in a number of different traits—e.g. maxillary canine height vs. overall body size.

Assessment of the correlates and degree of intraspecific variability in growth trajectories—and the relative susceptibility of various traits to environmentally-caused variability—have important implications for interpretation of small, geographically- and temporally-circumscribed samples of fossil hominins and other fossil populations. The spatiotemporal variability in the type and abundance of food is greater in the wild than it is in captivity; free-ranging primates, moreover, engage in higher activity levels and a greater variety of locomotor behaviors than captive (including "semi-free-ranging") populations. All of these differences can affect not only the degree of fatness, but also the development of the musculoskeletal system, whose growth responds dynamically to the stress and strain caused by locomotor and masticatory behavior; even coat color can be affected by nutritional and other environmental conditions such as prolonged exposure to direct sunlight. Furthermore, an organism's genotype is designed to produce an adaptive phenotype under natural conditions, via interaction with the organism's natural range of environments. Thus, while captive primate groups make experimentation much easier, data from wild groups are also extremely important in order to place morphological development of the phenotype in its evolutionary ecological context. A balance between studies on captive, wild and semi-wild (e.g. crop-raiding) primates should thus maximize internal as well as external validity (Altmann 1974; Arnold 1983).

According to conventional wisdom, interval data on true age from animals followed since birth is preferable to ordinal relative ages determined from dental eruption sequences, relative tooth wear, or both. Turner et al. (1997) have argued, however, that ordinal, relative dental ages may be preferable to absolute calendrical ages in cross-sectional analyses, since dental development tracks an animal's actual somatic developmental stage more reliably than does absolute, calendrical age; use of absolute ages can pool precocial and altricial individuals in the same category. While longitudinal studies of growth have obvious advantages over cross-sectional ones, longitudinal studies present their own conundra as well. One wishes to obtain a growth curve that characterizes an entire population or species, not just one individual; yet pooling longitudinal data from multiple individuals can lead to the construction of a "growth curve" that does not faithfully reflect the actual growth trajectory of any individual in the population. Thus, even when data are entirely cross-sectional and ordinal dental ages are used, growth data from free-ranging populations can be quite useful.

*Effects of food enhancement upon growth*—Altmann and Alberts (2005: their fig. 1), in a longitudinal study where absolute ages were known, found that individuals in anthropogenically food-enhanced environments grew faster (in body mass) than wild-feeding individuals; the difference in growth rate was much more pronounced in post-pubertal males than it was in females or pre-pubertal males (puberty was defined in males as the time of testicular enlargement). Post-pubertal males in both wild-feeding and food-enhanced conditions grew faster and for longer than did post-pubertal females. Thus Altmann and Alberts (2005) found that the qualitative ontogeny of sexual dimorphism remained the same regardless of diet, while the quantitative effect of diet upon growth rates, and the ultimate degree of intersexual divergence in body size, differed greatly depending upon diet and environment.

Altmann and Alberts (2005) also report that food-enhanced females attained menarche two years before wild-foraging females, which suggests that diet can have drastic effects upon life histories. Strum (1991) conducted a growth study of wild-feeding and food-enhanced *Papio*, and likewise found not only faster growth and larger eventual body size under food-enhanced conditions, but stronger sexual dimorphism in body size, with a greater sex difference in growth rate under food-enhanced conditions. Strum (1991) also found that, while food-enhanced free-ranging primates do grow faster and ultimately reach a higher maximum mass, they also stop growing earlier than wild-feeding primates. Thus females generally seem to respond to greater food availability with earlier onset of reproduction; males respond by increasing body mass. Such a response seems adaptively tailored to female- and male-specific optimal reproductive strategies in polygynous primates.

On the other hand, the data are not all in agreement on this point, even among cercopithecine species. Turner et al.'s (1997) study of vervet monkeys (*Chlorocebus pygerythrus*) found increased body mass in females (but not body length) at their

Naivasha site, a highly-cultivated area where the vervet monkeys were "notorious crop-raiders" by the authors' account. The increase in female body mass, not matched by any increase in male mass, decreased body mass sexual dimorphism at that site (see Turner et al.'s table 4).

*Does natural ecogeographic variation affect growth and dimorphism?*—I have argued that studies of free-ranging but food-enhanced primates, in comparison with wild-feeding primates, can suggest an upper bound of the effects of non-anthropogenic dietary conditions upon growth and dimorphism. Is there evidence from purely wild-feeding populations that supports such a possibility? While growth data *per se* is somewhat limited, there is a well-established literature on comparative body mass in wild primates, particularly in baboons, *Papio* spp. (reviewed in Dunbar 1990). Research on a very small sample of purely wild-foraging baboons by Altmann (1991) indicated that differences in foraging success (diet quality) among yearlings predicted fertility during adulthood, even within a single subpopulation; therefore it seems reasonable that substantial differences in diet could exist among geographic populations. Likewise, Post et al. (1999) found that in years where flowering of preferred food plants occurred earlier, young female red deer (*Cervus elaphus*) tended to grow faster and began their reproductive careers earlier—but the females' bulking-up actually reduced sexual dimorphism. Male red deer did increase in size relative to females in response to favorable environmental conditions—but in this case the relevant environmental variable was temperature, not diet (Post et al. 1999).

Dunbar (1990) collected data from the literature on body mass vs. mean annual rainfall for a number of baboon (*Papio* spp.) populations; he found a linear, positive relationship between rainfall and mean body mass, when populations with fewer than five animals sampled were excluded (Dunbar 1990: his fig. 3). The most plausible ecological explanation for the relationship is that rainfall causes differences in primary productivity (references cited in Dunbar 1990). Dunbar (1990) also claims that a U-shaped relationship between rainfall and body mass exists in Papio, but this claim is based upon a very few data points, and disappears when populations with very small sample sizes are excluded (Dunbar 1990: his fig. 3).

The postulated relationship between primary productivity, diet and mean body mass is strengthened by earlier research on *Papio*, which found a linear increase in body size with increasing rainfall (Popp 1983) and on howler monkeys, *Alouatta* (Froehlich and Thorington 1982). The *Alouatta* research was conducted on a smaller spatial scale and examined forest productivity directly, rather than using rainfall as a proxy (Froehlich and Thorington 1982), and thus is especially relevant. The *Papio* study by Popp (1983), on the other hand, found that body size of males but not that of females was affected by differences in rainfall—suggesting, in concert with the study of wild-feeding vs. food-enhanced baboons by Altmann and Alberts (2005), that natural differences in food availability among habitats could lead to differences in sexual dimorphism, not just in overall body size. The implication for interpretation of observed dimorphism in fossils is clear—one cannot assume that a small, geographically- and temporally-circumscribed sample of fossils represents a species-typical degree of dimorphism in overall body size. If, however, canine tooth sexual dimorphism (for example) is less affected by environmental variability than is overall body size, then observed dimorphism in fossil hominins' canines might be more reasonably interpreted as species-typical, and thus could form a plausible basis for reconstructing a fossil population's breeding system. Of course, hominin paleontologists are then faced with the fact that canine dimorphism is low even in the earliest hominins, and continues to decrease over geological time.

### *4.4: Proportions and relative growth of the limbs*

Animals that rely on leaping as a primary mode of locomotion generally have longer hindlimbs than forelimbs—a rule that holds true for organisms as diverse as frogs, kangaroos and primates. The more specialized the species is for leaping—the more it relies upon leaping to move about its habitat and obtain food or mates—the longer are the hindlimbs in proportion to the forelimbs; (e.g., sifakas: Indriidae, *Propithecus* sp.; tarsiers: Tarsiidae, *Tarsius* sp.). For example, Rodman (1979) compared pigtailed macaques (*Macaca nemestrina*) to longtailed macaques (*M. fascicularis*) and found that even within that genus, limb proportions differ in the expected direction: *M. nemestrina*, which is largely a terrestrial quadruped (i.e., it employs cursorial locomotion) has limbs of similar length, while *M. fascicularis*, a mostly arboreal quadruped that frequently leaps between trees, has proportionally longer hindlimbs. The proportionally longer hindlimbs of leapers undoubtedly function to increase leaping power, thus increasing the maximum diameter of arboreal gaps that can be safely crossed. Meanwhile, the limbs of terrestrial quadrupeds, of more equal length fore and aft, increase long-distance striding efficiency on the ground (Rodman 1979).

There has been some disagreement as to whether, within the hindlimb, leaping arborealists should have longer femora or tibiofibulae. Rodman (1979) found that the tibia/femur ratio (crural index) was higher in *M. fascicularis* than in *M. nemestrina*, and argued that this pattern was to be expected biomechanically, citing a passage from Hildebrand (1974, cited in Rodman 1979). Certainly highly specialized, high-speed cursors, for example many ungulate species such as horses (Equidae: *Equus* sp.) and gazelles (Antilopinae, within Bovidae), have longer lower limb segments (below the elbow or knee) relative to their humeri and femora; this condition enables greater horizontal sweep of the limb and thus facilitates coverage of greater distance per stride, at the expense of the power that might be had with a longer femur (unnecessary due to the absence of climbing behavior) (McGowan 1999: 185).

A longer femur relative to the tibia, by contrast, might then increase power for explosive leaping (McGowan 1999: 185). Indeed, Anapol et al. (2005), in another study of cercopithecine primates (*Chlorocebus pygerythrus* and *Cercopithecus mitis*), found proportionally longer distal limb segments in the more cursorial *Ch. pygerythrus* relative to the more arboreal *Ce. mitis*, suggesting that leaping arborealists may obtain an advantage (perhaps greater leaping power) from a proportionally longer femur relative to the tibia.

One widespread approach to the problem of limb proportions is to compare different species with regard to ratios—the ratio of total forelimb to total hidlimb lengths (intermembral index), ulnar to humeral lengths (brachial index), or tibial to femoral lengths (crural index). An allometric, regression-based approach may be preferable, however, since the allometric approach takes into account the possibility of non-linear relationships between growth rates (or, in the case of purely static allometry, relative size) of limb segments, while the use of simple ratios requires an assumption of linearity (though in some cases there is no reasonable alternative to analysis of ratios). Aside from that, methods of limb-segment measurement in living animals (which is tricky) can differ slightly yet systematically between studies (see below), which could produce spuriously different results. Thus I prefer to compare relative growth of limb segments within and between populations using allometric equations rather than indices.

## Methods

### *4.5: Populations and research localities*

Please see chapter two.

### *4.6: Field morphometry*

Please see chapter two.

### *4.7: Dental age scoring system*

In chapter three, my aim was primarily to conduct a more or less static comparison of *functional adults* between the *ochreata* and *brunnescens* subspecies, with respect to a number of traits—in many cases, secondary sexual traits. For chapter three it made sense, then, to define adulthood functionally: adults were males with descended testes or females with complete coverage of pink sex skin in the buttock region. For the analysis of male maxillary canines, for example, I simply included all males in which these teeth had erupted. In the present chapter, however, I wished to compare the *timing* of various ontogenetic events (such as body mass attainment, pubertal attainment, and so on) between environments and subspecies—thus some sort of more or less chronological age standard (as opposed to functional age or somatic maturity) was required. I did not know the true chronological age of the animals in this study (which were trapped only once each)—I thus used dental eruption to estimate ages and age classes. Dental age can serve as a fairly stable, roughly chronological standard against which to compare timing of maturity in various populations (see below).

I therefore constructed broad age classes (see below) for comparisons of groups (e.g., environment type) within age classes. These broad age classes were constructed so as to coincide with those used by Watanabe et al. (1987), whose published data are used here as a supplement to my own.

I will use herein the standard abbreviations to indicate type of tooth, capital letters indicating permanent teeth: M = molar, P = premolar, C = canine, I = incisor. Numbers following the letters indicate position in the mouth, from mesial (midline between incisors) to distal (back of mouth). Superscript indicates maxillary teeth, subscript indicates mandibular teeth; standard script indicates that both maxillary and mandibular are referred to.

*Subadult age: patterns of tooth eruption*—The eruption sequence of permanent teeth tends to be similar among cercopithecine species: for permanent dentition, most species follow the pattern M1-I1-I2-M2-P3-P4-C-M3 (Hurme and van Wagenen 1961; Nass 1977). Likewise, the chronological age of eruption of the permanent teeth also changes very little among congeneric species; Smith et al. (1994) provide data from four macaque species that indicate eruption of M1 at between 1.37 and 1.50 yr, and eruption of all permanent teeth by 5.75-6.02 yr. Likewise, data summarized by Iwamoto et al. (1987: their table 5) for from four macaque species indicates very low variability among species in eruption ages. There is also evidence that while age of tooth eruption is affected by environmental variables such as nutrition (Zihlman et al. 2004), age of tooth eruption is generally less affected by environmental factors than is, for example, the timing of puberty (Smith 1991 and references cited therein).

Of course, some teeth are of greater significance than others for age estimation. Some show very little inter-individual, within-population variation, while others show great variation; some are associated consistently with developmental milestones and some are not. For example, the use of M1 as an age marker is desirable due to its relatively low inter-individual variability, and its association among most primate species with the beginning of foraging independence and the juvenile period (the end of infancy) (Smith 1991). Another desirable characteristic of M1 is its high canalization and low variation within species; in captive *M. mulatta*, its eruption timing does not overlap at all with that of other permanent teeth (Hurme and van Wagenen 1961). M1 eruption also seems relatively little affected by environmental differences within species, and shows similar timing in males and females. In the Arashiyama West troop of *M. fuscata*, which lives in semi-arid shrubland in Texas with food provisioning, Nass (1977) found that M1 (upper and lower) erupt at age 2 years in both males and females; the result agrees with that of Mouri (1994), who studied animals of the same species that were a mixture of laboratory captives and "cadavers purchased from animal traders." Finally, M1 also shows high consistency among macaque species (Iwamoto et al. 1987; Smith et al. 1994).

Among the later-erupting teeth, first I1 and I2 (more or less jointly), then M2, erupt in sequence. Among the later-erupting teeth (P3, P4, C), there is some overlap and sometimes even changes in sequence within species (Nass 1977). The timing of eruption of M3 is far more variable within populations than that of the other teeth (Hurme and van Wagenen 1961; Nass 1977), and in at least one species (*M. fuscata*) M3 may become fully occlusal before $C^1$, but only in males (Mouri 1994). The longer time required for eruption of C in male primates, however, is probably simply a consequence of the much greater length of $C^1$ in males.

While the age of eruption of M3 can be quite variable within species (relative to the other teeth), an advantage of M3 is that, among primate species, the age of complete eruption of all M3 correlates as well as does M1 eruption with brain mass among primate species ($r = 0.97$ for both M1 and M3 eruption), and brain mass can be an indicator of developmental rate (Smith et al. 1994). Thus, not only is M3 eruption tied to a species' rate of development (life history), there is no evidence that *average* age of eruption of M3 is any less related to life history than is M1 eruption. On the other hand, the correlation between brain mass and M3 eruption (r = 0.97) could of course be caused by a mutual correlation of M3 eruption and brain mass with body mass; Smith et al. report, however, that the correlation between brain mass and M3 eruption remains moderately high (partial r = 0.82) when body mass is controlled (Smith et al. 1994: footnote to their table 6).

M3 is also more sexually-monomorphic in crown height, and thus in eruption timing, than is C; thus use of M3 as a developmental marker obviates the need for separate definitions of dental adulthood vs. adolescence for each sex. Use of M3 eruption as a marker of full adulthood also enables one to compare sexual maturation (descent of testes in males, sexual skin and nipple length in females) among populations using dental eruption maturation as an age standard. This possibility arises from the fact that, while timing of tooth eruption may be affected by environmental factors, it is probably less so affected than is somatic (e.g., reproductive, and skeletal) maturation (Smith et al. 1994). Thus dental eruption can provide a relatively stable background (canalized within species, conservative between congeneric species) against which to test for population differences in rate of somatic or reproductive development.

For the aforementioned reasons, it is desirable to use M3 eruption as an indicator of adulthood. On the other hand, this tooth presents a problem of high intra-population variability of eruption timing (relative to absolute chronological age). I therefore examined the data on captive *M. mulatta* of Hurme and van Wagenen (1961), and found that in that population the right-hand tail of the age distribution of $M^3$ (maxillary) eruption is much longer than that of $M_3$ (mandibular) eruption—especially in females, where $M^3$ eruption can sometimes occur extremely late. Furthermore, my sample of booted macaques includes seven individuals (*ochreata*: no. 15, female; no. 45, female; *brunnescens*: no. 62, 82 and 86, male; no. 73 and 78, female) in which $M_3$ was either erupting or occlusal but $M^3$ was still absent, confirming that in booted macaques (as in *M. mulatta*), $M_3$ erupts before $M^3$. Among those whose $M_3$ but not $M^3$ was occlusal, many were very much larger than one would expect for of a true adolescent, which also suggests that $M^3$ eruption can be quite delayed in booted macaques as it can be in *M. mulatta*. I therefore chose to use only $M_3$ eruption (to full occlusion) as the indicator of dental adulthood, the criterion that distinguishes adults from adolescents.

*Subadult dental age: broad age classes used*—For comparisons within broad age groups (e.g. between habitats), I defined the age groups as follows: (1) newborn: no permanent teeth, all-black natal coat; (2) infant: no permanent teeth, species-typical gray arms and legs; (3) juvenile: all four M1 erupted and fully occlusal but $C_1$ not erupted; (4) adolescent: $C_1$ erupted but $M_3$ eruption incomplete (not erupted to occlusal plane); (5) adult: $M_3$ erupted to the occlusal plane. Where my own field data were concerned, I based age classes upon my field notes, which were based upon detailed first-hand examination of eruption, occlusion and (in the case of molars) tooth wear (see chapter two).

The data table of Watanabe et al. (1987), used here to supplement my own field data, reports dental ages based on a study of *M. fuscata* by Iwamoto et al. (1987). I used Iwamoto's table 5 to align Watanbe et al.'s system of ages with my age classes as outlined above. I thus assumed that individuals to which Watanabe et al. (1987) assigned a dental age < 1.75 years were infants. I further assumed that those reported by Watanabe et al. as age of 1.75 through 3.5 yr (if female) or through 4.25 yr (if male) were juveniles. Those whose ages were given by Watanabe et al. as 3.75 through 5.5 yr (if female) or 4.5 through 5.5 yr (if male) I classed as adolescents. Those whose dental ages were given by Watanabe et al. as 5.75 yr or greater I classed as adults.

### *4.8: Behavioral observation methods*

My technicians and I made a total of 20 on-transect sightings of groups of various sizes. We also made numerous off-transect observations, but I did not include them in the statistical analysis for fear of potential bias—for example, most off-transect observations will have been made in or near base camps, which are always located near large creeks, where forest structure may differ from that of the interior hill forest. Most of the sightings (N = 17) were of *ochreata* at site B-3; a few (N = 3) were of *brunnescens* at site O-3 (see chapter two for transect methods and site descriptions). I combined data for the two subspecies and sites since my on- and off-transect observations did not suggest any obvious difference in locomotor behavior of forest-living monkeys of different subspecies. (Monkeys that live in highly disturbed forest near roads, for example at site O-1, tend to be far more terrestrial.)

Upon each sighting (a sighting being defined as one encounter within any 100m stretch of transect), my technicians and I recorded the number of individual monkeys that were visible, whether they were in a tree or on the ground, and how many individuals were in each location (tree vs. ground). We also recorded whether the monkeys were alarm-calling at or before the time we first spotted them, and whether the monkeys seemed alarmed or were fleeing from us. The macaques rarely fled or alarm-called upon our sighting them, and when they did so it was only *after* we first saw them, and was not associated with a change in stratum use (trees vs. ground). In no case did we locate monkeys at these sites by first hearing alarm calls (though we sometimes did so, off-transect, at other sites). Therefore I interpret these observations as indications of the monkeys' natural locomotor or positional behavior. In the absence of any evidence that the monkeys were alarmed by our presence, there is no reason to presume that because the monkeys were not habituated to behavior observation, they were normally terrestrial but climbed trees before they were detected. There is also no reason to think that the monkeys detected us before we detected them (nor that they particularly cared, for that matter), since my field technicians have many years' experience spotting animals in thick vegetation, and haplorhine primates' special senses (such as olfaction) are probably no more acute than ours. Thus I considered my on-transect behavioral data to be reliable and unbiased.

### *4.9: Statistical analyses*

I conducted all statistical analyses reported here with JMP software, version 7.0.2 (SAS Institute, Inc.). For allometric regressions I used reduced major axis regression. This type of regression has neither independent nor dependent variables; unlike least-squares regression, reduced major axis regression does not assume that the X variable is measured without error. I used an empirical method (principal components) to estimate the relative error of the X and Y variables in each regression. Slope estimates whose lower confidence limit (LCL, the lower end of the confidence interval) was > 1 were considered positively allometric (i.e., the Y variable increases faster than the X variable during growth). Those whose confidence interval (CI) overlapped with one were considered isometric (proportional change in X and Y variables). Those whose upper confidence limit (UCL) was less than one were considered negatively allometric.

Of course, sample sizes can affect the breadth of CIs, and so sample size should be taken into account when comparing the regression results reported in table 4.1. In most cases I reported 95% CIs, but when the LCL of a regression seemed substantially greater than one, I tested the robustness of the apparently positive allometry by increasing the stringency of the confidence interval (see caption to table 4.1). In this chapter (unlike much of chapter three) I generally used log CRL (i.e., crown-rump length, trunk length or sitting height) as the size standard (X variable) for allometry, except where CRL was itself the Y variable of interest. I used log CRL because, in some of the limb-length allometric regressions, use of log ($\text{mass}^{1/3}$) as the size standard (X) produced a curvilinear relationship (in spite of transformed data) with a statistically significant least-squares quadratic term—a phenomenon that makes linear methods (such as reduced major axis) inappropriate. The curvilinear effect with respect to body mass was probably due to the older and larger males "bulking up" with respect to body length in middle to late adulthood. This phenomenon also suggests that, where limb length allometry is concerned, use of log CRL rather than log ($\text{mass}^{1/3}$) may be more appropriate for species with sexual bimaturism (extended growth in males throughout adulthood), such as Sulawesi booted macaques (see chapter three).

The data analyzed here come from two studies of Sulawesi booted macaques—my own and that of Watanabe et al. (1987). Watanabe et al. employed slightly different methods than I did for measuring some limb segments—for example, Watanabe et al. measured the humerus distally to the condyle, while I measured to the olecranon process of the ulna. This difference in methods produced a consistent difference in our data which affected the Y-intercept of the regressions but not the slopes (producing parallel regression lines), and was easily corrected (see Results). The sample of Watanabe et al. is, to my knowledge, composed entirely of pet monkeys where booted macaques (*M. ochreata sensu lato*) are concerned (B. Suryobroto, pers. comm.). They obtained data from many wild monkeys from other Sulawesi macaque species, but I have not analyzed those data here.

Where limb proportions are concerned, sample sizes are smaller (see N column in table 4.1) because I obtained limb-length data only in the 2004-05 and 2007 research seasons, i.e., only for five primary-forest monkeys, and 31 orchard-forest monkeys. Limb length data from pet monkeys are from Watanabe et al. (1987). Unfortunately I do not have limb length data for the vast majority of the forest monkeys, which I trapped in 2002 prior to a change in morphometric protocol.

When comparing two groups of individuals, I generally used the Van der Waerden non-parametric test, which is as powerful as an analysis of variance (ANOVA) when errors are normally distributed (i.e., when ANOVA assumptions are met), and exceeds the power of an ANOVA when the assumption of normally-distributed errors is not met. Aside from its combination of power and robusticity, the Van der Waerden test uses normal scores (Z-scores from a normal distribution) rather than ranks, unlike other non-parametric tests—therefore far less information is lost compared to rank-based tests, and validity is greater (Conover 1999: 396-397). When comparing three groups, I used Kruskal-Wallis non-parametric tests. Both tests convert data to ranks and so are relatively insensitive to extreme values, thus avoiding chance bias in small samples. Likewise, I used box plots in many of the figures since these visually show medians, which are much less sensitive to large values than are arithmetic means. I used raw data in non-allometric comparisons of body size among groups, as there was no reason to transform the data. Body segment lengths (including CRL) were in mm and mass in kg.

When analyzing a larger set of data, in order to examine the effects of one or more independent variables (while controlling for other covariates) upon a single dependent variable of interest, I used general linear models (GLM) with normal distributions and identity link functions.

I report only two-tailed p values; in cases where there is a clear directional prediction, however, the reader may wish to consider the one-tailed p value as well, which is one-half the two-tailed value. In any case, I view statistical significance as a continuum, rather than as an either-or decision rule (Gigerenzer et al. 2004). I did not perform Bonferroni or other multiple-test adjustments to the p values, for reasons given in chapter three (Methods). My aim was merely to see whether the apparent association between two variables, or the differences in averages among groups, were likely due to chance in any given analysis, bearing in mind that subjective human judgement cannot be extricated from the process of data interpretation.

## Results

### *4.10: Whole-body growth: evolved or environmental differences?*

*Question one*: Are there evolved differences in whole-body growth rate, or in relative growth of the trunk (CRL) relative to body mass, between *ochreata* and *brunnescens*?

I showed in chapter three that while *ochreata* and *brunnescens* have diverged somewhat in relative breadth of the head, there are no significant differences between adults of the two subspecies in body size, in secondary sexual traits, or in post-pubertal allometric growth and sexual dimorphism thereof. I also provided some evidence that there may be a significant difference in whole-body growth between juveniles of the two populations, and I suggested that that difference is likely due to environmental differences (e.g., diet or activity level or both) between the populations. Indeed, it seems unlikely that a pair of recently-isolated sister populations would have diverged evolutionarily in juvenile growth rate, only to arrive at the same adult body size. Here I examine the hypothesis of environmentally-induced differences in juvenile growth rate in more detail than I did in chapter three.

In the present chapter, I examine both *ochreata* and *brunnescens* from three environmental conditions: forest-living (wild-feeding) monkeys, orchard-forest (crop-raiding) monkeys, and pet monkeys. Forest monkeys probably have the highest activity levels (large day ranges) and lowest caloric intake, thus the lowest energy balance.

Orchard-forest animals, which live mostly in secondary forest but make frequent forays into orchards to obtain domesticated fruit, likely have more moderate activity levels and higher caloric intake. Pet monkeys may have diets of varying quality, but have very low activity levels (they are usually chained to a pole with little possibility of horizontal or vertical movement), thus their energy balance is likely to be relatively high. These broad differences in diet and activity level afford an excellent opportunity for examining the effect of varying environments upon growth, relative growth, and the patterning of the phenotype in general.

Hypothesis 4.1: The eventual adult body size of booted macaques is largely evolved (genetic); the time needed to attain that size (the rate of approach) is largely environmental (determined by diet).

- Prediction 4.1.1: Due to differences in timing of growth, juveniles of the same dental age class from different environmental conditions (forest vs. forest-orchard vs. pets) will differ substantially from one another in body size, but adults will show little if any difference among environments.

I examined the sample as a whole (N = 119 for mass, N = 118 for CRL) to determine whether environment affects growth independently of subspecies (evolutionary history) and sex. I used a general linear model (GLM) with independent-variable main effects of environment, age class, and sex; no interactions were included. Environment exerted a strong effect upon body length (dependent variable = log CRL: chi-square =

29.89, $p < 0.0001$) but a weak effect, if any, upon mass (dependent variable = log (mass$^{1/3}$): chi-square = 4.51, $p = 0.105$), controlling for subspecies and age. There was no effect of subspecies upon either body length or mass, although of course there were strong effects of sex upon both length and mass (see chapter three).

After the broad total-sample analysis, I compared subgroups, pooling data from different sexes and subspecies in those cases where there were no apparent effects of sex or subspecies upon body size. I pooled data in these cases to increase sample size, and thus to increase the statistical power for detection of true differences (to reduce type II error).

*Infants*—First, it was necessary to determine whether there are sex differences between subadults (infants and juveniles), since obviously such differences exist by adulthood. (The GLM analysis, and the scatterplots with different symbols by subspecies and sex, demonstrated that there are no subspecific differences independently of environment and sex.) While there were few infants in the sample, I detected possible sex differences within the forest habitat in CRL, forest-living females ($N = 6$) being larger than males ($N = 7$) (Van der Waerden $Z = 2.297$, $p = 0.022$). Female forest-living infants also tended to be heavier than males, though the tendency was weaker than with CRL, due to a single outlier female (Van der Waerden $Z = 1.815$, $p = 0.070$). Because of this sex difference in size among infants, I was unable to pool data from males and females for between-environment comparisons. Thus I had to compare male and female infants separately from different environments, within sexes.

Sample sizes were very small due to the inability to pool infants of different sexes; in fact the female infant sample was too small to analyze. There were also too few orchard-forest infants for analysis. Therefore I compared males only, forest vs. pet environments. I found that male pet infants (N = 7) tended to be substantially larger in CRL than male forest infants (N = 7) (Van der Waerden Z = 3.024, p = 0.003) (fig. 4.1). There was also a tendency for male pet infants to be heavier than male forest infants (Van der Waerden Z = 2.323, p = 0.020).

*Juveniles*—Within environments, I detected sex differences in neither CRL nor mass in juveniles, using Van der Waerden tests (pets, CRL: Z = -0.832, p = 0.405; pets, mass: Z = -0.494, p = 0.621; forest, CRL: Z = -0.169, p = 0.866; forest, mass: Z = -0.385, p = 0.700). While sample sizes for each sex within each environment were very small, raising the possibility of type II error (pets: 14 males, 5 females; forest: 8 males, 4 females), visual examination of the scatterplots (not reproduced here) also makes it clear that pooling data from the two sexes is unlikely to produce any biasing effect. The possibility of a very slight, undetected bias must be weighed against the risk of type II error that could result from an overall between-environment comparison whose sample sizes within habitats are too small. Thus I decided to pool males and females in the between-habitat comparison of juveniles.

The comparison of juveniles among the three environments, sexes and subspecies pooled, revealed a substantial effect of habitat upon CRL, as was the case with the much smaller infant male sample (Kruskal-Wallis, chi-square = 10.627, p = 0.005). Examination of the scatterplot (fig. 4.2) makes it clear that the orchard-forest (N = 8) and pet (N = 19) juveniles jointly differ from the forest (N = 12) juveniles, the last being smaller than the former two. The orchard-forest and pet samples do not seem to differ substantially. There is a slight difference in the same direction where mass is concerned (forest juveniles being smaller), but the difference in mass could well be due to chance (Kruskal-Wallis, chi-square = 3.409, p = 0.182).

*Adults*—The sexes cannot of course be pooled where adults are concerned, and there are too few females in the sample for separate analysis. There were also very few pet males: only three for CRL comparisons. For mass comparisons, one of these three adult male pets (no. 259 in Watanabe et al. 1987) had to be excluded, since he was probably grossly obese (his mass was far greater relative to his trunk length than even the largest forest and orchard-forest males), thus for mass I only compared forest (N = 14) vs. orchard-forest (N = 8) monkeys. Among adult males, I found differences among the environments in neither CRL (Kruskal-Wallis, chi-square = 1.816, p = 0.403) (fig. 4.3) nor mass (Van der Waerden, Z = 0.299, p = 0.765). In the female data, the pet and orchard-forest individuals seemed relatively large compared to the forest females, but there were too few females for statistical comparison.

I conclude therefore that Prediction 4.1.1 is strongly supported where body length (CRL) is concerned but only weakly supported where mass is concerned, except in infants. The significant effect of environment upon body length that was detected by the GLM analysis is likely due to differences among infants and juveniles but not adults. Pets are likely to have the lowest activity levels, while orchard-raiding monkeys likely have the second-lowest activity levels, since their daily travel distances are likely shortened (relative to those of wild-feeding forest monkeys) due to concentration of high-quality food (i.e., foods domesticated by people). Thus it seems that the results here support those of Altmann et al. (1993) to some extent, who found that differential activity levels (i.e., energy expenditure) have a great impact upon growth.

### *4.11: Growth of the trunk relative to body mass*

Environmental effects upon length of the trunk (CRL, sometimes referred to here equivalently as "body length") seem stronger than effects upon body mass. If this apparent difference (thus far based only upon effect sizes and p values in static comparisons of age groups) is robust and real, it should also be reflected in relative growth rate of the trunk—infants and juveniles from the pet and perhaps orchard-forest environments should begin life with relatively long bodies relative to their mass, but the growth of their trunks should decelerate somewhat later on, so that adults from different habitats converge in body size.

- Prediction 4.1.2: Body length (trunk length, CRL) will show negatively allometric growth with respect to body mass (body mass as size standard on X-axis) in pet and orchard-forest environments but isometric or positively allometric growth in the forest environment. No difference between the subspecies, independent of environment, is expected.

Once again, I first had to determine whether there were systematic effects of sex or subspecies upon allometric growth of the trunk relative to body mass, to determine which data, if any, could be pooled. Since the forest and orchard-forest samples are potentially confounded by subspecies (most of the forest sample is *ochreata*, and all orchard-forest are *brunnescens*), I used the pet sample only to test for subspecific effects. The male pets included both subspecies, more or less equally represented (N = 12 male *ochreata* and N = 13 male *brunnescens*); there were too few females to construct separate regressions for female *ochreata* vs. *brunnescens*. Therefore I compared subspecies within males, within the pet environment. I found no significant difference in the subspecific regression lines (table 4.1); both slope estimates were < 1, although that of *ochreata* was somewhat lower. Both 95% CIs overlapped one, and broadly overlapped one another. One problem with this regression, however, was that the small sample sizes caused CIs to be excessively broad, and *brunnescens* are rather under-represented among medium-sized and large individuals.

I next wished to test for sex differences. Since there were too few females to compare the sexes within environments, I pooled environments and subspecies, conducting separate regressions for each sex. I found no evidence of any difference in length-mass allometry between females and males (table 4.1), with one exception: the largest males tended to cluster below the regression lines (I have not reproduced the male vs. female regression graph, as this clustering is visible also in fig. 4.4), undoubtedly due to "bulking up" of males in middle to late adulthood (increase in mass relative to length), a phenomenon probably related to sexual competition. It was, in fact, this "bulking up" that led me to use log CRL preferentially as a size standard in the limb-length allometric regressions (see below) since the relationship is more linear when CRL is used rather than mass.

Due to the apparent lack of subspecific and sex differences in trunk length allometry, I pooled subspecies and sexes to examine differences between environments. I found that, as expected, growth of the trunk relative to body mass is negatively allometric in pet and orchard-forest animals: these animals begin life rather long for their mass, but growth in the trunk later decelerates relative to overall body mass growth. Meanwhile, in the forest environment, growth of the trunk keeps pace with body mass increases (table 4.1; fig. 4.4). That somewhat explains the differences between immature animals between environments, and the convergence between environments in adult body length. A few caveats should be noted, however. First, while the 95% UCLs (upper confidence limits) of both the pet and orchard-forest regressions are < 1, the UCL of the pet regression is very close (0.999). The UCL of the orchard-forest regression is far more securely < 1. Aside from that, while the forest regression line is almost perfectly isometric and the others are negatively allometric, the 95% CIs of all three slopes overlap with one another. Therefore these regressions can be regarded as offering guarded support for Prediction 4.1.2.

### *4.12: Relative growth of the limbs: evolutionary and environmental effects*

*Question two*: Is relative growth of limb segments stable among populations in different environments (is it canalized, i.e., under strong genetic control)? Is it stable among species (evolutionarily conservative)? Is it stable between sexes (sexually monomorphic)?

To compare relative growth of body parts (ontogenetic allometry), it is necessary to separately compare ontogenetic allometry in various populations (with a separate equation constructed for each population). Static, interspecific allometric equations that pool several species, with one data point per species, can suggest constraints that may affect the course of evolution, but do not indicate differences in relative growth among species (Gould 1966; Gould 1975).

Hypothesis 4.2: Relative growth (ontogenetic allometry) of limb segments is evolutionarily conservative (resistant to short-term evolutionary change among subspecies), is highly canalized (under strong genetic control; resistant to environmentally-influenced change within subspecies), and is sexually monomorphic due to similar locomotor ecology between the sexes.

Prediction 4.2.1: There will be no difference in slope of limb segment allometries between subspecies *ochreata* and *brunnescens*, and no difference between the sexes.

Prediction 4.2.2: Within *M. ochreata sensu lato*, relative growth of limb segments will be the same (same slope) in three groups experiencing different dietary and locomotor environments: (1) pet monkeys, (2) orchard-forest (crop-raiding) monkeys, (3) forest (wild-feeding) monkeys.

There are a great many possible permutations of regressions for comparison of sex, environment and subspecies, each with log CRL or log ($mass^{1/3}$) as size standard. Therefore I first performed overall, total-sample regressions. Then, to determine which specific comparative regressions should be performed for further investigation (sex, subspecies or environment), I conducted general linear model (GLM) analyses on the total sample, separately for each limb segment as dependent variable. For each GLM analysis, the independent variables were (1) log CRL or log ($mass^{1/3}$); (2) subspecies; (3) sex; (4) environment. The environment comparisons are particularly important as some limb segments of the pet animals (e.g. humerus) were measured differently (by Watanabe et al. 1987) than the same segment was measured in the other animals (see Methods).

At first, I conducted separate GLM analyses, as well as regressions, for each limb segment with log CRL and with log ($mass^{1/3}$) as the size standards. It soon became apparent, however, that use of log ($mass^{1/3}$) as the size standard sometimes produced curvilinear rather than truly linear relationships, especially the regressions of log femur and log tibia lengths on log ($mass^{1/3}$), which had significant quadratic terms when I tried polynomial least-squares regression. I therefore report henceforth only GLM and regression results using CRL as the size standard (X variable).

The most common significant effects emerging from the GLM analyses were environment effects, although these almost certainly resulted from differences in methodology between Watanabe et al.'s (1987) pet sample, and my orchard-forest and forest samples. The humerus, ulna, tibia, and foot all showed significant environment effects, while the femur did not. The effect was particularly pronounced for the humerus and foot regressions, which showed parallel regression lines by environment, each widely separated by a large difference in Y-intercept (table 4.1). The differences in Y-intercept with identical slopes, in most cases, suggest that the differences are of methodological origin only. Only in the case of the tibia do the regressions differ between environments in both slope and intercept. The difference in slopes is very small, however, and the 95% CIs overlap greatly (table 4.1).

Aside from the artifactual "environment" effects, the GLM analyses did indicate possible effects of sex on relative growth of the tibia and foot; and a possible subspecific effect on relative growth of the foot. I further investigated these possibilities via regression. A regression of log tibia length on log CRL in pets, comparing males vs. females, showed no difference in slope or intercept between males and females, or between orchard-forest males and pet males (table 4.1). Likewise, a regression of log foot length on log CRL showed no difference between male and female pet monkeys; there was of course a large difference in Y-intercept between orchard-forest and pet monkeys (but not in slope) due only to methodological factors (table 4.1).

With regard to the ulna, the GLM analysis (environment, sex and log CRL as independent variables; log ulna length as dependent variable) yielded somewhat ambiguous results for a possible sex effect (chi-square = 3.376, p = 0.066). Regression results, with environments pooled, suggest that the ulna shows a slight tendency to positive allometry in males, but isometry in females (though the female sample is smaller, causing a much broader CI). The intercepts are different, but the regression lines cross each other before well to the right of the Y-axis, therefore the difference in intercept is uninterpretable. When I compared males vs. females within the pet sample only, however, the males' slope estimate fell below that of the females, and both CIs overlapped with one (table 4.1). The regression lines diverged only slightly, and the difference in slope was not credible upon examination of the scatterplot, due to the paucity of small females. I therefore conclude that there is no evidence for an effect of sex upon relative growth of the ulna.

I conclude therefore that Predictions 4.2.1 and 4.2.2 are both supported by the available data. Relative growth of limb segments is evolutionarily conservative, having not diverged at the subspecific level within ca. 9 kyr of isolation; it is sexually monomorphic, probably due to similar locomotor ecologies of males and females; and it is highly canalized, with no significant effect of environment. The latter result is especially notable since pet monkeys differ so radically from free-living monkeys in activity level, and therefore in energy balance, which can affect growth. It is also notable that overall body growth rate differs between environments, as does (possibly) relative growth of the trunk, while relative growth of the limbs seems far more canalized.

### *4.13: Limb proportions and proportional growth of limb segments*

*Question three:* Do any body segments grow faster than the others, and if so, why? If relative growth of body segments does differ, is the pattern stable between different environments (canalized) and subspecies (evolutionarily conservative)?

Hypothesis 4.3: Limb segments that were more important for efficient locomotion in a species' ancestral environment should grow faster than other limb segments, and outpace growth of the trunk. The hypothesized difference in relative growth between limb segments is expected to be evolutionarily conservative (among recently-diverged populations) and highly canalized due to constraining natural selection, and sexually monomorphic due to similar locomotor modes of males and females.

Prediction 4.3.1: The forelimb will grow isometrically or negative-allometrically with respect to the trunk (CRL). The hindlimb will grow faster than the trunk, i.e., positive allometry of hindlimb segments with respect to the trunk, regardless of environment, subspecies and sex.

*Forelimb*—For the humerus I pooled subspecies and sexes, since separate regressions showed no robust evidence for differences between these groups (see above). The humerus shows slightly but very robustly positive allometry with respect to the trunk (estimated slope = 1.21, 99.99% LCL > 1), which is against Prediction 4.3.1 (table 4.1). On the other hand, the degree of scatter around the total-sample regression line was higher than that for most other limb-length regressions, and separate analyses by habitat, sex and subspecies suggested that some degree of heterogeneity in the sample might contribute to the apparently positive allometry; for example, the male and *brunnescens* sub-samples seemed to have a disproportionate effect on the positive slope (table 4.1), although the female sample was small. While the heterogeneity by sex and subspecies was not statistically significant according to the GLM analysis (see section 4.9), it may be sufficient to cause artifactual effects upon the slope of the total-sample regression. Thus the results for allometry of the humerus are ambiguous: it may be positively allometric but the evidence is equivocal.

The ulna shows a weak tendency toward positive allometry, but the estimated slope is low (< 1.1) and the 95% LCL is below one. I therefore conclude that relative growth of the ulna is roughly isometric regardless of sex, environment or subspecies.

*Hindlimb*—The GLM analysis showed no significant effects of sex and subspecies upon relative growth of the femur; in fact there were no significant effects of environment either, suggesting that consistent measurement methods were employed by the two field studies (see Methods).

Of course, it is also possible that inconsistent methods obscured a real difference between sexes or subspecies, since I measured femoral length distally to the patella (knee flexed), while Watanabe et al. (1987) measured to the lateral condyle (a slightly shorter diastance). If this small methodological difference affected the analysis, (1) it would affect the y-intercept of the regression rather than its slope, whereas slopes (i.e., relative growth rates) and not y-intercepts are of most interest in this analysis; and (2) within the pet sample, the difference in y-intercept that was obscured in the full data set would appear. To further test for methodological confounding factors, therefore, I regressed log femoral length on log CRL within the pet sample only, comparing regressions for males vs. females (subspecies pooled), and separately for *ochreata* vs. *brunnescens* (sexes pooled). The lower 95% CLs of all slopes remained > 1, the 95% CIs overlapped substantially, and there were only small differences in intercepts (table 4.1).

Due to those small differences in y-intercept, I repeated the GLM analysis using only the pet sample (dependent variable = log femoral length, independent variables = subspecies and sex, N = 36). This GLM also detected no particular differences between sexes (chi-square = 1.372, p = 0.242) nor between subspecies (chi-square = 2.385, p = 0.123). It must be admitted, however, that a subspecific difference in y-intercept cannot be entirely ruled out, since N = 36 is a small sample size for a parametric test with three independent variables. (I interpret this GLM as a test for differences between sexes and subspecies in y-intercept, not slope, since in this statistical program a continous variable is used as a controlled covariate—essentially it is an analysis of covariance.)

The total-sample regression of log femoral length on log CRL was, like the humeral regression, very robustly postively allometric, with the 99.999% LCL > 1 (table 4.1). The total-sample scatterplot showed less error around the regression line, however, than did the total-sample regression for the humerus, reflected in a higher correlation coefficient (humerus: r = 0.94; femur: r = 0.98).

The femoral regression also remained consistently postively allometric within environments, with slope 95% LCLs > 1 and identical estimated slopes within the orchard-forest and pet environments, while the 95% LCLs of within-environment regression slopes for the humerus fell below one, rendering them isometric. Rather amazingly, in fact, the pet-only femoral regression slope remained significantly > 1 even when an LCL of 99.999% was used, despite the small sample size. In contrast, the pet-only regression for the humerus showed an LCL < 1 even at the 95% confidence level. Thus the postive allometric relationship of the femur is far more robust among environments than is that of the humerus.

When femoral allometry was examined separately by sex, the 95% LCL of the female regression fell below one, but that of the male regression remained robustly > 1. The same phenomenon occurred when the humeral regression was examined separately by sex. The humeral regression for males remained significantly > 1 when the LCL was placed at 99.9%; the femoral regression for males, however, remained significantly > 1 when a LCL of 99.999% was used (table 4.1).

When femoral allometry was examined separately by subspecies, the 95% LCLs for both subspecies' regressions remained > 1, while the 95% LCL of the humeral regression for *ochreata* fell below one (table 4.1). The LCL of the femoral regression for *ochreata*, moreover, remained > 1 even at the 99.9% confidence level, while that for *brunnescens* remains > 1 at the 99.999% level. The LCL of the humeral regression for *brunnescens* remained signifcant at the 99.9% confidence level (table 4.1).

Growth of the tibia relative to trunk length seems to be roughly isometric; there is a slight overall tendency toward positive allometry, but this tendency is not at all robust when relative growth is examined within sexes and environments (table 4.1). Males' tibiae may grow slightly more slowly than those of females (according to GLM analysis), but examination of a scatterplot shows that the difference is very small.

I conclude that the postive allometric relationship of the femur relative to body length is far more robust among environments than that of the humerus. The femoral regression is also more robust among sexes and subsecies than that of the humerus, but the difference in that case is more a matter of degree. Thus I conclude that Prediction 4.3.1 receives guarded support. It seems necessary, then, to help resolve any ambiguity by directly comparing growth rate of the femur to that of the humerus.

Prediction 4.3.2: The hindlimb will grow faster than the forelimb, regardless of environment, subspecies and sex.

I regressed log femoral length (Y) directly on log humeral length (X) to test further the prediction that femora should grow faster than humeri. I found parallel regression lines for orchard-forest and forest monkeys (my sample) vs. pet monkeys (the sample of Watanabe et al. 1987), due to methodological differences between the two studies (in the expected direction—see Methods). Slopes were identical for orchard-forest monkeys and pet monkeys (fig. 4.5). For both environments, the 95% and 99% LCLs for slope were > 1 (table 4.1), providing strong evidence for faster growth of the femur relative to the humerus—even within the rather small environment-specific samples—and for high canalization of relative growth of the humerus between environments.

For some unknown reason, however, the few forest monkeys for which I had limb-length data clustered exactly along the pet regression line even though they were from the same field study (mine) as the orchard-forest animals. If the prediction is wrong, and relative growth truly differs between environments, it should be similar in orchard-forest and pets, and different in forest (as with juvenile body length). Instead, the few forest animals cluster with the pets. I think, therefore, that the true reason for the forest animals' position is methodological, not biological. I did not include the forest animals in either regression analysis by reason of the unknown methodological problem, but I included them in figs. 4.5 and 4.6.

The difference in Y-intercepts necessitated separate regression analyses by environment, but such separation also reduced the power to detect robusticity in the relationship. I thus applied a rough correction factor to reconcile humeral measures between my study and that of Watanabe et al. (1987). I simply regressed log humeral length on log CRL separately for forest-orchard and pet environments, then (since the regression lines were almost perfectly parallel) subtracted the difference in Y-intercepts (0.07265) from log humerus measures from my orchard-forest sample, while not altering the log humerus measures from the pet sample. I then regressed this "corrected log humerus" measure on log CRL, to attempt a total-sample regression.

The result was a generally tight scatterplot with one exception: all five forest individuals that I trapped in 2005-06 (the only forest individuals for which I have limb-length data) fell on the pet regression line in the uncorrected log femur-log humerus regression, and thus fell well above the line on the corrected regression (fig. 4.6). For that reason I did not include them in either the uncorrected or corrected regression, as I think there must be some unknown methodological factor that differed between my 2004-05 and 2007 seasons. With the corrected, combined total sample, the slope estimate was nearly 1.2, and the LCL of the slope was now > 1 even at the 99.999% level of confidence (table 4.1).

I also regressed log tibia on log ulna to see if the highly robust positive allometry of the femur really is special. Regardless of how the sample was examined, however (total sample, by environment, by sex, and so on—see table 4.1), the relationship between tibial and ulnar growth was isometric, each keeping pace with the other.

### *4.14: Behavioral data on arboreality vs. terrestriality in* M. ochreata sensu lato

The faster growth of the femur relative to the humerus (and the trunk) may have to do with the largely arboreal locomotor pattern in forest-living *M. ochreata sensu lato*. To test this proposition, I used random transects to obtain data on arboreality vs. terrestriality of the macaques upon first sightings.

The macaques generally moved through the sub-canopy layer in large trees, among primary and secondary branches (immediately below the leafy main canopy), and to a lesser extent used the main canopy layer where most leaves were located. We rarely saw them use understory trees. Group spread of up to 200m occurred, and we occasionally observed lone individuals with no others in sight—not only males (as is expected in cercopithecines primates), but also females. The macaques also frequently used the crooks of primary branches (where the branch joins the main stem) for resting, reclining and grooming one another. On two occasions I observed the macaques climbing woody lianas (*ka'eo*) for access to the main canopy layer (after first leaping horizontally to the liana from the sub-canopy).

For each of the 20 on-transect sightings in my field data, I recorded the total count of individuals that were in trees when first sighted, vs. the number on the ground when first sighted. I then compared the number of animals observed in trees with the number observed on the ground for each of the twenty sightings. There were a total of 98 animals in trees and 6 animals on the ground upon initial encounters for the N = 20 sightings, meaning that the macaques spent 94% of their time in trees. A Wilcoxon signed-ranks test for matched-pair data (matched pairs were number of animals in trees vs. number on ground for each sighting) showed that booted macaques living in primary forest are largely arboreal, with Z (df = 20) = -84.5, $p < 0.0004$. The largely arboreal behavior of *M. ochreata sensu lato*, which involves hindlimb-powered leaping between trees and from trees to lianas, may account for the faster growth rate of the femur relative to the humerus.

## Discussion

### *4.15: Implications for trait-wise evolvability and evolutionary dynamics*

Whole-body growth, especially in body length (as opposed to mass) and especially in immature individuals, is highly susceptible to environmental perturbation. All the same, adults ultimately tend to converge toward the same body size, though judging by dental wear data on adults, primary-forest individuals (with their high activity levels) may take somewhat longer to reach the same body size attained earlier by orchard-forest and even by secondary-forest individuals. It is likely that juvenile growth rate, and probably also the timing of life-history milestones (such as descent of testes in males; pink sex skin and parity, indicated by elongated nipples, in females; and attainment of full body size in both sexes), are affected strongly by differences in diet and activity level (jointly, energy balance) among environments (Altmann and Alberts 2005; Ellison 1990). My impression is that that pattern is borne out in the data that I obtained. Environmental quality, moreover, may have an impact upon lifetime fitness, especially for females, via timing of the start of the reproductive career. Thus the timing of attainment of full body size, and also the length of the reproductive career (but not full body size itself), are affected by differences among environments.

The forest-living populations are presumably much more food-limited than are the macaques living in the other environments (orchard-forest and pet); or more precisely, the forest-living monkeys have a lower energy balance than monkeys in the other environments, since they must expend much energy to gather relatively little food. The smaller body size in juvenile forest-living monkeys (but not in adults) may not be particularly surprising, then, since this pattern seems similar to observed catch-up growth following periods of food scarcity in many human populations (Prader et al. 1963).

On the other hand, when children of relatively small humans are raised in food-enhanced environments, their more rapid juvenile growth is preserved in larger eventual adult size, especially in males (Froehlich 1970). A similar phenomenon, including the sex difference in effect of environment, has been observed in free-ranging baboons (*Papio* sp.) (Altmann and Alberts 2005; Strum 1991).

Thus my results suggest some degree of canalization of adult size, contra many studies of free-ranging primates and some studies of human growth. Another interesting result (though hampered by a very small sample) is the tendency of female infants to be larger than male infants in the forest environment. At any rate, the adult sample size of my study is not particularly large, and there is an obvious need for more data before one can reach firm conclusions.

It is unclear why there are differences in body length but weak differences, if any, in mass. Since mass is more ephemeral than body length (with greater circadian and seasonal variability), there may be more noise in the mass data. If this is true, one would predict that future studies with larger samples would detect a difference even where mass is concerned, although the effect upon mass might still be of lesser magnitude than that upon body length. That possibility is perhaps supported by the evidence for environmental differences in growth allometry of the trunk.

Limb proportions and relative limb growth are probably subject to very strong stabilizing selection within populations, which has likely resulted in canalization of growth patterns; it is unlikely that the effects of genetic drift between isolated populations ever successfully causes divergence in these traits, nor is it likely that even environments that differ radically in activity level (e.g. pets vs. free-ranging if slighly *manja* populations such as the orchard-forest sample) cause perturbation of genetically-determined relative growth. This degree of canalization of limb proportions is somewhat surprising in light of data from humans showing, for example, marked change in relative length of the legs caused by purely environmental factors (Ruff 1994: 94).

### *4.16: Implications for interpretation of fossils and other small, localized samples*

Before a morphological trait of a single individual or a small sample of individuals (as is often necessary in paleontology, and the neontology of little-known species) is interpreted as species-typical or its ecological significance is interpreted, we must have some idea, first, of how much variation in that trait typically exists within species; how the trait and its growth might differ between sex and age groups; how susceptible the trait is to non-adaptive divergence (such as via genetic drift) between recently-diverged populations; and the degree to which it can be affected by local (or seasonal) differences in diet quality and activity level.

The present study suggests that, within species, inferences from small, single-sex, or spatiotemporally (environmentally) heterogenous samples (e.g., McHenry 1992) are fairly secure where limb proportions are concerned, provided that allometric growth is taken into account. In fact, regression equations provided by this study might be helpful in interpreting immature fossil individuals of species for which adult limb proportions are little-known or unknown. When comparing overall body size of adults (whether proxies of stature or of mass), inferences from small local samples should also be fairly reliable, based on data presented here. Local (ecogeographic) differences in diet or activity level are more likely to affect immature individuals such as infants and juveniles, and have a greater effect upon body length than upon mass, if the data presented here turn out to be generalizable (replicated in a wide range of species). Thus, population-level inferences about overall body size (length or mass) based on small or localized samples of infants and juveniles should be made with care. Especially in juveniles, proxies of mass, when available (such as diameter of the femoral head) may be preferable to proxies of stature (such as limb segment lengths), though this question needs much more study.

### *4.17: A note on locomotor ecology of Sulawesi macaques*

Most previous studies (e.g., Anapol et al. 2005; Rodman 1979) of limb proportions vs. locomotion have been static comparisons among adults of well-differentiated species that are known *a priori* to differ in locomotor patterns. The present study builds upon previous efforts by examining growth and growth allometry within species and between recently-diverged subspecies that are not thought to differ in locomotor ecology; and tests for environmental effects upon growth and relative growth. My results supported those of Anapol et al. (2005), who compared arboreal blue monkeys to terrestrial vervet monkeys and found that blue monkeys had longer femora relative to their tibiae, than did vervets. My results somewhat contradict one aspect of Rodman's (1979) study, in that Rodman found that more arboreal macaques (*M. fascicularis*) have long tibiae relative to femora.

At least one other researcher who has studied a Sulawesi macaque species living in a closed-canopy rainforest environment (*Macaca nigra nigrescens* at Bogani Nani Wartabone National Park, northern Sulawesi) has observed largely arboreal behavior (Kohlhaas 1993). Others (*M. nigra nigra*: M. F. Kinnaird, pers. comm.; *M. maura*: S. Matsumura, pers. comm.) have observed a more even mixture of arboreal and terrestrial locomotion in Sulawesi macaque species, though my impression is that the study sites at which Kinnaird's and Matsumura's research were conducted have relatively open forest with little undergrowth (Kinnaird's study) or without a continuous, closed canopy (Matsumura's study). It is likely that neither of these conditions was typical of the ancestral environments of most Sulawesi macaques (at least during the Holocene), and both conditions likewise tend to discourage arboreal locomotion (Rodman 1991).

On the other hand, there could be evolved behavioral and ecological-niche differences between the Sulawesi species. I rather doubt it, however, since unlike the sympatric and syntopic pair of species observed by Rodman (1979) to have diverged in ecomorphologically in limb proportions and degree of arboreality (*M. fascicularis* and *M. nemestrina*), the Sulawesi macaques are distributed parapatrically, and share the same island-wide community of frugivorous potential competitors. Thus there has been no opportunity for disruptive selection and niche separation among the Sulawesi macaques.

Aside from the association between relatively rapid femoral growth and arboreality, an interesting result is the canalization of this growth difference—the lack of difference between macaques living in environments (pet vs. orchard-forest) that promote very different activity levels. This lack of difference suggests that femoral growth is under strong genetic control in these populations and evolved in the past to enable booted macaques, and perhaps Sulawesi macaques in general, to cover long distances efficiently in their search for fruit, and to gain access to canopy layer. Canopy-feeding allows the macaques to eat fruit such as *maniaga* and *eha* (see chapter two) before it can be consumed by pigs (Suidae, *Sus celebensis*), although macaques exploiting the canopy layer must also compete with birds, perhaps especially Sulawesi red-knobbed hornbills, *Aceros cassidix*, which can soar above the canopy and quickly survey large areas for ripe fruit. My research team observed a tendency for booted macaques to descend to the ground slightly more often during the dry season, when fruit is scarce, than in the rainy season, though I am unsure that there are enough data to date for a statistical comparison of locomotion between seasons.

*Tables*

**Table 4.1.** Allometric data from reduced major-axis regressions. M = male, F = female; O = ochreata, B = brunnescens; P = pet, Or = orchard-forest, Fo = forest (primary). Limb segment lengths: hum = humerus, fem = femur, tib = tibia, foot = foot + pedal digit III. Int = Y-intercept. N = sample size. LCL = lower limit of 95 % confidence interval for slope; UCL = upper limit of 95% confidence interval for slope. *99% LCL > 1. **99.9% LCL > 1. ***99.99% LCL > 1. ****99.999% LCL > 1. †Log humerus length corrected for differences in measurement method between studies—see Methods. Lengths in mm, mass in kg. Sample sizes (N) were smaller for regressions involving limb lengths of forest animals because limb length data were obtained for only five forest animals.

| Y | X | Sample | Slope | LCL | UCL | Int | N |
|---|---|---|---|---|---|---|---|
| log CRL | log (mass$^{1/3}$) | MOP | 0.917 | 0.741 | 1.135 | 2.448 | 12 |
| log CRL | log (mass$^{1/3}$) | MBP | 0.975 | 0.848 | 1.122 | 2.421 | 13 |
| log CRL | log (mass$^{1/3}$) | M | 0.956 | 0.894 | 1.021 | 2.409 | 75 |
| log CRL | log (mass$^{1/3}$) | F | 0.978 | 0.885 | 1.080 | 2.409 | 43 |
| log CRL | log (mass$^{1/3}$) | Fo | 0.992 | 0.934 | 1.053 | 2.387 | 56 |
| log CRL | log (mass$^{1/3}$) | Or | 0.868 | 0.795 | 0.949 | 2.434 | 25 |
| log CRL | log (mass$^{1/3}$) | P | 0.891 | 0.794 | 0.999 | 2.441 | 37 |
| log CRL | log (mass$^{1/3}$) | all | 0.971 | 0.922 | 1.022 | 2.407 | 118 |
| log hum | log CRL | O | 1.102 | 0.946 | 1.283 | -1.033 | 18 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| log hum | log CRL | B | 1.202 | 1.095** | 1.319 | -1.001 | 49 |
| log hum | log CRL | M | 1.235 | 1.110** | 1.374 | -1.095 | 47 |
| log hum | log CRL | F | 1.111 | 0.941 | 1.312 | -0.775 | 20 |
| log hum | log CRL | Or | 1.051 | 0.917 | 1.205 | -0.582 | 25 |
| log hum | log CRL | P | 1.059 | 0.979 | 1.146 | -0.655 | 37 |
| log hum | log CRL | all | 1.211 | 1.110*** | 1.321 | -1.033 | 67 |
| log ulna | log CRL | M | 1.076 | 1.005 | 1.153 | -0.658 | 47 |
| log ulna | log CRL | F | 1.002 | 0.816 | 1.230 | -0.475 | 20 |
| log ulna | log CRL | MP | 1.043 | 0.968 | 1.123 | -0.573 | 25 |
| log ulna | log CRL | FP | 1.105 | 0.894 | 1.366 | -0.730 | 12 |
| log ulna | log CRL | all | 1.069 | 0.997 | 1.146 | -0.642 | 67 |
| log fem | log CRL | O | 1.248 | 1.113** | 1.400 | -1.095 | 18 |
| log fem | log CRL | B | 1.191 | 1.116**** | 1.271 | -0.939 | 49 |
| log fem | log CRL | P | 1.194 | 1.167**** | 1.278 | -0.950 | 37 |
| log fem | log CRL | Or | 1.193 | 1.041 | 1.367 | -0.944 | 25 |
| log fem | log CRL | M | 1.228 | 1.155**** | 1.305 | -1.034 | 47 |
| log fem | log CRL | F | 1.081 | 0.951 | 1.228 | -0.657 | 20 |
| log fem | log CRL | MP | 1.198 | 1.100 | 1.304 | -0.961 | 25 |
| log fem | log CRL | FP | 1.164 | 1.027 | 1.320 | -0.867 | 12 |
| log fem | log CRL | OP | 1.248 | 1.113 | 1.400 | -1.095 | 18 |
| log fem | log CRL | BP | 1.200 | 1.090 | 1.322 | -0.961 | 19 |
| log fem | log CRL | all | 1.203 | 1.138**** | 1.271 | -0.971 | 67 |
| log tib | log CRL | MOr | 1.024 | 0.855 | 1.226 | -0.550 | 17 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| log tib | log CRL | MP | 1.113 | 1.005 | 1.232 | -0.771 | 25 |
| log tib | log CRL | FP | 1.088 | 0.911 | 1.300 | -0.708 | 12 |
| log foot | log CRL | MOr+Fo | 1.106 | 0.962 | 1.272 | -0.435 | 22 |
| log foot | log CRL | MP | 0.962 | 0.865 | 1.070 | -0.371 | 25 |
| log foot | log CRL | FP | 0.981 | 0.784 | 1.228 | -0.428 | 12 |
| log fem | log hum | P | 1.136 | 1.066* | 1.210 | -0.230 | 37 |
| log fem | log hum | Or | 1.135 | 1.053* | 1.223 | -0.283 | 25 |
| log fem | log hum† | all | 1.195 | 1.127**** | 1.268 | -0.344 | 67 |
| log tib | log ulna | P | 1.046 | 0.967 | 1.131 | -0.117 | 37 |
| log tib | log ulna | Or+Fo | 0.936 | 0.847 | 1.033 | 0.108 | 30 |
| log tib | log ulna | MP | 1.074 | 0.985 | 1.171 | -0.175 | 25 |
| log tib | log ulna | MOr+Fo | 0.943 | 0.818 | 1.086 | 0.094 | 22 |
| log tib | log ulna | M | 0.971 | 0.903 | 1.044 | 0.039 | 47 |
| log tib | log ulna | F | 0.919 | 0.806 | 1.048 | 0.147 | 20 |
| log tib | log ulna | all | 0.964 | 0.907 | 1.024 | 0.053 | 67 |

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*Figures*

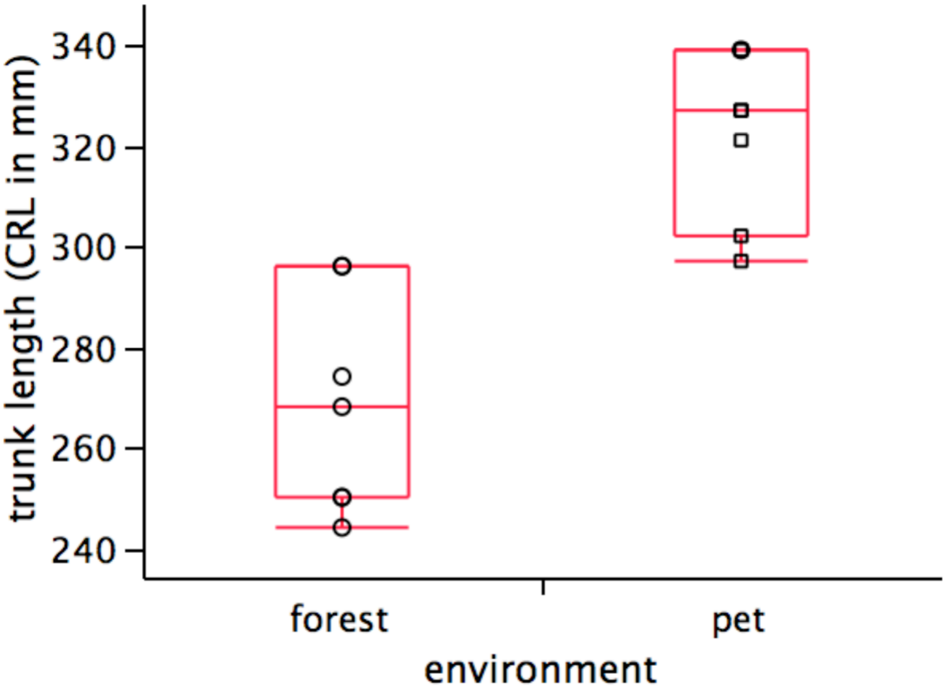

**Figure 4.1.** Trunk length (crown-rump length, CRL) of male infants in two environments: forest (N = 7) vs. pets (N = 7). Raw data shown, in mm. Van der Waerden Z = 3.024, p = 0.003. Differences in mass were slightly less pronounced (Z = 2.323, p = 0.020). Female infants tended to be larger than male infants within environments, therefore male and female samples could not be pooled. There were too few females for a separate between-environment comparison of females, and there were too few orchard-forest infants for that environment to be considered. The central horizontal line in each box plot is the median. In all figures, symbols as in chapter three: circles = male *ochreata*; squares = male *brunnescens*; diamonds = female *ochreata*; triangles = female *brunnescens*.

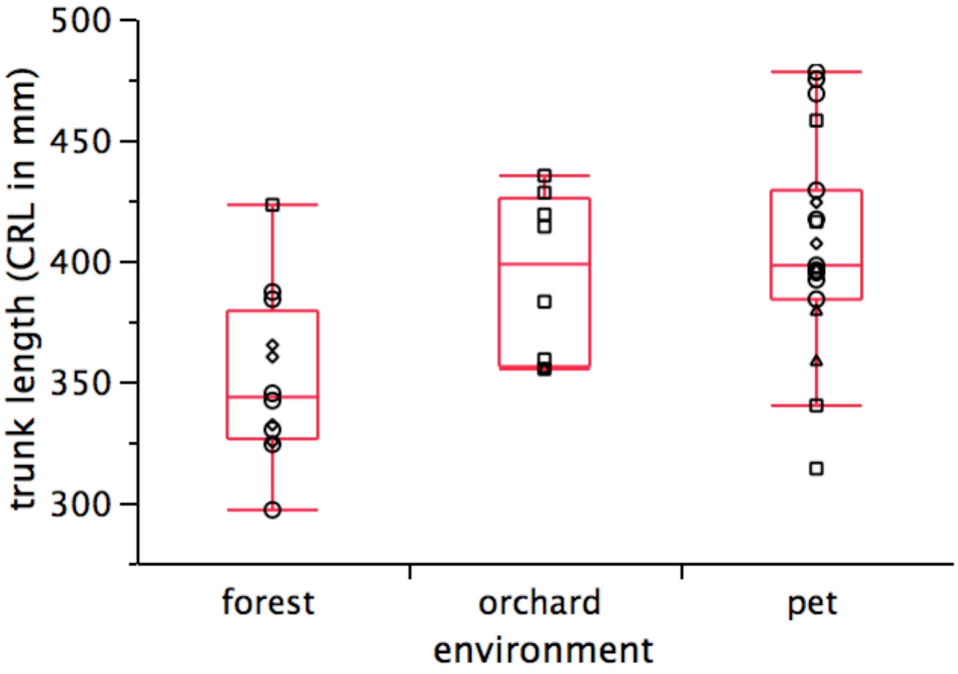

**Figure 4.2.** Trunk length (crown-rump length, CRL) of juveniles in three environmental conditions: forest (N = 12), orchard-forest mosaic (N = 8), and pet (N = 19). Sexes were pooled due to a lack of sex differences in CRL and mass at this age (tested separately within each environment). Trunk length is smaller in forest juveniles than in the other two environments (Kruskal-Wallis chi-square = 10.627, p = 0.005. There was no detectable difference in body mass among environments (Kruskal-Wallis chi-square = 3.409, p = 0.182).

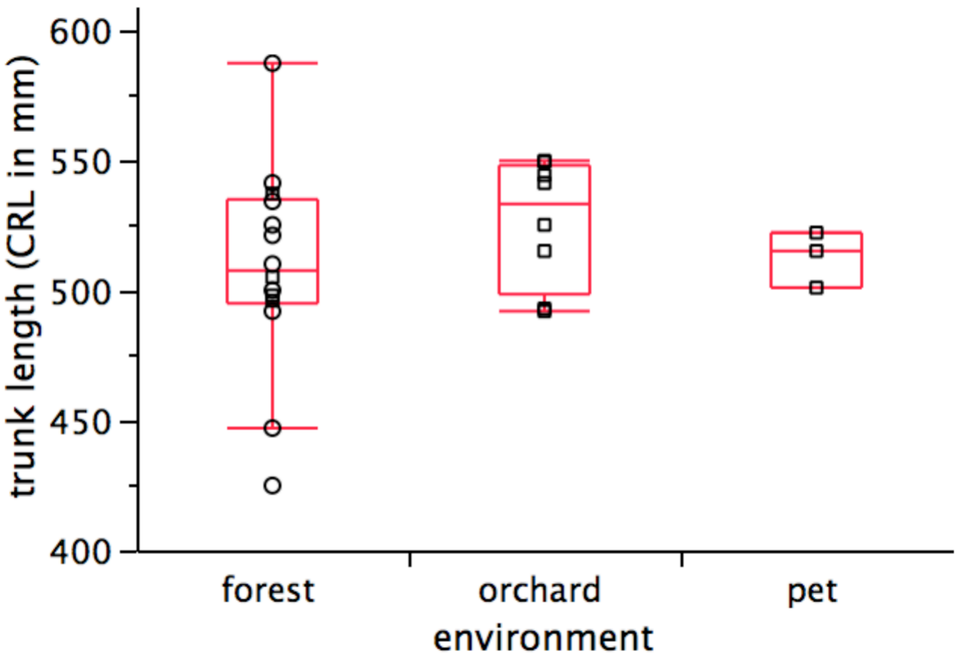

**Figure 4.3.** Trunk length (crown-rump length, CRL) of adult males in three environmental conditions: forest (N = 14), orchard-forest mosaic (N = 8), and pet (N = 3). There is no detectable effect of environment upon trunk length in adult males (Kruskal-Wallis chi-square = 1.816, p = 0.403). Also note that forest-living *brunnescens* males appear near the center of the forest males' distribution, reinforcing the point that there are no subspecific differences in size among adults (see chapter three). There is also no effect of environment upon adult male mass (forest vs. orchard-forest only: Van der Waerden Z = 0.299, p = 0.765). There were not enough adult females in the pet and orchard-forest environments for statistical comparison, but the few orchard-forest females seemed relatively large.

**Figure 4.4.** Allometric relationship of log trunk length (crown-rump length, CRL) to log body mass. An abnormally obese adult male pet (no. B259, rightmost data point) was excluded. A newborn (no. 44, lower left corner) was included in total-sample regression but excluded from the forest regression (to make fair comparison of environments). Solid red line = total sample regression; dotted blue line = forest; dashed green line = orchard-forest; dot-dashed orange line = pets. Please see table 4.1 for regression parameters. Some curvature downward away from the line is apparent in the largest individuals; this may reflect bulking up by males of all habitats in later adulthood, a late increase of mass relative to body length. Food-enhanced (or activity-reduced) populations such as pets and orchard-forest monkeys are relatively long for their body size in early life, but forest animals catch up in body length, apparently via slightly faster growth in length relative to mass; thus body proportions among habitats converge in adulthood. While the slopes of the various environmental conditions are not significantly different from one another (95% CIs overlap), CRL is isometric in the forest environment, but negatively allometric (signif. < 1) in pet and especially in orchard-forest environments (see table 4.1).

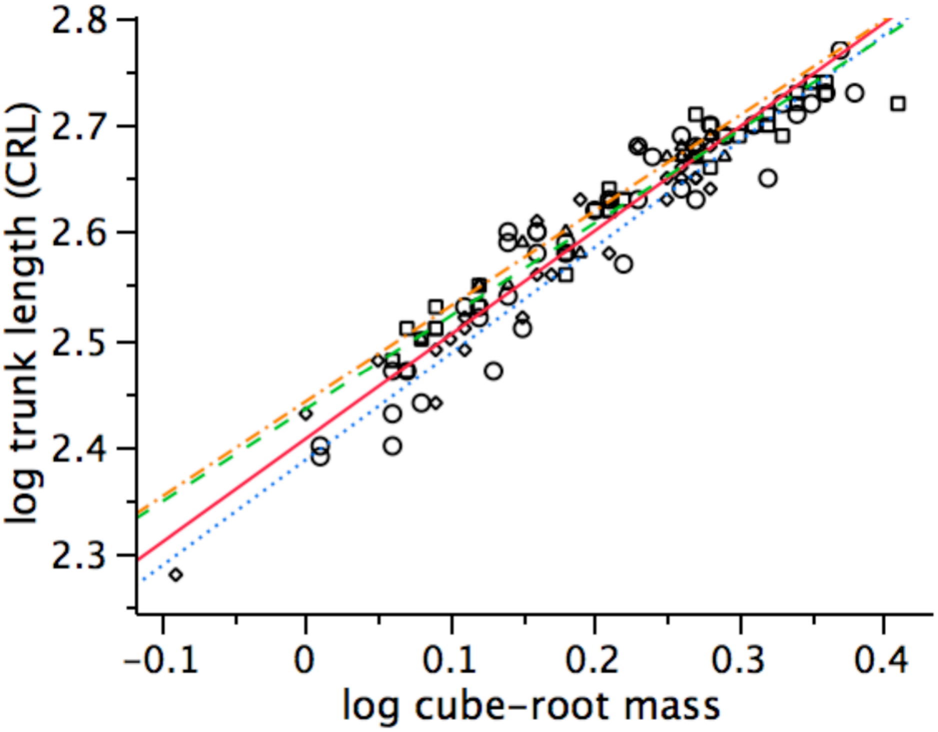
log trunk length (CRL)
2.8
2.7
2.6
2.5
2.4
2.3
−0.1
0
0.1
0.2
0.3
0.4
log cube−root mass

**Figure 4.4**

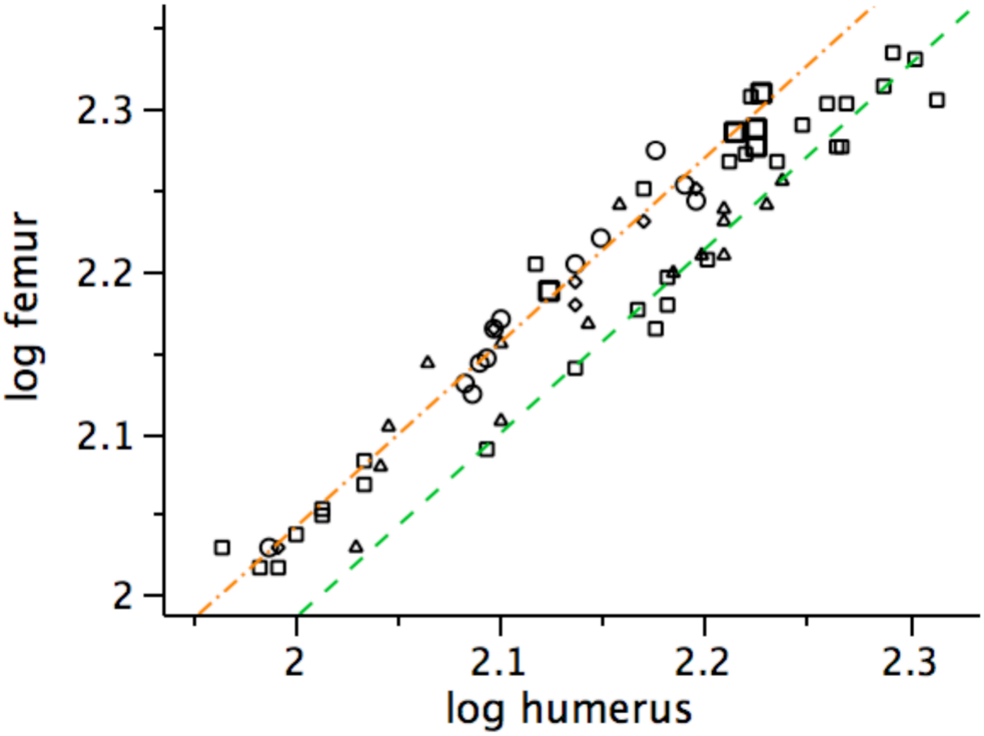

**Figure 4.5.** Direct regression of log femoral length on log humeral length, showing faster growth of the humerus. There are two parallel regression lines due to differences in measurement methodology (see Methods) between the present study's orchard-forest sample (dashed green line) and the pet sample of Watanabe et al. (1987) (dot-dashed orange line), but note the identical slopes (see table 4.1). The parallel lines indicate that there is no difference in relative growth between environmental conditions, thus canalization of relative femoral growth (unlike whole-body growth, and relative growth of the trunk) is very high. Note that the forest animals (large squares) cluster with the pet animals, for unknown reasons that are probably methodological (see text).

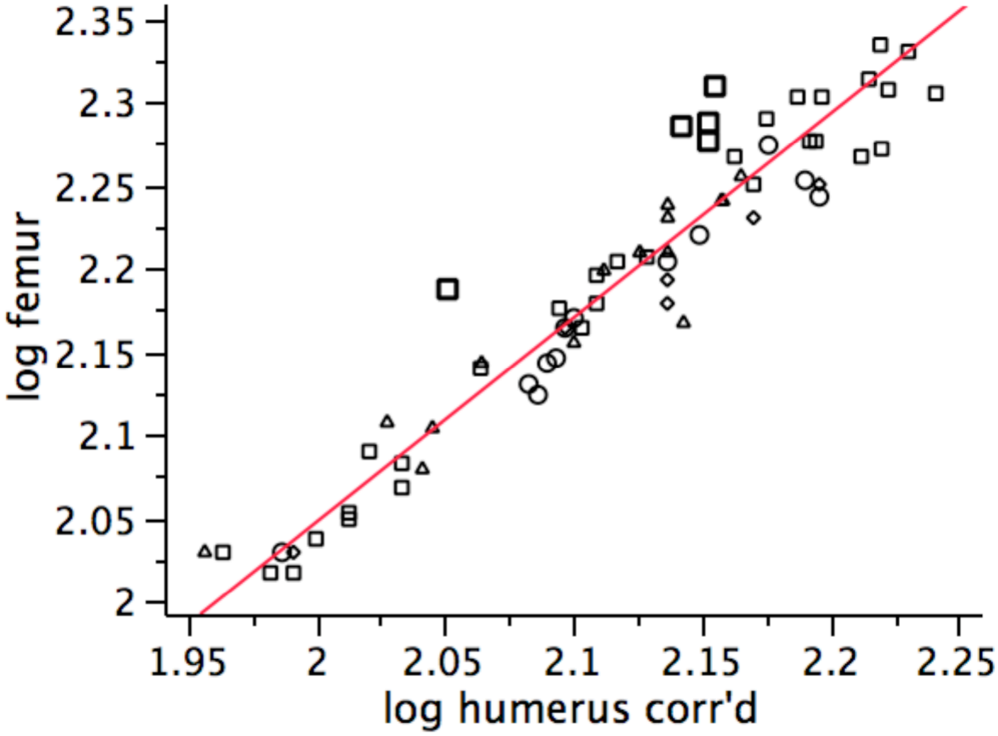

**Figure 4.6.** Regression of log femoral length on log humeral length, after the latter was corrected for differences in measurement methodology between studies. Note that, again, the forest animals (large squares) appear above the line. They were not included in the regression analysis as they are thought to differ for methodological reasons. The slope of the regression line remains significantly > 1 even when the confidence limits are increased to 99.999% (see table 4.1).

## Chapter Five

## Conclusion:

## Differential selective constraints upon morphological characters?

In chapters three and four, I found evidence (albeit indirect) that parallel natural selection in both *ochreata* and *brunnescens* may enforce stasis in a number of somatic traits. The results further suggest that limb proportions—specifically, the relative growth of the limb segments—may be the body part that is subject to the strictest evolutionary control. Evidence supporting that inference includes not only the lack of difference between subspecies in relative growth of the limbs, but also the high canalization of growth within subspecies, among environmental conditions. Growth of the trunk, for example, relative to body mass does not show canalization as great as that of the limb segments, as it seems to differ subtly among environmental conditions. Thus the importance of the limbs in propulsion of the body through the forest canopy—I infer that it must have been highly and equally important in both subspecific populations—probably caused both evolutionary stasis and canalization.

The size of male secondary sexual characters such as testes and especially the upper canines has likewise remained stable, in spite of indirect evidence (strongly positive allometry, strong sexual dimorphism relative to body size sexual dimorphism, high coefficient of variation) for strong sexual selection on these traits within subspecies.

Again, it seems likely that natural selection in the broad sense—in this case sexual selection—has played a constraining role and enforced stasis between the subspecies.

Head breadth (chapter three) is perhaps the trait least constrained by parallel, stabilizing selection and is thus freer to diverge between the populations. The hypothesis that divergence in relative head breadth (reduced in *brunnescens*, relative to the other Sulawesi species) has occurred via genetic drift is consistent with the fact that *brunnescens* is an insular peripheral isolate with a small population size relative to *ochreata*. The case for divergence by drift is also strengthened by the subtlety of divergence between the populations in this trait, and by the lack of a known effect of head breadth on ecological performance in macaques. The hypothesis of differential susceptibility of cranial shape to divergence by drift also agrees with results obtained for New World primates (Marroig and Cheverud 2004) and for Neandertals (Weaver et al. 2007). It is consistent with evidence presented by Nei (2007) and Lynch (2007), and theoretical arguments by Ho and Saunders (1979) suggesting that the tendency of natural selection to constrain evolutionary divergence, and the tendency of genetic drift in small populations to facilitate divergence, have perhaps not been widely appreciated.

In other words, evolution may be facilitated as much by the absence of natural selection as by its presence, depending upon the ecological and psychophysical circumstances, and upon the trait in question. It might be possible, then, to think of evolutionary divergence as resulting from a rare release from the processes that normally enforce stasis—such as parallel, stabilizing natural selection among populations and gene flow from large subpopulations (Eldredge et al. 2005; Estes and Arnold 2007).[1] Of course, there is nothing mysterious about what might cause such a release—small effective population sizes, changes in biotic or abiotic ecological circumstances, subdivision of a population's range, or some combination of these, can all potentially lead to the opportunity for divergence (as reviewed in chapter one). Of course, the wrong combination can lead back to stasis.

I pause here to concede the obvious—that the methods used in this dissertation for inferring the presence, direction and intensity of natural selection are very indirect and focused upon only one pair of populations, albeit in great detail. It will be necessary in the future to attempt replication of these results in other pairs of allopatric populations, preferably from a wide array of mammalian taxa. It would also be desirable to have more detailed and direct measures of selection, as well as to use quantitative methods to test for genetic drift. While replication is desirable, the nature of research on the effects (constraining or otherwise) of ecological selection requires a reasonable amount of ecological and environmental detail in order to contextualize the results; thus studies with detailed data collected from a small to moderate number of species would be highly desirable.

Of course, one would ideally like to know more about the regulatory details of the development of traits analyzed in this dissertation. The ideal study would integrate molecular and histological studies of development with gross studies of development, divergence and stasis like the one performed here, while simultaneously including more detailed ecological data that I have done here. It should be noted, however, that there is no substitute for the study of gross morphology, since it is largely at that level that ecological performance occurs.

Thus I believe that, even in the age of molecular genetics, morphology is not a bad place to start when addressing any particular evolutionary question. I hope—as many others have also noted, of course—that functional genomics will make it possible for biologists to move beyond analysis of model "systems" (model organisms) and, in non-model organisms, to build upon studies of gross morphology and ecology with greater molecular and developmental detail—combining mechanistic rigor with an appreciation for the diversity of life and the oft-surprising vicissitudes of evolution. On the other hand, the comparative evidence that has been gathered so far suggests that the broad details of genetics and developments are highly conserved among all vertebrates, indeed among all animals to a great extent—the differences seem to occur in the details of timing and rate of transcription of certain genes.

What this conservatism of mechanism means is that even if a study of gross morphology never extends down to the molecular level (in a particular species or genus), we need not think ourselves entirely ignorant as to the likely molecular mechanism of divergence, or stasis as the case may be.

## Note to chapter five

[1] The concept of evolutionary diversification as a release from normative stasis (or punctuated equilibrium) has been controversial, particularly as to its degree of originality as an idea. I treat it here as merely a difference in emphasis or approach, not as a revolutionary new idea, as it was noted in passing by Darwin (1859). On the other hand, natural selection was noted in passing by many authors before 1859, but it was Darwin who explained its importance and prevalence in nature.

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