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# Feeding Ecology and the Rise of Primate Intelligence:

## With Special Reference to the Orangutan

by

Paul L. Vasey

B.A. (Honours) University of Alberta 1989

THESIS SUBITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF MASTERS OF ARTS

in the Department

of

Archaeology

Simon Fraser University
June 1991

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ISBN 0-315-78201-3

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# APPROVAL

**Name:** Paul Vasey

**Degree:** Masters of Arts (Archaeology)

**Title of Thesis:** Feeding Ecology and the Rise of Primate Intelligence: With Special Reference to the Orangutan

**Examining Committee:**

**Chairperson:** Dr. E. Nelson

Dr. Biruté Galdikas
Senior Supervisor, Professor

Dr. Richard Shutler, Jr.
Professor Emeritus

Dr. Charles Crawford
External Examiner
Professor, Department of Psychology,
Simon Fraser University

Date Approved: June 10, 1991

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# **Abstract**

It is argued that the behaviours traditionally described as hominid "prime movers" in fact constitute part of a shared pongid/hominid behavioural repertoire and are a concomitant by-product and consequence of direct selection for higher order intelligence. Furthermore, in order to understand the origin of the behaviours deemed the "prime movers" of hominid evolution, an examination of pongid intelligence is necessary. Orangutans (Pongo pygmaeus) are the most phylogenetically conservative of all the pongids and, unlike the chimpanzee and the mountain gorilla, they have never radiated out of the climax tropical forest where pongid intelligence initially evolved. Consequently, it is argued that orangutans should be *the* great ape under consideration during any investigation of pongid intelligence.

Primatologists have long debated the relative importance of food acquisition problems versus social problems as selective mechanisms influencing the evolution of primate intelligence. Unlike all other anthropoid primates, wild orangutans are characterized by a unique semi-solitary adaptation with correspondingly infrequent social interaction. As such, literature pertaining to orangutan social intelligence has, to date, been scant and is unamenable to review. Therefore, this thesis provides a preliminary investigation into the role feeding ecology played as a selective mechanism favouring orangutan intelligence. In the process of doing so, it is demonstrated that the extreme complexity of orangutan feeding ecology necessitates that they constantly process large amounts of environmental information. This is demonstrated throughout all phases of the food acquisition process including: food recognition, searching/foraging and handling/processing. Over time, natural selection would have favoured the more intelligent orangutan individuals who were capable of processing the large amounts of complex information associated with feeding problems they encountered. As such, feeding ecology probably played a large role as a selective mechanism favouring the rise of orangutan intelligence.

# Acknowledgements

Over the past two years I learned much about the role of an academic, both from the preparation of this thesis and from the publications and conference papers that I worked on throughout my stay here in the Department of Archaeology at Simon Fraser University. Successful completion of my M.A. degree, however, would have been impossible were it not for the assistance of the following people:

To begin with, I am exceedingly grateful to the Department of Archaeology and to the chairman Dr. Jack Nance, for awarding me with a Graduate Fellowship during my second last semester at S.F.U.. Without this financial support, there is little doubt that my completion time would have been much longer than two years. Furthermore, I was able to work on two papers for publication during this period of support, which would have also been impossible without the fellowship.

Jack Nance, Jon Driver, Ingrid Nystrom, Yvonne Marshall, Andrew Barton, Linda Bannister, Denise Kask, Erle Nelson and Richard Shutler, Jr. all helped guide me through the tangled bureaucracy of the university system. Each of these people provided helpful information and were always willing to answer my questions concerning university policy on various issues.

Murrielle Nagy, Veronica Smith and the Department of Anthropology at the Univeristy of Alberta were kind enough to allow me to use their offices and computers during the preparation of parts of this thesis. Randy Preston provided valuable comments on an earlier draft of this thesis.

Many individuals provided support, encouragement and most importantly, friendship, during some dark hours when I thought I would never be able to make it through the program. These individuals include: Grant Lemke, Teri Clark, Linda Fedigan, Mary MacDonald-Pavelka, Lisa Duncan, Lindsey Oliver, Nick Teo, Murielle Nagy, Cidalia Duarté, Jeff Bailey, Sue West, Elizabeth Crocker, Eldon Yellowhorn, Lorraine Erikson, Jeff Vasey, Todd Vasey, Eva Linklater, Shauna McRanor, Lisa Gould, Donna Morrison, Valerie Gobeil, Jane Fitschen, Yvonne Marshall and Catherina Purss. By taking the time to listen to my concerns or ideas of the moment each of these people help me achieve my fullest potential during my time at S.F.U.. In this regard, I am particularly indebted to Christopher Knüsel

who's "never-give-up" attitude was truely a wellspring of inspiration.

Special thanks goes to my parents, Leonard and Dorothy Vasey. Both my parents help me make the move to Vancouver and then provided weekly support via telephone conversation. Most importantly, they did not question the choice I made to become a primatologist, nor did they prod me to seek education in a more conventional discipline.

I would like to thank Dr. Charles Crawford for serving as my external examiner during my thesis defense and for the many thought provoking conversations we shared over the past two year. His "devil's advocate" converstation style prompted me to reformulate many of my ideas concerning evolutionary theory, sociobiology and the nature of intelligence.

I would like to thank Dr. Biruté Galdikas, firstly, for accepting me as her first western graduate student for which she served as senior supervisor. Dr. Galdikas was kind enough to share many of her interesting ideas on primate behaviour and evolution with me and I have benefited from her unique world view. I am most grateful to Dr. Galdikas for allowing me the opportunity to co-author several papers with her, one on adolescent female orangutan social and sexual behaviour, one on sociobiology in primatology, one which poses the question of 'why orangutans are so smart', and one on species recognition in hominid paleontology. Her willingness to co-author these papers provided me with a forum in which to introduce my ideas to other academics and to develop my skills as a researcher and writer. I am exceedingly greatful for this opportunity, for it allowed me the chance to experience how much I enjoy research and writing. I feel that my association with Dr. Galdikas has been extremely productive and, in reflecting on the past two years, we both have much to be proud of.

Charles Darwin had Thomas Huxley; my "bulldogs" were Dr. Richard Shutler, Jr. and Ingrid Nystrom. I owe extra special thanks to both of these people for more than any others they were responsible for my success over the past two years. They acted as surrogate parents, advisors, teachers, friends and *always* made me feel good about myself and my work. It was a great solace to know that they were in their offices daily and were always willing to stop what they were doing and provide positive reinforcement. At the university, where so much negative behaviour finds an atmosphere in which to flourish, knowing that Dr. Shutler and Ingrid acted completely without interest to themselves made it all tolerable . As a student of animal behaviour, both Dr. Shutler and Ingrid are my reminders that human beings can defy the explanatory powers of sociobiology.

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# Chapter 1: On the Pongid/Hominid Behavioural Repertoire

## 1.1 Introduction

This thesis provides a preliminary investigation into the role feeding ecology played as a selective mechanisms favouring orangutan intelligence and encephalization. In the process of doing so, it is demonstrated that orangutans are not the lackadaisical creatures that they are often portrayed to be. Instead, the complexity of their feeding ecology necessitates that orangutans constantly process large amounts of environmental information. This is demonstrated throughout all phases of the food acquisition process including: food recognition, searching/foraging and handling/processing. Over time, natural selection would have favoured the more intelligent orangutan individuals who were capable of processing the large amounts of complex information associated with their feeding niche. As such, feeding ecology probably played a large role as a selective mechanism favouring the rise of orangutan intelligence. It is argued that any investigation of orangutan intelligence and encephalization carries with it implications not only for orangutan adaptation, but for hominid behavioural evolution as well.

## 1.2 Non-Human Primates as Models for Hominid Evolution

An unfortunate reality of palaeoanthropological inquiry is that the majority of evidence pertaining to early hominid lifeways does not survive taphonomic processes or, as is the case for behaviour, does not preserve at all. Consequently, much of the paleoanthropologist's work remains highly speculative and is relegated to the realm of educated guesswork. Paleoanthropologists temper their speculation, however, by examining how extant primates have adapted to their social, physical and biotic environments. The use of primate models for reconstructing hominid origins is by no means a direct and simple process since no two species experience extactly the same ecological pressures throughout their evolutionary histories. That is, the behaviour exhibited by a non-human primate cannot be demonstrated as mirroring early hominid behaviour. Morphologically, physiologically and behaviourally, every species is a unique product of an evolutionary path traveled once and only once. Recognizing this important point, Fedigan

(1982: 4) states:

> "No matter how closely chimpanzees (<u>Pan troglodytes</u>) may appear to resemble us, they are certainly not on their evolutionary way to becoming humans, and their present situation is not one of the way-stations along which our own species travelled. Nor does their behaviour, represent the biological core of our own behaviour, stripped of it's cultural oramentation. Simply it represents the behaviour of an animal with which we share some relatively recent common ancestor... Yet, given such assertions, it is small wonder that many people continue to think incorrectly of monkeys as not-quite humans, as primitive creatures retarded on the path to humaness."

Although non-human primates cannot act as mirrors reflecting every nuance of the early hominid condition, they can serve as metaphors which help *approximate* how the early hominids lived. Approximating extinct hominid lifeways using extant non-human primates is theoretically feasible, because all the primates share a common phylogenetic history. This shared phylogenetic history constrains the range of adapations to ecological stimuli members of the Primate Order can accommodate. For example, an aerial predatory niche, similar to those filled by hawks, may become vacant, but the massive structual reorganization necessary for any primate to fill such a niche (not the least of which would be the evolution of wings!), makes the prospect of such an occurance entirely unlikely. Because a shared phylogentic history constrains all the primates, all members of the Order *may* respond in broadly similar ways given a particular set of ecological parameters (Kinsey 1987). Parrellel evolution between the Old World and New World monkeys bears witness to this fact; more than 30 million years of separate evolution has resulted in similar evolutionary solutions to similar ecological problems owing to a shared phylogenetic history (Fleagle 1988).

Hominids are also constrained by their primate phylogenetic history and consequently, they too may respond to ecological stimuli in a manner similar to that of the other primates. As such, every primate species may serve a role in interpreting how early hominids adapted to their environment. For example, in posing the question: 'What were the consequences, for early hominids, of having dexterous, gripping hands' we can theoretically turn to the most unlikely of primate models, the aye-aye (Daubentonia madagascariensis), or the ukari (Cacajao spp.), or the mandrill (Mandrillus sphinx), since all the primates share the benefits and constraints of manipulative hands. More commonly, however, because of the close phylogenetic relationships between the pongids and the hominids, the great apes (especially the chimpanzee) are favoured by paleoanthropologists who seek primate models to reconstruct hominid behaviour.

## 1.3 On the Pongid/Hominid Behavioural Repertoire

Most palaeoanthropological hypotheses concerning hominid origins are founded on the assumption that the behavioural adaptations which modern humans possess, but which the great apes do not, allowed the first transitional hominid to radiate into a savanna niche and avoid competition from forest dwelling pongids. Hunting, gathering, tool use, bipedality, language, food sharing, culture, ecological separation underlying a sexual division of labour, and transportation of items to a central home base have each been cast as *the* "prime mover" responsible for inducing pongid-hominid speciation and as hallmarks of the hominid condition (Table 1) (Washburn & Lancaster 1968; Isaac 1978; Zihlman & Tanner 1978; Campbell 1988). Survival on the open savanna, it is often argued, was dependent on the expression of these "unique"

## Table 1:

**The behaviours traditionally advanced as unique unto the hominids and as the "prime movers" of hominid evolution include:**

| | |
|---|---|
| Physical Behaviours: | -Bipeadality |
| Foraging Behaviours: | -Savanna dwelling<br>-Hunting/scavenging<br>-Gathering<br>-Transportation of food to "Home base" |
| Techological Behaviours: | -Tool use/making |
| Social Behaviours: | -Food sharing<br>-A sexual division of labour as reflected by an inter-sexual ecological separation |
| Cognitive Behaviours: | -Language capacities<br>-Proto/culture |

hominid behaviours and, as such, natural selection favoured those transitional hominids who exhibited them as part of their daily behavioural repertoire. Traditionally, it has been suggested that once these distinguishing behaviours became part of the proto-hominids' daily behavioural pattern they served as prezygotic "isolation mechanims" (Mayr & Provine 1980) which imposed barriers to gene flow with parapatric pongid populations. That is, these behaviours inhibited sexual interaction and exhange of genetic material between members of adjacent pongid and hominid populations.

Paleoanthropologists, in general, envision the origin and evolution of the behaviours traditionally forwarded as the "prime movers" of hominid evolution as: 1) appearing at the point of the pongid-hominid speciation and 2) as being the product of direct selection due to extreme ecological pressures such as reduced tree cover, heat, aridity and predation, experienced in the ancestral savanna niche. Implicit in this assumption is that these behaviours only gain major adaptive significance with the emergence of hominids and that they consititute irrelevant components of wild pongid adaptations. Beginning with Jane Goodall's (1963) observations of tool use and tool manufacture among chimpanzees in the wild, one by one the behaviours held as hallmarks of the hominid condition (Table 1) have fallen by the wayside as each has been found to be a *component* of wild pongid adaptations. Evidence now indicates that these behaviours constitute part of a shared pongid-hominid behavioural repertoire (Table 2). Thus, the behavioural differences that separate the pongids from the hominids must be measured by degree rather than kind. Hence, the origin of the behaviours forwarded as the "prime movers" of hominid evolution must have occurred long before pongid-hominid divergence. As such, a true understanding of the origin and evolution of the behaviours deemed so cruical for hominid emergence requires an examination of the *pongids* as well as the hominids.

The infrequent expression of these behaviours by wild pongids speaks strongly to the suggestion that the capacity for these behaviours was not the product of directional selection. Had these behaviours been products of direct selection wild pongids would be manifesting them more frequently. Why infrequently expressed behaviours evolved among the pongids need not be a source of confusion once one considers that "Natural selection may build an organism 'for' a

**Table 2**

**Research Indicating at Shared Pongid/Hominid Behavioural Repertoire** *

| **Behavioural Hallmark** | **Researcher(s)** | **Pongid** |
|---|---|---|
| Hunting/Meat Eating: | Sugardjito & Nurhuda 1981 | Orangutan |
| | Tutin & Fernandez 1983 ** | Gorilla |
| | Badrain & Malenky 1984 | Bonobo |
| | Boesch & Boesch 1989 | Chimpanzee |
| Gathering and Transport of Food: | Boesch & Boesch 1984b | Chimpanzee |
| | Chevalier-Skolnikoff et al. 1982 | Orangutan |
| Tool Use/Making: | Galdikas 1982 | Orangutan |
| | Kano 1982 | Bonobo |
| | Boesch & Boesch 1984b, 1990 | Chimpanzee |
| | Wood 1984 | Gorilla |
| | McGrew 1987 | Chimpanzee |
| Proto/culture: | McGrew, Tutin & Baldwin 1979 | Chimpanzee |
| | Galdikas 1983 | Orangutan |
| | Goodall 1986 | Chimpanzee |
| | de Waal 1989 | Bonobos |
| Language: | Shapiro 1982 | Orangutan |
| | Patterson & Linden 1981 | Gorilla |
| | Savage-Rumbaugh et al. 1989 | Chimpanzee & Bonobo |
| | Miles 1990 | Orangutan |
| Food Sharing: | Teleki 1973 | Chimpanzee |
| | Horr 1977 | Orangutan |
| | Silk 1978 | Chimpanzee |
| | Kuroda 1984 | Bonobo |
| | Bard 1990 | Orangutan |
| Ecological separation: | McGrew 1979 | Chimpanzee |
| | Galdikas & Teleki 1981 | Orangutan & Chimpanzee |
| Bipe adalism: | MacKinnon 1974 | Orangutan |
| | Dixson 1981 | Gorilla |
| | Susman 1984 | Bonobo |
| | Bauer 1977 | Chimpanzee |

* Included are only a few of the many citations I could use to support the claim for a shared pongid/hominid repertoire.

** Although not meat eating *per se*, this article discusses a faunal component, termites, in the diet of one population of gorillas.

specific function or group of functions..., [but] the 'purpose' need not fully specify the capacity of that organism. Objects designed for definite purposes can, as a result of their structural complexity, preform many other tasks as well..." (Gould 1980: 57). In short, "Structure has latent capacities" (Gould 1980: 57). In line with Gould (1980), the pongid/hominid behavioural repertoire as expressed by the great apes, represents a consequence and concomitant by-product of directional selection for some other adapation. Because the behaviours that constitute part of the shared pongid/hominid behavioural repertoire were not a product of directional selection, any understanding of their origin and evolution, is dependant on an understanding of the basal adapation which *was* being selected. It is this basal adaptation which laid the basis for the behaviours deemed the "prime movers" of hominid evolution. Therefore, an examination of this basal adaptation should be of great interest to paleoanthropologists.

I argue, as has Galdikas (1978b: 307), that the basal adaptation allowing for the shared pongid-hominid behavioural repertoire was, in large part, increased intelligence as reflected by an encephalized brain.

Among the pongids, higher intelligence probably did not evolve as a specific ability, but rather as a more general adaptation for problem solving which was not domain specific. The rise of a non-domain specific intelligence among the pongids would have allowed for the increased information processing abilities (Jerison 1983, 1985) and behavioural flexiblity (Napier 1970; Parker 1978; Burton 1984) necessary for expression of the behaviours which constitutes the shared pongid-hominid repertoire (Table 1).

Orangutans are the most phylogentically conservative of all the pongids. That is, of the extant pongids, orangutans were the first to have evolved. Unlike the chimpanzee (Pan troglodytes) and mountain gorillas (Gorilla gorilla beringei) they have never radiated out of the climax tropical forest where pongid intelligence initially evolved (Pickford 1983). As such, any investigation into the origin and evolution of pongid intelligence should involve and examination of how wild orangutans utilize their higher order intelligence. Examination of wild orangutan intelligence may serve to elucidate selective mechansims that favoured the evolution of pongid intelligence in general, and by extension, the mechanisms which laid the basis for the pongid-hominid behavioural repertoire. In order to fully understand the behaviours modern humans share with the great apes, but which have been hypothesized as cruicial to the hominidization process, we must first understand the origin and evolution of pongid intelligence.

As Cartmill (1990: 188) states:

> "To understand the origin of anything, we must have an overarching body of theory that governs both the thing itself and its precursor to successors. Without such a body of theory, we have no way of linking the precursor to its sucessors. We are also left with a body of knowledge that cannot be understood as an implication of larger and more fundamental generalizations about the world, but is fated to remain logically isolated in a theoretical vaccum."

## Chapter 2: The Costs and Benefits of Brain Size

### 2.1 Introduction

Of all animals, primates have the largest brain/body ratios, with the pongids and the hominids represent the zenith of this trend (Jerison 1973). From an evolutionary perspective relative enlargement of the brain over time is a fascinating process because of the extreme benefits and costs associated with maintenance of brain tissue. In this chapter, the costs and benefits of possessing an enlarged brain/body ratio are explored. Analysizing such cost and benefits provides a theoretical background for understanding why higher order intelligence would evolve and the contexts in which it would be favoured by natural selection.

### 2.2 The Cost of Large Brains

The brain is, metabolically speaking, an extremely expensive organ to maintain (Hofman 1983a, b; Armstrong 1985; Martin 1984; Milton 1988). Among humans, 20% of the of the total energy generated by body metabolism is utilized by the brain, while the brain's cortex metabolism is about 43% higher than the weight-specific metabolic rate of the entire brain (Hofman 1983a, b; Armstrong 1985; Milton 1988). Regardless of an organism's physical or mental state its brain tissue requires large and continuous supplies of oxygen and glucose to maintain the basal metabolic rate (Hofman 1983a, b). Oxygen is used for the aerobic oxidation of glucose and almost no energetic reserves of $O_2$ stored for reserve use (Hofman 1983a, b; Armstrong 1985). Because brain maintenance requires a constant supply of energy in the form of oxygen and glucose, hypoglycaemia can lead to stupor and rapid, irreversible damage to the nervous system (Hofman 1983a, b; Armstrong 1985). It follows, that those species which can sustain a high $O_2$ and glucose delivery, can afford the metabolic costs of large brain maintenance (Milton 1988; Gibson 1986). Reflecting on the combined costs and benefits embodied by maintenance of a large brain/body ratio, Richards (1985: 121) states "...while the possession of a large, expensive-to-run brain may help ensure the success of primates in the tropics, I believe that it may also be important in limiting their distribution to areas with an abundance of high-quality food."

Due to the extreme metabolic cost associated with brain maintenance one would expect natural selection to favour a reduction in relative brain size in the absence of a significant adaptive value. Thus, a major task faced by the paleoanthropologist is explaining why primates require such large brain/body ratios. Part of the answer to this question lies with the extreme benefits enlarged brain/body ratios impart to their possessors.

### 2.3 The Adaptive Value of Large Brains: Intelligence, Information Processing, & Behavioural Flexibility

Traditionally, it has been assumed that the adaptive benefit bestowed by large brain/body ratios was increased intelligence. The correlation between brain size and intelligence has, however, always been more intuitive than obvious. Much of this situation is owed to the fact that intelligence is one of the those abstract concepts that everyone recognizes in pratice, but which lacks any agreed upon definition. For example, Humphrey (1976: 304) states that "An animal displays intelligence when he modifies his behaviour on the basis of valid inference from evidence", while Parker (1978: 304) believes that "When an individual recognizes an early step towards the solution of a complex problem, it exhibits one facet of what we mean by intelligence." Markl (1985) defines intelligence as the ability to relate different unconnected pieces of information in new ways and to apply the results in an adaptive manner, while Piaget and Inhelder (1971) define intelligence as the differentiation and coordination of actions on objects.

Jerison's (1983, 1985; also see Burton 1984) concept of intelligence deserves special consideration, as it functions to bring together the seemingly disparate viewpoints of other researchers. He equates intelligence with the brain's capacity to process external and internal information concerning the environment and the body (Jerison 1973, 1983). The greater the brain's capacity to process information, the more advanced the intelligence level of the organism. Hence, intelligence *is* information processing ability (Jerison 1983, 1985).

Jerison (1983, 1985) argues that the biological units of information processing, the "modules", are found throughout the surface of the brain, in the neocortex. The brain's modules each contain approximately 2,000 neurons and occur repeatedly accross the surface of the neocortex (Szentagothai 1978; Jerison 1983). Research shows that the modules are remarkably uniform across species in terms of their morphology and density, with about 2,000 modules occurring per $cm^2$ of cerebral cortex (Szentagothai 1978; Eccles 1979; Rockel et al. 1980; Jerison 1983). Jerison (1983) concludes that if the module is accepted as the unit of information processing, a fundametal measure of an organism's intelligence (as measured by information processing capacity) will be brain size ( as measured by the brain's surface area). In other words, increased intelligence is a function of an encephalized brain, where encephalization represents the amount of additional brain mass an organism prosesses above and beyond its basic somatic needs. Convolutedness and fissurization increase the brain's surface area and, therefore, increase the number of information processing modules. This might confound Jerison's (1983, 1985) conclusions were it not for the fact that the degree of convolutedness and fissurization increases positively with brain size. Thus, it seems that brain size (as measured by the brain's surface area) can be used as *one* relevant indicator of intelligence (as measured by information processing capacity) (Jerison 1973, 1983, 1985; Parker & Gibson 1979; Lynn 1990).

Higher level intelligence as a function of brain size, forms the basis for another adaptive trait, behavioural flexibility (Napier 1970; Parker 1978; Burton 1984). As the cognitive capabilites of the organism become increasingly refined, there is an increase in both the range of stimuli that will elicit any given response and in the range of responses that can be elicited by any given stimuli (Parker 1978). In other words, behaviour can be tailored to the uniqueness of a situation, so that individuals can respond in an adaptive manner to a situation which has never been encountered before and which may never be encountered again.

In sum, an enlarged brain per body weight forms the basis for the increased intelligence (as measured by information processing ability) (Jerison 1973, 1983, 1985; Lynn 1990) and behavioural plasticity (Napier 1970; Parker 1978; Burton 1984). The positive correlations between an encephalized brain, information processing ability (intelligence) and behavioural flexiblity makes each trait inseparable from the others. Thus, in discussing the evolution of the encephalized primate brain, one is simultaneously investigating the evolution of primate information processing ability (intelligence) and behavioural flexiblity.

Although the the increased information processing ability and behavioural flexiblity associated with enlarged brain/body ratio bestowed great benefits to the posessor, in and of themselves, these traits cannot be thought of as explanations for the rise of primate intelligence because in isolation, they have little adaptive meaning. To understand why higher order intelligence evolved among primates, one must ascertain the contexts in which increased information processing ability and behavioural flexiblity are rendered necessary for survival. The issue of context specificity and the adaptive value of large brains is dealt with in the following section.

## 2.4 Context Specificity & the Adaptive Value of Large Brain/Body Ratios

We humans, the species with the largest brain/body ratio to ever have evolved, may find it paradoxical that bigger brains are not always more adaptive. In light of the metabolic costs associated with brain maintenance the mere fact that intelligence and behavioural flexiblity are positively correlated with brain size does not account for why large brains evolved among primates. The benefits of intelligence and behavioural flexiblity are relative, and depend on the ecological and social context in which an animal exists. Features of an organism's environment must necessitate possession of intelligence and behavioural flexiblity in order for them to be rendered adaptive and to be selected for. Hence, intelligent behaviour to one animal may be irrelevant behaviour to another animal faced with different adaptive problems.

Consider, for example, the sportive lemur (Lepilemur mustelinus) which Jolly (1988: 373) refers to as "...no one's candidate for the most intelligent primate." The sportive lemur has among the lowest brain/body ratios of any primate (Bauchot & Stephan 1966) and inhabits a niche that is narrow and simple in structure, especially when compared to the niche occupied by orangutans. The overwhelming bulk of the sportive lemur's diet consists of leaves (91%) with a small proportion of flowers (6%) taken from only three species

(Charles-Dominique & Haldik 1971). Observations reveal that throughout their lives, sportive lemurs confine themselves to a handful of trees over a 0.1 - 0.3 ha. area (Richard 1987; Russell, pers. comm. in Jolly 1988). The high cellulose, low energy diet of the sportive lemur necessitates that they it spend the majority of the day alone and immobile, while their specialized large intestine works to extract the maximum amount of nutrients possible (Charles-Dominique & Haldik 1971; Richards 1987). Because the environmental and social stimuli encountered by the sportive lemur is so uniform, repetitive and limited in quantity, the advanced intelligence and behavioural flexibilty conferred by large brains are of little value. On metabolic grounds alone, the sportive lemur would be unable to support a large brain/body ratio due to its nutritionally low quality diet. The possession of a large brain capable of processing unpredictable and complex stimuli, and responding in a flexible and varied manner, would be a vast overstatement of the sportive lemur's requirements; somewhat analygous to using a jackhammer in opening a walnut. Lacking any adaptive context which necessitates an encephalized brain and increased intelligence, the phylogenetic history of the sportive lemur has simply been characterized by selection for such traits.

In short, the adaptive value of a large brain, and its correlates, expanded information processing capabilities and behavioral flexiblity, is context dependent. In order to understand why primates evolved large brains, primatologists must search for the selective mechanisms, *the contexts*, which render advanced intelligence and behavioural flexiblity necessary for survival.

## 2.5 Social Problems Versus Ecological Problems & the Rise of Orangutan Intelligence

Primatologists have long questioned the relative importance of social problems (Jolly 1966; Burton 1984; Cheney et al. 1986; Parker 1987; Byrne & Whiten 1988a; Cheney & Seyfarth 1990) versus ecological problems (Parker & Gibson 1977, 1979; Wrangham 1977; Galdikas 1978b; Parker 1978; Clutton-Brock & Harvey 1980; Sigg 1986; Milton 1981; Sigg & Stolba 1981; Terborgh 1983; Menzel & Juno 1985; Gibson 1986) as selective mechanisms favouring primate encephalization and intelligence. For example, students of primatology have marveled at the highly social nature of their subjects. Most primates spend many hours in proximity to one another traveling, feeding, playing, grooming, fighting, mating, and sleeping. They formulate life-long relationships that transend generations and interact in complex ways according to their kinship, age, sex and individual history. Research suggests non-human primates perceive elements of their social systems and use this information to manipulate the behaviour of conspecifics for personal benefit (Burton 1984; Bryne & Whiten 1988a; Cheney & Seyfarth 1990). In this way primates are capable of using others as 'social tools' indicating that "...primate intelligence is not just 'social', but *Machiavellian* in its origins" (Whiten & Byrne 1988a: 6). Because the social lives of most primates appear so complex, primatologists have suggested that the need to solve social problems was the major selective mechanism influencing primate intelligence and encephalization (Jolly 1966; Burton 1984; Cheney et al. 1986; Parker 1987; Byrne & Whiten 1988a; Cheney & Seyfarth 1990). More specifically, the ability to recognize one's self, other individuals and relationships, to participate in triadic interactions and to deceive, have all been cited as hallmarks of "Machiavellian" social intelligence (Whiten & Byrne 1988b).

According to the "Machiavellian" social intelligence hypothesis, social situations are highly "reactive" necessitating that group living primates continuously monitor the behaviour of conspecifics and accommodate their behaviour as the social mileu evolves (Whiten & Byrne 1988a). Individuals capable of processing complex social information could manipulate the behaviour of conspecifics and influence the outcome of interactions for their own personal benefit. Those individuals able to attribute intentions, beliefs, knowledge and emotions to others rather than simply predict behaviours, would be far more adept in the social arena, because they could manipulate what another individual thinks rather than simply how it behaves (Cheney & Seyfarth 1990). Attribution necessitates that the individual represent two, possibly contradictory, mental states at once. Social expertise of this magnitude would require an expanded ability to deal with disparate types of rapidly changing information and to store and recall such information. In short, faced with these types of social problems, there would be ever greater selection in favour of increased intelligence and, by extension, encephalization.

Because orangutans are not group living, their higher order intelligence has always seemed problematic when viewed from the perspective of the Machiavellian social intelligence hypothesis. Nevertheless, orangutans have not shunned their anthropoid heritage. Galdikas (1985) demonstrates the social potential of wild orangutans, while Galdikas and Vasey (1991, in press) argue that orangutans possess (although rarely express) a higher order "Machiavellian" social intelligence. Research by Bard (1990) indicates that orangutans are capable of using gestures as "social tools" to manipulate others as early as three and a half years of age. Orangutans appear capable of recognizing themselves, other individuals, their own personal relationships and the relationships of others, and they put this social knowledge to use during acts of coalition and deception (Galdikas & Vasey 1991, in press). This provides evidence (but does not prove) that orangutans are capable of recognizing: 1) the mental states of others, 2) that others may not be privy to the same information they are, and 3) that the mental states of others may differ from their own (Galdikas & Vasey 1991, in press). If this is true, it would mean orangutans could influence what others think and not just what others do (Galdikas & Vasey 1991, in press).

Unlike all other anthropoid primates, wild orangutans are characterized by a unique semi-solitary adaptation with correspondingly infrequent social interaction (Galdikas 1985). As such, literature pertaining to orangutan social intelligence has, to date, been scant (with the exception of Galdikas 1978b; Galdikas & Vasey in press, 1991). Given the lack of published data on orangutan social intelligence, the focus of the following chapter will be the role of feeding ecology, rather than social problems, in the rise of orangutan intelligence.

# Chapter 3: Feeding Ecology & The Rise of Primate Intelligence With Special Reference to the Orangutan

## 3.1 Feeding Ecology & The Rise of Primate Intelligence: Theoretical Background

During their waking hours, wild primates spend a disproportionate amount of time engaged in feeding activites. Recent research has dispelled the myth of the tropical forest as a bountiful storehouse of easy to obtain food (Richards 1977; Milton 1981; van Schaik 1986; Galdikas 1988), illuminating the fact that primates inhabiting tropical forest often have a difficult and time consuming task feeding themselves. Because so much time is spent feeding and because food acquisition is intimately linked to survival and reproduction, primatologists have begun to investigate the role feeding ecology plays as a selective mechanism mediating the evolution of primate intelligence. The basic premise underlying this body of thought is that as the foraging matrix of a primate becomes increasingly complex, there is ever greater need for an encephalized brain which can process disparate types of information, as well as store and recall such information rapidly and efficently. Individuals with larger brains per body weight would experience lower mortality and higher lifetime reproductive success because of their advanced ability in solving foraging problems. In short, as the problems a primate faced in feeding itself increased, there would be ever greater selection in favour of encephalized brains and the advanced intelligence and behavioural flexibity they confer. What then, is the specific nature of foraging problems that would favour higher order intelligence?

Early attempts to link primate intelligence with feeding ecology cast hunting/meat eating as the selective mechanism favouring the evolution of the encephalized primate brain (Washburn & Lancaster 1968). Incorporation of a substantial meat component into the diet, it is argued necessitated the monitoring of prey activity rythms, coordinating movement during the hunt in a cooperative manner, and delaying carcass consumption so that meat could be shared with conspecifics not present at the kill site. All of these behaviours were thought to be dependent on the behavioural flexibility and intelligence a large brain/body ratio confers. As such, hunting and encephalization (and, by extension, intelligence and behavioural flexiblity) formed a spiraling feedback loop whereby each favoured increasing refinement of other in a evolutionary symbiosis.

Initially meant to account for trends of encephalization among the *hominids*, the inability of researchers' to generalize the principles of this hunting hypothesis across the primate lineage meant that the general trend for increased encephalization throughout primate evolutionary history could not be accounted for. All non-human primates, with the exception of the tarsiers (Bearder 1987), are essentially vegetarians, indicating that the hunting/meat eating could not have been the cruicial factor mediating encephalization throughout the phylogenetic history of the Primate Order. Moreover, field data on non-human primates revealed that the diet of some non-human primates, such as chimpanzees, savanna baboons (Papio spp.), and capuchin monkeys (Cebus spp.), contained a substantial component of meat, yet researchers questioned whether such species exhibited intelligent behaviour such as planning, cooperation or reciprocity during predation episodes (Busse 1978; Smuts 1981; Fedigan 1990; personal observations of Cebus capucinus). These observations cast doubt on the causative relationship between predatory behaviour/meat eating and intelligence and prompted primatologists to investigate how exploitation of plant food might favour intelligence and encephalization. It readily became apparent that the acquistion of plant foods was not as innocuous and effortless as it superfically appeared.

Because the majority of primates feed at the first tropic level on plant material, their food acquisition behaviour does not involve a pursuit component during which they must subdue fleeing prey. Instead, as a prelude to ingestion, food acquisition by primates can be broken into three phases: 1) food recognition 2) search/foraging, and 3) handling/processing. Depending on the niche a primate occupies, increasingly complex information processing may be required during each of these phases for successful ingestion of food and nourishment of the body. Primatologists have questioned how each of these three feeding phases might become increasingly complex, so as to necessitate increased intelligence and thereby act as selective mechanisms favouring encephalization. More specifically, dietary diversity as reflected by an opportunist/generalist adaptation (Parker 1978; Galdikas 1978b; Milton 1981), the need to memorize and monitor food sources that are irregularly distributed in time and space (Parker

& Gibson 1977; Wrangham 1977; Galdikas 1978b; Parker 1978; Clutton-Brock & Harvey 1980; Milton 1981; 1988; Sigg & Stolba 1981; Terborgh 1983; Menzel & Juno 1985; Sigg 1986) over a large supplying area (Menzel 1978; Clutton-Brock & Harvey 1980) and extractive foraging on embedded foods (Parker & Gibson 1977, 1979; Gibson 1986) have all been argued to place a high selective premium on intelligence and behavioural flexibility conferred by enlarged brain/body ratios. Add to this the need to decide when to leave a food patch given decreasing returns for energy and time expended, the need to avoid predators while foraging, and the need to acquire adequate food when faced with inter- and intra-specific competitors and the challenge of feeding oneself becomes a formidable task.

As discussed in Chapter 2, inferring the presence or absence of intellectual capacities among other species is a difficult task because intelligent behaviour as manifested among one species may be irrelevant behaviour to another. In short, the adaptive significance of intelligence is context specific. In an attempt to account for this problem, Menzel and Wyers (1981) outline four criteria by which intelligent foraging behaviour might be empirically assessed and which are referred to throughout this chapter whenever orangutan behaviour is discussed. These four criteria include:

(1) the ability to remember and to plan ahead

(2) the ability to account for stimuli that are momentarily absent

(3) a lack of a rigid one-to-one relationship between stimuli and responses; (various behavioural patterns are used to obtain the same goal)

(4) the ability to take into account a relatively large number of variables, rapidly and simultaneously.

I now turn to the evidence which sheds light on the role feeding ecology played during the evolution of primate intelligence, in general, and orangutan intelligence, in particular.

### 3.2 Recognizing Food: The Dietary Diveristy Hypothesis

The first step an orangutan, or any primate, faces in feeding itself is recognizing what to eat. To make this decision, inanimate objects in the primate's range must be categorized as edible, nutritional, non-toxic and/or medicinal based on several of traits including size, texture, colour, and physical construction (criterion 3 & 4). In other words, a "taxonomy" of dietary and non-dietary items must be constructed (Burton 1984: 77). If the need to recognize appropriate food was an important selective mechanism influencing primate intelligence, then brain size and intelligence should be positively correlated with dietary diversity as reflected by an opportunist/generalist adaptation (Parker 1978). In other words, as the number of potential food items a species eats increase, so to does the species' need to recognize, store and recall information pertaining to each food item. This contrasts with the adaptive situation faced by specialist primate species such as the sportive lemur which occupies very narrow niche and thus, does not need to recognize, store and recall large amounts of information pertaining to its food items. Consquently, the sportive lemur has one of the lowest brain/body ratios of all the primates. What evidence is there that the need to recognize appropriate food items was an important selective mechanism favouring encephalization among the large brained, intelligent orangutans?

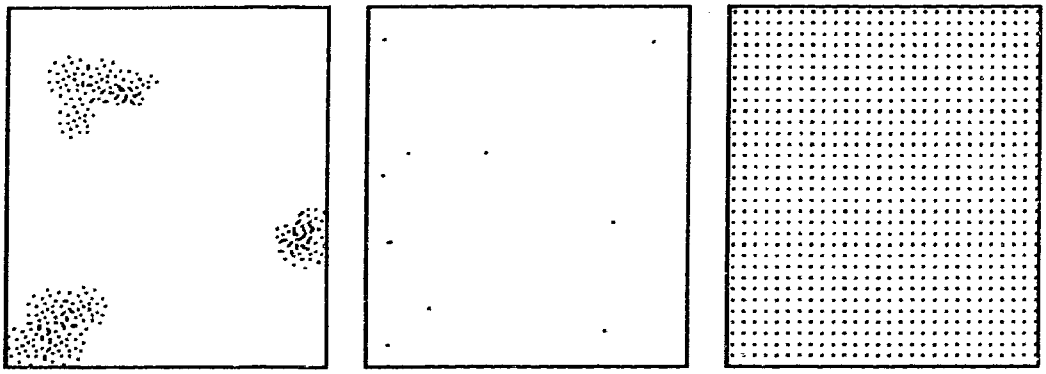
With a diet characterized by a complex mix of fruit, leaves, bark, sap, insects, shoots/stems, honey and fungi and which varies markedly from month to month, orangutans can definitely be described as opportunistic foragers (Galdikas 1988). Moreover, the dietary breadth exhibited by orangutans is truely remarkable among primates. At Tanjung Puting National Park, Indonesian Borneo, 317 food types have already been identified and it is reasonable to assume that orangutans at this field site actually use more than 400 food types (Galdikas 1988). Galdikas (1978b) argues that wild orangutans are capable of remembering and recognizing the over 300 different food types utilized at her Bornean field site, because they rarely experiment with new (and potentially toxic) foods (criterion 1, 2 & 4). Often, orangutans do not taste food prior to ingestion or rejection, but merely inspect it visually or handle and smell it (Galdikas 1978b). In the case of toxic food items, this behaviour suggests that the absence of direct toxicity inducing nausea is not necessary for toxicity to be inferred (criterion 2) because the orangutan remembers (criterion 1) the food item based on past experience.

Food availability regularly fluctuates in rainforest habitat (Richards 1977; Milton 1981; van Schaik 1986; Galdikas 1988). The orangutans' ability to recognize a large number of food items greatly reduces their risk of starvation or malnutrition during periods of food scarcity. Furthermore, food recognition reduces the need to experiment with food and thus, the possiblity of ingesting poisonous toxins. Since the orangutans health and survival depend on obtaining nutrients from such an enormous number of food sources, many of which are seasonal in productivity, the need to recognize, store and recall several criteria for each of the vast array of potential food items indicates considerable selective pressure. Hence, for the case of the opportunistic orangutans, it appears that dietary breadth played a significant evolutionary role in encephalization and intelligence.

### 3.3 Finding Food: The Food Distribution Hypothesis

Once primate recognizes appropriate food items it must decide where to search, or forage, for them. The difficulty of finding food varies, however, depending on how preferred food is distributed throughout a primate's range.

Folivores are not under intense selection pressure tc remember the location and phenology of leave sources because leaves are denser and more uniform in time and space relative to fruit (Fig. 1)(Milton 1981).



Clumped
(eg: Fruit)

Scattered
(eg: Non-social Insects)

Even
(eg: Leaves)

Fig 1: A Schematic Representation of the Three Types of Food Distribution. Orangutan food sources are clumped in their distribution.

Instead, the foraging success of folivores appears dependent on very regular patterns of movement which maximize the probability of encountering appropriate leaf sources (Milton 1981). By contrast, the search/forage phase of food acquisition of frugivorous primates is particularly complicated because, unlike leaves, fruit is irregularly distributed both in space *and* in time throughout tropical forest habitats (Fig. 1) (Richards 1977; Milton 1981; van Schaik 1986; Galdikas 1988). This means that fruit trees within a primate's home range are not only irregular in their location, but they are also irregular in their timing of productivity. Consequently, fruit is rarely an abundant resource in the tropical forest. The dynamic nature of tropical forest fruit sources enforces that frugivorous primates, such as the orangutan, must continuously make complex decisions regarding the area in which to forage so that time and energy are not wasted randomly moving about encountering unproductive fruit patches or no fruit patches at all. The need to remember, store and recall information pertaining to the location of irregularly distributed fruit sources, so that time and energy expendature could be minimized while foraging and malnutrition or starvation could be avoided, suggests considerable selection pressure favouring the evolution of primate intelligence. Higher order intelligence would allow frugivorous primates, like the orangutan, to "cognitively map" (Menzel 1978) irregularly distributed food patches within their home range and use this information to plan economically efficient travel routes to and from food sources in a premeditated fashion. Time and energy spent in travel could be minimized by choosing the shortest routes between cognitively mapped food sources. In other words, a least distance policy (Menzel 1978) between goals could be employed.

An added advantage to any frugivore possessing a cognitive map of fruit sources in its range, would be the ability to monitor the phenological patterns of fruit sources in their range. In other words, individuals possessing cognitive maps of their environment could, upon encounter with a productive fruit tree, use their knowledge of the location of other food sources to make a systematic check of all other trees of that species throughout their range. The ability to cognitively map irregularly distributed food patches within one's home range and to monitor the varying phenological nuances of such food patches necessitates possession of a large brain capable of processing vast amounts of spatial and botanical information and responding to such information in a very flexible manner. What evidence exists to support the hypothesis that the intelligence exhibited by frugivorous primates such as the orangutan has evolved so that the locations of food sources which are irregularly distributed both in time and space can be remembered? Do orangutans use this information to maximize encounter rates with productive food sources while minimizing time and energy expenditure in travel? Do orangutans use cognitive maps to monitor the phenological patterns of food sources in their ranges by making systematic checks of similar productive species?

Among orangutans, such capacities are indicated by their use of remarkably efficient routes to reach out of sight (criterion 2), productive food patches (MacKinnon 1978; Rodman 1979; Galdikas 1978b). The ability to take "shortcuts" is perhaps the clearest single piece of evidence for cognitive mapping (Menzel 1978). This behaviour entails the need for detailed individual memory of environmental features (criterion 1), as well as the ability to represent several such features in quantitative terms so that a least distance policy can be employed in a premeditated fashion (criterion 4). In other words, in using cognitive maps, orangutans appear capable of representing several unseen environmental features in a simultaneous fashion (criterion 2 & 4), rapidly quantifying distances between such features (cirterion 4) and then, on the basis of this information, choosing the shortest and most energy efficient travel route to reach their 'goal' (criterion 1 & 3). Orangutans seemed to excell at this over primatologists equipped with compasses, maps and cut trails (Galdikas 1978b). MacKinnon (1978:122) notes:

> "It is quite clear that orangutans do not amble aimlessly around their ranges taking pot luck. They move in a very purposeful and deliberate fashion. To plan such [economically efficient] routes they must not only have a very good knowledge of what is where, but they must also have a good sense of direction, distance, and travel time."

A least distance policy as exhibited by orangutans has been similarly demonstrated for captive chimpanzees (Menzel 1978). Menzel (1978) posed the basic question of whether captive chimpanzees (Pan spp.) could remember food locations and organize their food search in such a way as to get the best possible reward in the shortest possible time and with the shortest possible mileage. From an adjacent cage a small group of chimpanzees were shown the location of eighteen randomly hidden food items in a one acre field. The test animals and a group of control animals (who did not observe the hidden food locations) were then released into the field. Results show that the test chimpanzees found 12.5 out of a possible 18 food items per trial, while the control animals found only .21 items per trial. The test chimpanzees never wandered randomly about the field, but instead searched unerringly according to a least-distance principle. The control chimpanzees mainly obtained food by begging and following the test chimpanzees. These results indicate that the test chimpanzees were able to remember the location of a large number of irregularly distributed food items and use this information to maximize the rate of food acquistion, while minimizing their time and energy expenditure by using a least distance policy (Menzel 1978). In other words, the test chimpanzees formed a cognitive map of the distribution of resources throughout their one acre feild and then used this information to forage efficiently. Menzel (1978: 402, 407) concludes:

> "From the several thousand test trails I conducted in outdoor situations over a period of several years, I am of the opinion that chimpanzees'

> spatial memory...is probably better than our own would be in the same situation. ...'Cognitive mapping' is not the only possible explanation of the above facts, but it describes the facts more accurately and succinctly than any alternative term of which I am aware."

Most detailed research on primate cognitive mapping abilities has been carried out on captive animals (Menzel 1978; Menzel & Juno 1985). In the wild, the primatologist's ability to concretely state that their subjects remember the locations of food and use a cognitive map to optimize their foraging is severely limited (Jolly 1988). In captive situations the "environment" can be manipulated so that the "goal", the costs and benefits normally associated with foraging, and the subject's motivation (eg: hunger, thirst, fear etc.) can be ridgidly controled by the researcher. By controling for these variables, an experimental foraging problem can be designed for which (normally) only one optimal solution exists and no intermediate goals exist to confound the the subjects' attainment of this solution. More specifically, four main problems confound the field primatologist's ability to infer the possession of cognitive maps (Sigg & Stolba 1981; Sigg 1986): 1) It is difficult to infer whether the subject reached a food patch by chance or by goal directed travel. 2) It is extremely difficult to know the actual goal of a travelling primate because it may combine a number of different goals in one single route. 3) In the wild, a least distance policy to conserve maximal amounts of time and energy is not necessarily *the* optimal solution to a foraging problem since the animal must also account for risk to predation, body temperature regulation and vegetational cover (which may go unnoticed by the field research). 4) Animals may search out food sources according to a high probability of their productivity or in order to monitor their imminent productivity. An inablity to control for these variables has meant that field studies of the relationship between irregularly distributed resources, cognitive maps and intelligence are largely lacking.

One exception to this trend has been the field study by Boesch and Boesch (1984b) on the wild chimpanzees of Taï National Park. Boesch & Boesch (1984b) provide evidence that these wild chimpanzees possess cognitive maps which allow them to remember features in their environment, such as nut trees, and use this information to employ a least distance policy when moving between such features. In order to exploit the nuts of one tree species (Panda oleosa) these chimpanzees must carry hammer stones to the goal tree. Hammer stones occur in proximity to the nut trees, but are randomly distributed at varying (unseen) distances around it. Results show that once a tree had been selected the chimpanzees almost always (95% of the time) choose to use a tool that required the least amount of time and energy to transport. These results suggest that the chimpanzees were able to remember and quantify the location of abandoned hammer stones relative to numerous nut trees. Using this information they were then able to select the hammer stone that required the least distance to transport it to the desired nut tree. The authors suggest that the exploitation of a nutritionally rich and irregularly distributed food source, under conditions of poor visiblity, contributes to the high development of spatial capacities in the Taï chimpanzees (Boesch & Boesch 1984a). If this hypothesis is correct, then poor visibility due to dense foliage may have been an important environmental pressure favouring cognitive maps among orangutans.

The only other detailed study of cognitive mapping among wild primates was carried out by Sigg and Stolba (1981; Sigg 1986) on Hamadryas baboons (Papio hamadryas) in Ethiopia. In one sense, Hamadryas baboons are the ideal wild primates with which to study the presence/absence of cognitive maps, because their survival centres around finding two basic goals: water by day and safe sleeping cliffs by night. Because the grassland plateaus that Hamadryas baboons inhabit are so desolate, intermediate goals are less likely to influence these animals' travel patterns to and from water and cliffs. Hence, researchers studying this primate have a more concrete understanding of the "goals" that might motivate their subjects' travel patterns. Results from this study reveal that topographical features and predators do not funnel the Hamadryas baboons movements, nor do they move about randomly. Instead, the baboons repeatedly travel along defined routes 500m in length and 150 m in width and use these in novel combinations depending on their daily "goals".

Could topographical features be directing the movements of orangutans in a manner that mimicked the non-random indicative of higher order intelligence? At some of the mountainous sites where orangutans have been studied such as Ketambe in Northern Sumatra (Rijksen 1978), steep slopes and deep valleys may funnel orangutan movement in a non-random pattern that mimics the premediated movement characteristic of higher order intelligence. If this is the case, topographical features would confound the primatologists' attempts to infer intelligent mainfestation of cognitive mapping abilities. Such an explanation seems highly improbable for the Tanjung Puting orangutans of Indonesian Borneo, however, in light of the flat, featureless, uniform topography found at this site (Galdikas 1978a). No topographical features analogous to mountains or valleys exist at Tanjung Puting which would limit an orangutan's choice of movement in a non-random fashion. It appears that, irrespective of topography, orangutans at Tanjung Puting use arboreal pathways in novel combinations depending on the targeted food source (criterion 3 & 4) (Galdikas 1978b).

During their study of hamadryas baboons Sigg and Stolba (1981; Sigg 1986) attempted to find evidence for "cognitive mapping" other than the classic "shortcut". They hypothesized that the pattern of approach towards an unseen "goal" *should* be distinct from the usual manner of travel. Their results show that the baboons accelerated their travel at least 500 meters before making eye contact with their 'goal'. This suggests that the animals were cognitively representing their destination and could thereby anticipate their approach to unseen environmental features. Along these lines, orangutans at Tanjung Puting were often observed veer suddenly from their previous route and travel more rapidly than usual just prior to making visual contact with their "goal" (Galdikas 1978b). Upon reaching the "goal" this noticeably rapid pattern of travel would cease. Movement of this sort suggests that orangutans use cognitive maps to anticipate their approach to an unseen (criterion 1, 2 & 3) feature within their range.

Aside from remembering the location of food sources, primates may use cognitive maps to monitor the productivity of trees in their range. For example, individuals possessing cognitive maps of their environment could, upon encounter with a productive fruit tree, utilize their knowledge of tree locations to make a systematic check of all other trees of that species throughout their home range on the chance that such trees would be productive. In a single day, for example, orangutans frequently encounter more than one productive stem of the same rare, irregularly distributed species (Galdikas 1978b; Galdikas, personal communication). This suggests they use their memory of food sources locations (criterion 1) to make systematic checks of food sources (criterion 2) that have a high probabilty of being productive

(Galdikas 1978b), thereby maximizing their encounter rate with food sources. By monitoring food sources in this manner, orangutans demonstrate a rudimentary understanding of plant species' synchronicity in productivity.

Similarly, there is some evidence that chimpanzees use cognitive maps to make systematic checks of similar *types* of food sources. Recall Menzel's (1978) research, which provided evidence that chimpanzees use cognitive maps to employ a least distance policy between hidden food sources. Menzel's (1978) chimpanzees were very quick to learn any non-randomness in the experimental design. For example, if food was hidden too often in the same general class of places (eg: clump of grass), the control chimpanzees immediately spotted this regularity and raced to check similar classes of places in the enclosure (Menzel 1978). This behavioural pattern suggests that chimpanzees can recognize *types* of productive food sources (analogous to tree species) and then make systematic checks of similar types of food sources. Upon encounter with a productive fruit tree, wild chimpanzees may use their ability to recognize *types* of food sources, to make a systematic check throughout their range for other members of the productive tree's species.

While a productive food source may cue an orangutan to systematically monitor the productivity of other such food sources in the area, there is also evidence that orangutans monitor the phenological state of food sources that are *not* productive. At Tanjung Puting, orangutans were frequently observed to enter trees, visually inspect the leaves, bark or fruit, discard the food item and then exit the tree (Galdikas 1978b). Because the orangutans were not ingesting any food on such occasions it appeared as if they were monitoring the state of the trees' productivity (Galdikas 1978b). In other words, an orangutan might observe the phenological state of a tree, conclude its fruit was far from ripe or its leaves too mature and toxic and then not bother re-checking mature stems of that tree species until some weeks later when fruit matured or a new flush of young leaves bloomed (Galdikas 1978b). This behaviour involves remembering the location and phenological cycle of the food sources (criterion 1), assessing its present phenological state based on several conditions that change through time (eg: color, size, physical construction etc., of leaves, fruit, flowers etc.)(criterion 3 & 4), and predicting the future productivity potential of the food source based on its present state (criterion 2). The following example from Galdikas (1978b: 303) serves to illustrate these points:

> "...an adult female, who in previous days had visited and exploited several durian trees, suddenly veered off into an area that to that time was outside her known home range. She travelled more rapidly than usual and barely foraged. During this rapid travel she passed through two different wild durian trees, neither of which was fruiting.... After passing through [and inspecting] the second durian tree, the adult female returned to a part of her home range known to us. That she was inspecting the phenological state of the two durian trees is evidenced by the fact that, even though we eventually accumulated over one thousand hours of observation on this particular individual, we never again observed her passing within one hundred meters of either of those two specific durian trees."

The orangutans' ability to remember and monitor unproductive food sources without being cued by a productive source may be a key behaviour consequence of selection for their high intelligence, large brain/body ratio and ability to cognitively map their ranges.

Although the evidence for the orangutans' ability to monitor the phenological state of food sources even when such sources are *not* productive is anecdotal, controled research carried out on captive saddle-back tamarins (Saguinus fuscicollis) under laboratory conditions indicates this tiny Callithricidae utilizes cognitive maps to monitor food availablity at various productive and *unproductive* locations as well (Menzel & Juno 1985). Menzel and Juno (1985) studied foraging behaviour in captive saddle-back tamarins to test whether this tiny New World primate species was capable of remembering the visual appearance and relative position of different food related objects from one day to the next. Over alternating days of a thirty day period, the experimenters randomly placed two novel objects at random into the tamarins' cage until a total of thirty objects were present. On the first day novel objects were placed into the cage, they contained (or were in proximity with) bits of candy. On subsequent days of the experiment the objects were not in association with candy. Results indicate that the tamarins moved directly towards those locations that previously yielded food and that failing to find food at such locations, they moved to novel food locations (eg: objects placed in the cage that day). Hence, a single reinforced trial and relative novelty affected results in a positive manner (Menzel and Juno

1985). The tamarins' direct and rapid movement to food sources strongly suggests that they remember the spatial location of food sources using a cognitive map, thereby minimizing time and energy expended during travel. The pattern of repeated movement back to unproductive food sources suggests that saddle back tamarins monitor the productivity of such food sources in an attempt to maximize encounter rates with productive food sources. The exceptionally rapid learning abilities of the tamarins coupled with their highly perceptive nature allows them to cognitively map their environment and thereby remember and monitor the location of changing food sources (Menzel & Juno 1985).

On the basis of the studies described in this section, it appears evident that many non-human primates, from the tiny Callitrichids to the great apes, use cognitive maps to remember the location of irregularly distributed food sources throughout their ranges. Moreover, they use this information to maximize encounter rates with productive food sources while minimizing time and energy expenditure in travel by choosing the shortest travel routes to their 'goals'. There is limited evidence that non-human primates also use cognitive maps of their environment to monitor the phenological patterns of food sources in their ranges by making systematic checks of trees which have a high probability of being productive. Orangutans are no exception to these findings and exhibit higher order intelligence as defined by Menzel and Wyer (1981) throughout the search/forage phase of food acquisition. Since many primates demonstrate higher order intelligence while searching/foraging for spatio-temporally irregularly distributed food, the need to remember the location of such food sources and to monitor their phenological patterns may have been a major selective force favouring primate intelligence. Given the validity of this hypothesis, primate brain size should be positively correlated with increasingly irregular spatio-temporal distribution of food sources.

Milton (1981, 1988) tested this prediction by examining the feeding ecology and relative brain sizes (Clutton-Brock & Harvey 1980) of two Neo-tropical primates, the folivorous howler monkey (Aloutta palliata) and the frugivorous spider monkeys (Ateles geoffroyi). Because fruit is more irregular in its spatial and temporal distribution than leaves, the frugivorous spider monkeys are faced with a more difficult task in locating and monitoring their food sources (Milton

1981, 1988). Moreover, the patchy distribution of fruit within tropical forests intensifies competition between spider monkey individuals so, unlike howler monkeys, they are unable to forage in a large cohesive unit and rely on group knowledge regarding food sources. Spider monkeys respond to this pressure by foraging in dispersed subgroups or alone and as such, Milton (1981, 1988) argues forceably that selection pressure is far more intense on them as *individuals* to learn the locations and phenological patterns of fruit patches. Because the dietary realm of their environment is constantly changing the individual must continuously adapt to a variable environment (Parker 1978; Milton 1981,1988). Consequently, very little of their behaviour can be genetically programed as fixed action patterns. Using the index of progression (I.P.)(Appendix 1) and the encephalization quotient (E.Q.) (Appendix 1) as measurements of relative brain size, Milton's (1981,1988) research bears out the predictions of the spatio-temporal food distribution hypothesis: spider monkeys whose frugivorous diet is more irregular in its spatio-temporal distribution exhibit brain/body ratios two times larger than howler monkeys, whose folivorous diet is more evenly dispersed.

On a broader scale, Clutton-Brock and Harvey (1980) sought to test the predictions of the spatio-temporal food distribution hypothesis across all the taxonomic levels of the Primate Order. Analysizing the comparative brain size (CBS) (Appendix 1) of 118 species of primates, their results mesh well the predictions of the hypothesis and echo those of Milton (1981,1988): frugivores whose dietary staple is irregular in spatio-temporal distribution all had significantly greater CBS's than folivores, whose diet of leaves is much more evenly distributed in space and predictable over time. Because fruit is so patchy both in time and space, the authors concluded that frugivorous primates require extensive information storage and processing abilities in order to find and monitor fruit sources (Clutton-Brock and Harvey 1980).

The spatio-temporal food distribution hypothesis can account in large part for the differences in brain/body ratios witnessed between folivores and frugivores. An explanation as to why the frugivorous orangutan possess such extremely large brain/body ratio relative to most other frugivorous is not so readily apparent, however. Contrasting the phenological conditions faced by one orangutan population at Tanjung Puting, with the phenological conditions faced by a different frugivore at another site serves to shed light on the issue of why orangutans possess such large brain/body ratios. Spider monkeys studied at Barro Colorado Island in the Panama canal (Milton 1981, 1988) are appropriate primate subjects to compare with orangutans because both are frugivores, both are anthropoid primates and, most importantly, phenological data exist for both sites.

In reference to her study site on Barro Colorado Island, Milton (1981, 1988) has argued that some degree of *predictablity* is associated with the spatio-temporal distribution of tropical plant foods, so that once the location of a food source is found it remains constant in space. Furthermore, she states that a measure of predictablity is also associated with the phenological pattern of each tree *species* and that this element of predictablity could be exploited by primates to "counteract" (Milton 1981: 536) irregular productivity over time. In other words, after being cued by one productive food source, a primates could monitor the productivity of other trees of the same species on the chance that members of the species exhibit synchronicity in productivity. While I certainly agree with Milton's

(1981) hypothesis, the phenological conditions may be much more complicated for orangutans of Tanjung Puting.

At Tanjung Puting, as at Milton's field site on Barro Colorado Island, fruit is much more patchy in its spatio-temporal distribution than are leaves (Galdikas 1988) and thus, orangutans and spider monkeys are faced with a much more difficult task in locating and monitoring their dietary staple, relative to folivores. The flowering and fruiting patterns of individual species within the rainforest at Tanjung Puting do not follow predictable yearly cycles in the manner of temperate forest species. Each tree species seems to have its own flowering/fruiting cycle which is apparently triggered by very specific combinations of climatic conditions. Unlike Milton's (1981, 1988) field site, however, the situation for a frugivore at Tanjung Puting becomes increasingly complex, when one considers that tree species which do fruit in a given year vary greatly in the amount of fruit produced, even among trees of similar girth (Galdikas 1978b, 1988). This can result in some trees *within the same* species producing no fruit while others are laden with fruit. Another phenomenon affecting the availability of seasonal food resources is the "empty harvest" syndrome (Galdikas

1978b, 1988). This phenomenon occurs when the crop of a tree species appears abundant, but upon closer inspection the flesh of the fruit is either defective (unedible) or not developed at all. Clearly, synchronicity in productivity among fruit tree species is by no means a uniform phenomenon at Tanjung Puting and therefore, the element of phenological predictablity which occurs at Milton's (1981, 1988) field site is a much less reliable guideline for these orangutans.

In sum, the phenological data from Tanjung Puting reveals a much more complex distribution of food in time than occurs at Milton's (1981, 1988) field site in Panama. The *extremely* complex and irregular distribution of food sources in time (and secondarily in space) may have been a major selective mechanism favouring the evolution of intelligence and encephalization as exhibited by orangutans. These adaptations would allow for "cognitive mapping" of environmental features and the ability to monitor food sources regardless of their productivity state. Their possession of cognitive maps allows them to minimize travel costs while maximizing their encounter rate with productive food sources. "For such a heavyweight frugivore this is the difference between survival and starvartion" (MacKinnon 1978: 122).

## The Home Range Size Hypothesis

As a primate's home range expands, so too does the amount of dietary information pertaining to the spatio-temporal distribution of food that must be learned, stored and recalled (Clutton-Brock & Harvey 1980). Primates occupying extensive ranges need to store and process larger amounts of complex information concerning the spatio-temporal distribution of food, relative to those occupying small ranges, who are in daily contact with a large proportion of their food sources. If an enlarged home range necessitates expanded information processing capacities, an enlarged brain/body ratio should be positively correlated with home range size.

Examination of the large brained orangutans' extensive ranging patterns mesh well with these predictions. Although adult females at Tanjung Puting spend most of their lives in a home range encompassing five to six km$^2$, recent evidence from Gunung Leuser Reserve Sumatra indicates that some adult females do not occupy home ranges, but instead wander over large areas that remain to be mapped (Galdikas 1978; te Boekhorst et al. 1990) During the adolescent life stage, orangutans of both sexes wander throughout an area substantially larger than their mothers' home range (Galdikas 1978a). Moreover, the lifetime range of adult male orangutans in all areas studied thus far is so extensive that is has yet to be documented precisely (Galdikas 1979; Rodman & Mitani 1987). Galdikas (1979, 1988) notes that during the first four years of her ongoing study of wild orangutans all adult males ranged extensively within and outside of her 35 $km^2$ mile study area. This is suggestive of the possiblity that orangutan males are the most extensively ranging of all known non-human primates.

Given that the size of an individual's home range is "...presumably determined in part by how much spatial and object information can be assimilated" (Menzel 1978: 398) observations of orangutan ranging patterns suggest evidence for extensive information processing abilities. The need to store, process and recall botanical data relevant to such vast ranges suggest considerable selective pressure. As such, an increase in range size was probably an important selective mechanism favouring orangutan intelligence and encephalization.

## 3.4 Handling Food

## The Extractive Foraging Hypothesis

Once found, a food item may require handling, or processing, prior to ingestion in order to render it edible. Depending on the food type, processing can range from simply removing fruit from a branch to much more intricate manipulation of the food object. Food processing reaches its most complicated form with extractive foraging on embedded foods (Parker & Gibson 1977, 1979; Gibson 1986). Extractive foraging involves feeding on unseen (embedded) foods which must be removed from the matrix in which they are encased, or separated from inedible or toxic attachments prior to consumption (criterion 2). This requires, firstly, that the primate be able to visualize the presence of unseen food and conceptualize the states of "in" versus "out" (Parker & Gibson 1979). Following this, the primate must adapt its processing behaviour in a manner specific to each embedded food type encountered, so that the food's formidable and unique physical or chemical defense systems can be overcome. This requires manipulation of the embedded food item using several limbs (and sometimes the tail) simultaneously and in a co-ordinated fashion often according to a heirachically dependant sequence of behaviours. Furthermore, embedded foods may be manipulated relative to surfaces that act as anvils or objects that act as tools so that the primate must to able to conceptualize the relationships between objects, space, gravity and force. Clearly, the intelligence and behavioural flexibity conferred by encephalized brains would be advantageous during such food processing situations.

Gibson (1986) illustrates quite eloquently the profound food processing advatages conferred by higher order cognitive abilities in her contrast of mammalian versus lower order vertebrate feeding techniques. She states:

> "Frogs, for example, sit motionless in wait for flying insects. When one is spotted, the tongue lashes out, captures the insect and is with drawn into the mouth. Prey are recognized by conformance to a rather stereotyped visual image of size and movement (Lettvin et al. 1959) . No evidence exists for the ability to construct visual images of prey of highly varied shapes, sizes, and habits. If these animals can anticipate or follow prey movements, this is not evident from their feeding behaviour. Escaping insects are not pursued.
>
> From a manipulative standpint, prey are captured through a single motor act involving one

> anatomical organ. Food is swallowed without prior breakdown and without chewing. This feeding technique is clearly efficient. It is also limiting. Frogs can feed only on insects that will identify themselves by movement and can be swallowed whole....by contrast, mammalian feeding techniques commonly manifest simultaneously and sequentially coordinated movements of the lips, tongue, teeth and hands. As a consequence, mammals possess major feeding advantages over most reptiles. Specifically, they break their food into component parts prior to ingestion and, hence, can feed on foods too large to be swallowed whole or containing indigestible elements such as shells, bones, or attached sticks. When combined with masticatory skills and salivation, this ability to subdivide food prior to ingestion also results in a relatively speedier digestive system which can, in turn, fuel a higher metabolic rate and a larger brain size." (p. 95)

Parker and Gibson (1977, 1979) have suggested that radiation into a plant food niche wherein complex processing of food prior to ingestion was necessary, would have induced encephalization, in response to selective pressure for an increased capacity for problem solving. In other words, extractive foraging on embedded foods may have been an important selective mechanism favouring the rise of primate intelligence. What evidence exists to demonstrate that primate intelligence in general, and orangutan intelligence in particular, evolved in response to a need to solve the complex problems posed by the processing of embedded food?

Examples of extractive foraging among primates are numerous and cut across taxanomic levels (Gibson 1986; King 1986). For example, mountain gorillas (Gorilla gorilla), baboons (Papio spp.), Japanese macaques (Macaca fuscata) and crab eating macaques (M. fascicularis) dig up the unseen, underground storage organs of plants (DeVore & Hall 1965; A. Goodall 1979; Wheatley 1982; Iguchi & Izawa 1990) and the aye-aye (Daubentonia madagascariensis) bores into seeds, coconuts, bamboo pith and litchie nuts to extract the edible contents with the aid of its specialized incisors and skeletal-thin third finger (Iwano & Iwakawa 1988). Similar anecdotal examples can be found throughout the primatological literature, but field studies which focus on extractive foraging are lacking (see Gibson 1986 & King 1986 for reviews).

The most extensive literature on extractive foraging comes from studies on capuchin monkeys (Cebus spp.) (Izawa & Mizuno 1977; Izawa 1979; Terbourgh 1983; Chevalier-Skolnikoff 1989, 1990; Visalberghi 1987, 1990; Anderson 1990) and chimpanzees (Pan spp.)(Struhsaker & Hunkerler 1971; Sugiyama & Koman 1979; Sugiyama 1981; Kortlandt &

Holzhaus 1987; Boesch & Boesch 1981, 1983, 1984b; Sumita 1985). Most of these studies focus on nut cracking behaviour with and without the aid of tools. The study by Izawa and Mizuno (1977) on palm-fruit cracking by wild black-capped capuchins (Cebus apella) is representative of the kind of extractive foraging *without* tools that is frequently seen among wild capuchins and chimpanzees. During this study capuchins used two differing processing techniques depending on the ripeness of the palm fruit (Astrocaryum chambira). The first technique involved puncturing the palm-fruit with a canine, sucking out the juice, and then banging the puctured nut against a bamboo anvil three times to force an edible, yogurt-like albumen out onto the anvil. The second technique was used when the nut's albumen solidified. It involved smashing the nut against the joint of a bamboo stem until it cracked and then peeling the husk and rind back to expose the fruit's juice and albumen. This study alone indicates that during food processing bouts Cebus are capable of coordinating several body parts simultaneously (they use two hands to grasp fruit, their tail to balance themselves and their torsos as levers to generate force); their processing behaviour involves a complex sequence of hierachically dependent behaviours; they can work towards obtaining a goal in the absence of the motivating stimulus (the unseen palm juice and albumen); they can conceptualize the object-object (palm-fruit/bamboo anvil) and object-force (smashing fruits to crack the husk) relationships and they use different processing techniques to attain the same goal. In short, Cebus demonstrate all four of the criterion outlined by Menzel and Wyers (1981) as indicative of higher order intelligence as manifested during food acquisition behaviour.

Similarly, the nut cracking by chimpanzees of Taï National Park, Ivory Coast is representative of the kind of extractive foraging with tools exhibited among chimpanzees and captive capuchins (Boesch & Boesch 1981, 1984b; Visalberghi 1987). Depending on the species of nut being cracked these chimpanzees use different processing techniques. Panda nuts (Panda oleosa) are opened exclusively on the ground with stone "hammers" due to the extreme hardness of their shells. Commonly, four to six panda nuts are collected at once and carried to an exposed tree root or stone which serve as an anvil. At the anvil the nuts are carefully positioned and opened with precise blows which vary in intensity. The first blows must be powerful in order to crack the panda nut shells and the following ones must be careful, gentle blows to free the almonds. Continued powerful blows to the panda nut will smash the meat along with the shell making the meat, for the most part, inedible. Often the nut needs to be repositioned at least three times during the cracking process, so that the blows can be delivered precisely.

By contrast, coula nuts (Coula edulis) are collected in batches of 12-15 and are either cracked on the ground where they fall or in the trees were they are collected. Coula cracking on the ground is simlar to panda cracking except that wooden clubs are often used to crack the softer shelled coula nuts, suggesting that the Taï chimpanzees can cognitively grasp the physical properties between wood and stone as material for tools. Cracking coula in the trees is considerably more difficult than either of the previous techniques. To crack coula in the trees a chimpanzee must anticipate its actions and carry a hammer into the trees. Once there, it must then engage in a complex balancing act for, when cracking one nut, the others must be held in the mouth or foot. To eat the Coula nut once it is cracked, the mouth must be freed by transferring the uncracked nuts to one hand while balancing the hammer on a branch and using the other hand to eat with. Then, everything must be switched back to begin cracking again. To prevent the Coula from falling while cracking it in the trees the chimpanzee holds it on the branch with the thumb and forefinger of one hand between blows with the hammer. While off collecting more nuts in the trees, the hammer is left to balance on the horizontal branch. It soon becomes clear that these chimpanzees are capable of coordinating several body parts simultaneously; their processing behaviour involves a complex sequence of behaviours; they can work towards obtaining a goal in the absence of the motivating stimulus (the unseen nuts); they can conceptualize the object-object (nut/anvil) and object-force relationships as witness by their selection of "hammers" with differing physical properties depending on the species of nut being cracked and they use different processing techniques to attain the same goal. In short, chimpanzees, like Cebus, demonstrate all four of the criteria outlined by Menzel and Wyers (1981) as indicative of higher order intelligence as mainifested during food acquisition behaviour.

Paradoxically, while tool use by captive and ex-captive orangutans often surpasses that of the other pongids, both in quantity and variety, only the common chimpanzee (Pan troglodytes) has been observed to use tools to get food in the wild (Wright 1972; Beck 1980; Galdikas 1982; Lethmate 1982; McGrew 1989). Nonetheless, orangutans frequently process/handle food items without tools prior to ingestion (MacKinnon 1974; Galdikas 1978b, 1988; Rijksen 1978; Chevalier-Skolnikoff et al. 1982; Wheatley 1987). At Tanjung Puting numerous food types and species, including embedded foods, were processed. Nuts and fruit encased in shell or husk were cracked open, inedible and toxic attachments were detached from the edible portion of food items, the underground storage organs of plants were dug up, insects such as wood boring termites were extracted as was honey contained in bees' nest.

When handling embedded foods orangutan processing behaviour was characterized by several complex, coordinated and simultaneous object manipulatory movements of several body parts (criterion 4) (Chevalier-Skolnikoff et al. 1982). Some foods such as bakunyit fruit were processed according to oraganized behavioural sequences which required successful completion of each sequence in the correct order to successfully render each item edible. Successful execution of an organized sequence of behaviour to transform a food item to a processed state is based on mental representation of conditions not present and the ability to plan ahead (criterion 1 & 2) (Chevalier-Skolnikoff et al. 1982). Attached substrates, such as level branches, were sometimes used as anvils while processing embedded foods. Food processing with the use of an attached substrate involved rapid and simultaneous coordination of substrate-food-body-force relationships (criterion 4) (Chevalier-Skolnikoff et al. 1982). The processing technique orangutans choose varies according to the food item being handled, and some food items such as the burr covered fruit *Chaeotocarpus castanocarpus* or bantian nuts (*Mezzetia leptopoda*) were processed using a variety of techniques (criterion 3). For example, *C. castanocarpus* was processed by rubbing handfuls of the fruit around a branch substrate, until all the burrs were removed; alternatively these fruits were processed by rubbing them on the back of the free hand (Galdikas 1978b, 1982). The extremely hard shelled bantian nuts were processed using three techniques: 1) removal of the shell with the teeth only, 2) removal of the shell with the teeth as the mouth is covered with the back of the hand, the wrist or both hands or alternatively 3) removal of the shell as in (2) except in order to intensify the forced directed to crack the shell, the orangutan, while hugging a tree, pressed its cheeks against the tree trunk.

Prior to food processing, orangutans commonly gathered up a number of embedded food items and transported them to a specific place. Transportation of food in this manner suggest the orangutans were capable of conceptualizing their impending food processing behaviour and account for this by carrying food with them to the desired processing location (criterion 1 & 2) (Chevalier-Skolnikoff et al. 1982). The transport of objects for the purposes of food processing has been similarly demonstrated among chimpanzees (Boesch & Boesch 1984b). Possibly orangutans were motivated to transport embedded foods to an appropriate substrate (anvil) so they could be processed more efficiently. Alternatively, they may simply have sought a more comfortable arboreal substrate on which to sit and feed.

The result of the studies described in this section indicate that higher order cognitive behaviour is involved with the complex processing of embedded foods and may have been an important mechanism selecting for intelligence among primates. Given the validity of this extractive foraging hypothesis, primates brain size should be positively correlated with increasingly dependence on embedded food sources. Gibson (1986) examined this prediction by comparing encephalization indices of progression (I.P.)(Appendix 1) of 25 primate genera with foraging behaviour. Results demonstrate that among prosimans, New World Monkeys, Old World Monkeys, and Hominiodea, the largest relative brain sizes occur in omnivorous extractive foragers. Gibson (1986) concludes that primate extractive foragers require expanded information processing abilities to recognition embedded foods and to perform the complex sensorimotor coordinations necessary to process such food.

Further quantitative evidence in support of the extractive foraging hypothesis is provided by application of Piagetian development theory to the sensorimotor behaviours manifested during the processing of embedded foods. Piagetian theory is a systematic framework for categorizing behaviours according to their cognitive complexity that is based on hierachical stages of sensorimotor development. Use of this framework has revealed that primate extractive foragers manifest the most advanced levels (5 and 6) of Piaget's sensorimotor intelligence series (Parker & Gibson 1977, 1979; Gibson 1986;

Chevalier-Skolnikoff et al. 1982; Chevalier-Skolnikoff 1989, 1990). Piagetian sensorimotor intelligence levels 5 and 6 involve the ability to conceptualize object-individual-space-gravity-force relations without a one-to-one (stereotyped) relationship between the stimulus and reponse. Moreover, the ability to sequence behaviours based on mental representation of objects or conditions not present is equivalent to stage 6 sensorimotor intelligence.

The problems encountered during extractive foraging on embedded foods and during food processing in general, may have been important selective mechanisms favouring primate intelligence. This stance appears particularly plausible given the possitive correlation between brain size and omnivorous extractive foraging (Gibson 1986). Food processing may have played a particuarily important role in the evolution of orangutan intelligence, however, because of this pongid's heavy dependence on embedded foods. Intelligent individuals in the ancestral Tanjung Puting orangutan population who could process food, particularly embedded food, and thereby render it edible, gained access to a wide range of dietary items whose physical construction and chemical defenses effectively prohibited utilization by many other species (Chevalier-Skolnikoff et al. 1982). It follows that natural selection would have favoured such individuals, their genes for large brain/body ratios and, by extension, their higher order intelligence.

### 3.5 Summary

To summarize, primatologists have suggested that each of the food acquisition sequences: food recognition, search/foraging and handling/processing may become increasingly complex, so as to act as selective mechanisms favouring the rise of intelligence. Data from several studies demonstrate the positive correlation between intelligence and dietary adaptations including: opportunism, irregular spatio-temporal food distribution, home range size and extractive foraging on embedded food. The positive correlation between intelligence, brain size, and these dietary adaptations lends support to the conclusion that feeding ecology may have played a major role in the evolution of primate intelligence and encephalization.

Orangutans exhibit higher order intelligence (as defined by Menzel and Wyer [1981]) during all phases of the food acquisition process. Moreover, use of Piagetian theory indicates orangutans exhibit the highest levels (stage 5 and 6) of sensori-motor development while processing/handling food. Expression of higher order intelligence by orangutans is necessary for survival given the complex nature of their feeding niche. Thus, orangutan intelligence may be the product of a long phylogenetic process whereby natural selection favoured large brained, intelligent individuals who demonstrated a competitive advantage when faced with food acquisition problems. The genes of such individuals would have been preserved and perpetuated over time fostering the evolution of encephalized brains and higher order intelligence. Since all primates encounter difficult problem solving tasks during food acquisition the question of why orangutans have such large brain/body ratios relative to other primates remains only partially answered.

For several reasons which relate to their uncommonly difficult food acquisition problems, the selection pressure favouring increased intelligence among orangutans may have been more intense throughout their phylogenetic history relative to most other primates. Firstly, the dietary breath exhibited by orangutans is enormous. Consequently, relative to most other primates, orangutans may be under more intense selection pressure to recognize many different kinds of food. Secondly, the spatio-temporal distribution of orangutan fruit sources may be much more irregular than experienced by primates at other field sites and may greatly confound the search/forage phase of their food acquisition behaviour. Thirdly, although orangutans have been studied for decades, the home ranges of adults at some sites have yet to be mapped. This suggests that a male orangutan may range a greater distance over its lifetime than any other primate species. This extensive ranging behaviour may complicate the seach/forage phase of the food acquisition process because so much botanical and spatial information must be processed. Finally, the orangutans particularly heavy reliance on a variety of embedded food resources makes for numerous problems that must be solved during the processing/handling of food items prior to ingestion. In conclusion, a close examination of the orangutan's feeding ecology reveals that the foraging problems argued to be a selective mechanisms favouring intelligence among primates are particularly intense in the case of the orangutan. When viewing primate foraging problems on a continuum from simple to difficult, the orangutan's foraging problems can be seen as representing the extremely difficult end the continuum. Adaptation to the feeding niche occupied by orangutans would have required a concommitant increase in intelligence. As such, feeding ecology must have played an important role as a selective mechanism favouring the rise of orangutan intelligence.

# Chapter 4: Proposed Study and Conclusions

## 4.1 Introduction

The long term, continuous field study by Biruté Galdikas at Tanjung Puting National Park, Indonesian Borneo, has provided a wealth of information pertaining to the orangutans overall feeding ecology. Galdikas (1988) has intensively documented the extraordinary dietary breadth of wild orangutans. Consequently, if the need to recognize many different food items was an important selective mechanism favour orangutan intelligence, than the recognition phase of food aquisition must have played a substantial role in the evolution of orangutan intelligence. Galdikas (1978b; 1988) has also provided preliminary evidence that orangutans use cognitive maps while searching/foraging for food to make shortcuts between 'goals' and to make systematic checks of food sources. Moreover, Galdikas (1978b; Chevalier-Scholnikoff et al. 1982) has demonstrated that orangutans utilize and process embedded food.

Preliminary documentation of cognitive mapping and processing of embedded foods by Galdikas (1978b) provides a foundation for more intensive studies concerning how the food searching/foraging and handling/processing phases of food acquisition influenced the evolution of orangutan intelligence and encephalization. Given the difficulties of studying orangutans, each of these food acquisition phases should be considered for study separately. In the following section, I outline a proposal for studying orangutan food handling/processing behaviour. Such a study has implications not only for orangutan adaptation and intelligence, but also for the paleoanthopologist who seeks to reconstruct the behaviour of the earliest hominids.

## 4.2 Proposed Study

A review of the literature concerning extractive foraging and food processing among orangutans suggest several lines of study that deserve attention. The goals of the study proposed herein can be summarized as such:

1) To describe: 1) the amount of time wild orangutans allocate out of their daily budget to processing food, 2) the species they exploit in this manner, and 3 ) the behavioural sequences involved in processing each species.

2) To discern which, if any of several variables, influence manifestation and efficiency of this behaviour. Variables to be examined include: age, sex, size, number of dependents under care, availability of resources and group size.

3) To compare the results of this study with studies of chimpanzee food processing behaviour, particularly those carried out by Boesch and Boesch (1981, 1984b) at Taï National Park, Ivory Coast.

4) To discuss the implications of this study's results for hominid evolution.

### 4.3 Study Site & Methodology

I propose to study food processing/handling behaviour of wild orangutans at Tanjung Puting National Park, Indonesian Borneo, an area of lowland tropical rainforest. Tanjung Puting is an excellent site for studying orangutans because: 1) many of the orangutans in the area have been habitated, 2) research facilities exist at Dr. Biruté Galdikas' Camp Leakey, and 3) the tree capopy is lower here than in other areas which orangutans occupy (Galdikas, personal communication). I will conduct my study over a period of two years from the fall of 1991 to the fall of

1993. This period of time is warranted by the well documented difficulty of collecting data on orangutans. Methodology will follow that outlined by Galdikas (1978b) in order to facilitate comparisons of my data with hers. Whenever possible, focal animal observations (Altmann 1974) will consist of whole day follows, from the time the animal leaves its nest in the morning until the time it builds another nest at night and ceases movement. Focal animal data is gathered on one individuals at a time for a set period, following which the observer changes the focus of their data collection to another "focal" animal. During the time in which the focal animal is observed, all the behavioural patterns which it exhibits (eg: sit, locomote, groom) are recorded. Following Galdikas' (1978b) guidelines for subject selection adult males will be favoured as target individuals over adult females and adult females will be favoured over immatures when groups are encountered. However, when adult female/sub-adult male groupings are encountered target observations will be alternated between the two age/sex classes over successive days of observations. This discriminatory selection process is related to the difficulty experienced in finding adult and sub-adult males owing to their complex ranging behaviour (Galdikas 1978a). Focal animal data will be gathered on individuals of all age/sex classes and the component of the data concerning food processing will be analyzed in order to ascertain which, if any, of the variables outlined above influence orangutan food processing.

### 4.4 Age as a Variable Influencing Food Processing

In comparison to other mammals the great apes have extremely prolonged postnatal maturation periods, during which time they are fed, protected and socialized (Goodall 1986; Fossey 1979; Horr 1977). Among orangutans postnatal dependency lasts about eight years (Galdikas & Wood 1990). During this time the pongid infant learns foraging techniques, such as food processing, from his/her mother. An age related difference in efficiency and time spent food processing has been reported for the chimpanzees at Gombe, with young dependents exhibiting inefficient and "messy" processing techniques (Silk 1978). Rijksen (1978) mentions that younger orangutans appeared to find the spines of the durian fruit painful to touch and are unable to detach and open this fruit efficiently. Given that infant and juvenile individuals lack the strength exhibited by older age classes and that they are still learning and perfecting those skills necessary to process food, such inefficient behaviour is to be expected. In light of this information, it is expected that infant and juvenile orangutans will spend less time processing food and process fewer types of food relative to adolescent, subadult and adult individuals. When younger age classes do participate in processing behavior, it is expected that they will not be as efficient at the behavior as their elders. Efficiency will be measured by number of food items processed per unit of time. Units of time will be in minutes, in order to facilitate data comparison with the work by Boesch and Boesch (1981, 1984b) on chimpanzee food processing.

## 4.5 Sex, Size and Number of Dependents as a Variables Influencing Food Processing

Sex differences in time spent processing food and efficiency at the activity have been reported for two extractive foragers: the common chimpanzee and the Cebus monkey (Goodall 1986; Boesch and Boesch 1981, 1984b; McGrew 1979; Visalberghi 1987). More data needs to be collected before sex differences in food processing by Cebus are fully understood, but the general behavioral pattern which emerges from the chimpanzee studies is one in which females predominate over males in both time spent and efficiency at food processing. Explanations for the existence of sex differences during foraging fall under two main categories: 1) sexual dimorphism in size and strength (Boesch & Boesch 1981, 1984b) and 2) nutritional constraints on the female (McGrew 1979; Wrangham & Smuts 1981).

With few exceptions (all among monogamous primates), male primates tend to be larger than females (Hrdy 1982). Such sexual dimorphism enforces differences in the life histories of male and female primates (Selander 1972; Galdikas & Teleki 1981; Wrangham & Smuts 1981; Hrdy 1982). It has been suggested, for example, that the larger size and greater strength of male chimpanzee renders them "phylogenetically retarded" in their ability to control body posture, movement and strength with the result that they are ineffective food processers (Boesch & Boesch 1984b: 437). This phylogenetic limitation in body coordination renders male chimpanzees less effiecient at exploitation of embedded foods. Consequently, an analysis of their diets demonstrates that, relative to females, male chimpanzees do not allocate as much time to foraging on embedded foods over the lifetime (Boesch & Boesch 1981, 1984b). Female chimpanzees, by contrast, are better able to control their strength due to their smaller size. Greater control over body coordination renders them more capable of the finely differentiated movement which prove necessary given the sometimes exacting nature of food processing (Boesch & Boesch 1984b: 437). Thus, among chimpanzees, it appears that control of body strength, rather than overall body strength is the key factor influencing processing efficiency. As such, female chimpanzees excell over males at this phase of the food acquisition process. A cross-species comparison reveals that human females are also superior to males in certain behaviours requiring manual dexterity (Garai & Scheifeld 1968; Ember 1981).

In contrast, among orangutans, it seems that the males' greater size and strength allows them, rather than inhibits them, to process very hard, embedded foods such as bantian nuts (Galdikas 1978b; Wheatley 1987). Galdikas (1978b: 217) implies that male orangutans are more efficient when processing bantian nuts (M. leptopoda) due to their greater strength, but she does not detail this sex difference.

Furthermore, adult male orangutans spend considerably more time than the adult females foraging on terrestrial termites, a resource thought to be nutritionally rich relative to leaves, bark or even fruit (Galdikas & Teleki 1981). It is possible that the males greater size and strength permits them to rip open termite infested logs that females are less able to access and also affords for greater protection from terrestrial predators. Predator avoidance may restrict the smaller bodied adult females to the canopy where they forage on plant matter. Thus, at least during bantian nut processing and possibly termite foraging, control of strength seems not to be at issue for the orangutan; instead, how much strength can be applied to open the embedded resource seems to be the key to successfully processing.

The effects of differential size and strength on sex differences during food processing remains to be detailed among orangutans. If such a difference exists, a review of the literature is not a good indicator of which sex will predominate. It must be ascertained whether 1) control of strength allowing for finely differentiated movement, as opposed to 2) overall amount of strength (allowing for increased intensity of force delivered to the embedded food object) is important during orangutan food processing. It is conceivable that both play a role, depending on the resource being processed. If this is the case, sex differences will not be consistent across all embedded resources foraged on, but instead will vary given the type of food item processed.

The second common explanation for the existence of sex differences during foraging involves nutritional constraints on the females resulting from pregnancy, childbearing, lactation, child transport and among some primate species, food sharing with offspring (McGrew 1979; Wrangham & Smuts 1981). Due to these constraints females are thought to be more dependent on high quality resources that have a predictable energy return and present little danger to immature dependents during exploitation. Lactating and pregnant human females require a supplement of 1000 kcal per day (Gunther 1971 quoted by McGrew 1979) and there is little doubt that orangutan females are faced with similar requirements. Moreover, orangutans mothers carry their infants for about four years and are one of the few non-human primates in which active sharing of solid and premasticated food takes place from the mother to her infant and juvenile offspring

(Horr 1977; Chevalier- Skolnikoff et al. 1982). The importance of some form of high quality food in their diet takes on even more importance when one considers that a large component of the female orangutans diet consists of bark and leaves and that they may at any time be "juggling" toxin loads to avoid poisoning (Galdikas 1978a, 1988). In an evolutionary sense, the quality of the mother's diet during the prenatal period cannot be stressed enough, as its quality can have longterm effects on the life-history and reproductive success of her offspring (Widdowson & McCance 1975). It is significant that an orangutan mother and her juvenile and infant offspring died following an anomalous period of intensive bark and leaf exploitation due to a shortage in seasonal resources (Galdikas1978b: 229). As discussed above, the small size of the females and the presence of dependents prevents exploitation of terrestrial resources such as nutritionally rich termites. Embedded food items obtained during arboreal extractive foraging may provide a high quality food resource with a predicable energy return (Gibson 1986) and no danger to dependents during exploitation. As such, exploitation of embedded food could provide the means for females to meet the higher energy requirements imposed by nutritional constraints.

Since parous females may be under selection pressure to obtain high quality food items, the number of dependents under care will be analyzed as a variable influencing 1) the amount of processing engaged in by a female as well as 2) the individual's food processing efficiency. Given the validity of the nutritional constraint hypothesis, females who are pregnant or lactating should process food more than mothers who simply share with dependents. By the same reasoning, sharing mothers should process food more than nulliparous females or those with independent offspring. Absence of this pattern would suggest that females are not as dependent on embedded foods as assumed, but instead are meeting their nutritional needs in other ways.

Sex differences in foraging are particularly compelling for the anthropologist given recent interest in the "Woman the Gatherer" model for hominid evolution which casts gathering by females as the prime mover during hominid evolution (Tanner 1981; Tanner & Zihlman 1976; Zihlman 1978). The authors argue that the combination of moving into a savanna

environment and sharing with one's offspring resulted in females being selected for as more efficient gatherers and food processors than males. The chimpanzee literature indicates that female chimpanzee are superior food processors relative to males and chimpanzees mothers frequently share difficult to process foods (Silk 1978) adding support to this reconstruction of early hominid lifeways. Data gathered pertaining to sex differences in food processing among orangutans will have important implication for fleshing out the "Woman the Gatherer" scenario.

## 4.6 Availability of Food Resources as a Variable Influencing Food Processing

Although the number of food types contained in the diet of the wild orangutan is extremely large for a primate, observations clearly indicate that certain food types are preferred to others (Galdikas 1978b, 1988). Bark and leaf eating plummet during months when fruit species become abundant suggesting that fruit is the preferred food category. However, even among various edible fruit species, some types are favoured over others with preferred species being returned to again and again while in fruit and less preferred species being largely ignored (Galdikas 1988). Thus, food items which are preferred by the orangutans constitute a greater percentage of the total monthly diet when in season, whencompared to those food resources less favoured. Given the amount of effort required to process embedded foods, one could argue they would be a less desirable food source and as such would be exploited only when a lack of preferred seasonal food sources are available. Galdikas (1978b) implies that this is the case for at least one embedded food resources, M. leptopoda. Conversely, given the high nutritional value of embedded food one could also argue that some would be preferred food items and, as such, would be exploited whenever in season to the exclusion of less preferred items. With these possiblities in mind, resource availablity will be analyzed as a variable influencing the amount of food processing exhibited each month. This will clarify which embedded resources are preferred by the orangutan and will illuminate whether the embedded food niche is the primary focus of the wild orangutans foraging adaptation, or whether or not it represents a secondary foraging adaptation which the orangutan relies on during periods of food scarcity.

## 4.7 Group Size as a Variable Influencing Food Processing

Group living primates have a variety of reasons for which they may choose to associate with other members of their species. These can include the following:

1) Individuals depend on their presences in the group to maintain their status,
2) Co-operative territorial defense,
3) Co-operative hunting or flushing of prey,
4) Predator protection,
5) Reproductive advantages gained by association with estrous females,
6) Social needs associated with psychological health and well-being.

Given that male dominance heirarchy among orangutans is maintained at great distance by long calling, that orangutans spent the bulk of their time alone as adults, that they do not hunt, and that their large bodies and arboreal nature affords them predator protection; (Galdikas 1978a, 1978b, 1983) it may seem odd that one would even address the affects of group size and sociality on their foraging behaviour. However, even orangutans have a capacity for sociality that is more often than not ignored by researchers (exceptions include: Edward 1982; Galdikas 1985). Under the appropriate reproductive and ecological conditions all orangutans interact socially and will travel together for several days.

The cost primates incur for the benefits of group living is frequently manifested as a reduction in time spent foraging. For example, in a group of nut cracking chimpanzees, the more socially active males suffered a reduction in processing efficiency due to a greater amount of time devoted to social vigilance (Boesch & Boesch 1984b). This lack of efficiency resulted in a lower return of energy per unit of processing time relative to females. Consequently, males spent less time processing nuts and instead concentrated their energy on more profitable resources which allowed for social interaction. Uehara (1986) believes the tendancy of male chimpanzees to move about in groups may be the reason why they predominate over females in the capture and consumption of prey. Similarly, Visalberghi (1987) suggests group size may effect Cebus processing performance and influence sex differences in the behavior. Along these lines, it is assumed that during periods of social interaction, orangutans will allocate time to monitoring the behaviour of their companions. Hence, group size and social vigilance are expected to be negatively correlated with time spent food processing and food processing efficiency.

## 4.8 Summary & Conclusion

The behaviours traditionally held up as unique unto hominids and as the "prime movers" of hominid evolution (Table 1), in fact, constitue part of a shared pongid/hominid behavioural repertoire. The capacity for such behaviours evolved long before the origin of the hominids and their role as "prime movers" of hominid evolution should thus be re-evaluated. Because the pongids exhibit behaviours thought to be uniquely hominid, answers as to the origin and evolution of such behaviours should be sought through an examination of hominid *and* pongid adaptations. That wild pongids do not exhibit the particular behaviour in question on a habitual basis strongly suggests that these behaviours were not the products of directional selection. In order to fully understand the origin and evolution of these behaviours, one must examine the basal adaptation that allowed for their existence and which *was* directly selected for. It is argued herein, that this basal adaptation was increased intelligence (information processing ability [Jerison 1983, 1985]) as reflected by an enlarged brain/body ratio.

Primatologists have long questioned the relative importance of ecological problems (Parker & Gibson 1977, 1979; Wrangham 1977; Galdikas 1978; Parker 1978; Clutton-Brock & Harvey 1980; Sigg 1980; Milton 1981; Sigg & Stolba 1981; Terborgh 1983; Gibson 1985; Menzel & Juno) versus social problems (Jolly 1966; Burton 1984; Cheney et al. 1986; Parker 1987; Byrne & Whiten 1988a; Cheney & Seyfarth 1990) as selective mechanisms which may have favoured the evolution of primate intelligence. Unlike all other anthropoid primates, wild orangutans are characterized by a unique semi-solitary adaptation with correspondingly infrequent social interaction. Literature pertaining to orangutan social intelligence has thus, been lacking (exceptions include Galdikas 1978b; Galdikas & Vasey in press, 1991). Given the lack of published data on orangutan social intelligence, the focus of this thesis has been the role of feeding ecology, rather than social problems, in the rise of orangutan intelligence.

With the exception of the tarsiers (Bearder 1987), all the primates feed primarily at the first tropic level, so that their food acquisition does not involve subduing fleeing prey. Instead, as a prelude to ingestion, primate food acquisition involves three phases: 1) food recognition, 2) search/foraging, and 3) handling/processing. In the past, primatologists have pondered how each of these three food acquistion phases would become increasingly complex so as to necessitate, and select for, higher order intelligence. Orangutans exhibit higher order intelligence during all phases of the food acquisiton process. A broad, opportunistic diet, extremely irregular distributibution of food in time and space, extensive ranging patterns and heavy reliance on embedded foods that require complex processing, all function together to necessitate, and to favour, the orangutan's higher order intelligence within the ecological domain.

In the past primatologists have sought to disentangle the relative importance of ecological versus social variables as selective mechanisms favoring the evolution of primate intelligence (Cheney & Seyfarth 1988, 1990). It is unlikely, however, that a simple and dicotomous answer exists to be found. Primate intelligence is the product of a complex and inseparable tangle of both ecological and social mechanisms. Even among the relatively asocial orangutans social problems played an important role in shaping intelligence (Galdikas 1978; Galdikas & Vasey, in press 1991). Moreover, feeding ecology and social problems are not the sole mechanisms favouring orangutan intelligence. For example, Chevalier-Scholnikoff et al. (1982) argued that the contingences of orangutan locomotory adaptation necessitate, and would have selected for, higher order intelligence.

Food processing by orangutans, while briefly mentioned in the literature, has yet to be studied intensively in the wild. Researchers indicate, however, that food processing by wild orangutans occurs frequently and may have been an important selective mechanism favouring the evolution of orangutan intelligence and encephalization. Thus, a study such as the one proposed herein is warranted.

In conclusion, I have attempted to gain a deeper understanding into the hominid condition by stepping back and viewing hominids as part of a long evolutionary history. Because "the roots of uniquely human adaptations lie deep in the ecological adaptations of [our] arboreal frugivorous pongid ancestors, long before the gradual dessication of the

African or Asian tropical rainforests forced these ancestors into increasingly terrestrial modes of behaviour on the savannahs" (Galdikas 1981), a true understanding of the origin and evolution of the behaviours deemed hallmarks of the hominid condition requires an examination both the hominids *and* the pongids. In the end, I am left with the overwhelming impression that our hominid nature is but a profound expression of our pongid heritage.

## Appendix 1:

## Allometry: Measuring the Brain/Body Relationship

In order to make cross-species comparisons in brain size some method of controlling for the confounding effect of body size is necessary. Though the relationship between brain and body size is probably better documented than any other allometric relationship, there is little concensus of opinion on the most useful method for calculating brain size relative to body size. Not surprisingly, absolute brain size is largest in the largest species such as whales and elephants, but when measured as a percentage of body weight brain size appears largest in the *smallest* mammals (Mace et al. 1980). Clearly, the relationship between brain size and body size is not a linear one. That is, brain size and body size do not scale in a 1:1 fashion. Instead, brain weight scales to approximately 2/3 power of the body weight (Jerison 1973). This non-linear relationship between brain size and body weight is commonly described in the form of the following equation (Mace et al. 1980):

$$y = a \cdot x^b$$

or

$$\log (y) = \log (a) + (\log [x] \cdot b)$$

where $y$ = brain weight
$x$ = body weight
$b$ = slope of the best fit line
$a$ = elevation of best fit line.

Based on this equation, various authors have attempted to measure relative brain size among species. Bauchot, Stephan and their colleages attempted to quantify relative brain size using their index of progression (I.P.)(Stephan & Andy 1969; Bauchot & Stephan 1964; Pirlot & Stephan 1970). The I.P. was calculated as the ratio between species brain size and the predicted brain size value for a basal insectivore (eg: shews, tenrecs, hedgehogs) of the same body size. This approach has been critisized based on the assumption that the brain/body relationships in contemproary insectivores reflect those of primitive mammals and can be extrapolated to apply to species outside their size range (Clutton-Brock & Harvey 1980).

Avoiding the problems inherent with using relative brain size measurement for basal insectivores as a basis for other mammals, Jerison (1973) attempted to quantify relative brain size using his encephalization quotients (E.Q.). The E.Q. equals observed brain weight for each species divided by the predicted brain weight. Predicted brain weight is calculated based on the following equation:

$$\text{Predicted Brain Weight} = 0.115\ (\text{Body weight})^{0.664}$$

or alternatively,

$$\log(\text{predicted brain weight}) = \log(0.12) = 0.67 \cdot \log(\text{body weight})$$

Essentially the E.Q. of a species represents that species' point devation from the best fit line created when plotting brains weight against body weight for all mammals. Jerison (1973, 1983, 1985) suggests that the E.Q. of a species represents the amount of additional brain matter an animal has over its basic somatic needs. As with Bauchot & Stephan index of progression, Jerison's encephalization quotient is not without its methodological problems. Specifically, attempts to examine relative brain size among species are confounded by the fact that the relationship between brain size and body size within taxomonic Families differs from relationships calculated across a taxomonic Order (Clutton-Brock & Harvey 1980). The wider the taxonomic affinity of a group of species the steeper the slope of the best fit line of brain weight plotted against body weight. The consequence of this is that larger species belonging to the same genus will tend to show small relative brain sizes compared to smaller species (Clutton-Brock & Harvey 1980). As such brain/body differences between Families must be considered separately from brain/body differences within them (Clutton-Brock & Harvey 1980).

Clutton-Brock and Harvey (1980) attempted to quantify relative brain size, while controlling for the confounding variable of taxonomic level using a measure of comparative brain size (CBS) (or alternatively, relative brain size [RBS][Sawaguchi 1990]). CBS measures for each genera represent a genera's deviation from the taxonomic Families best fit line for the brain/body ratio. The CBS for a genera can be calculated using the following equation:

$$\begin{gathered}\text{CBS (for a given genus)} = \\ \log(\text{brain wt.}) - (\text{elevation for Family} + \text{slope for Family} \cdot \log[\text{body wt.}])\end{gathered}$$

This background to the brain/body allometric relationship provides a means of comparing the relative brain size between species while controlling for the confounding affects of body size and taxonomic affinities.

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