GEOGRAPHIC AND SEX DIFFERENCES IN POSITIONAL BEHAVIOR OF ORANG-UTANS

by

JITO SUGARDJITO
Research and Development Center for Biology,
The Indonesian Institute of Sciences (LIPI)

JOHN G. H. CANT
Medical Sciences Campus, University of Puerto Rico

ABSTRACT

The basic aim of this paper is to present a synthesis of the field work that we have been conducting on the positional behavior of orang-utans. The data have been collected from two study sites, of which one was at Ketambe, Gunung Leuser National Park, northern Sumatra and the other at Mentoko, Kutai National Park, eastern Kalimantan. We attempt to interpret positional behavior in an ecological context, and we evaluate several hypotheses, some of which can not be tested conclusively at the present time.

GEOGRAPHIC DIFFERENCES IN MALE BEHAVIOUR

Female orang-utans of all ages are virtually entirely arboreal in both Sumatra and Kalimantan, whereas adult males in Sumatra are very largely arboreal. They travel between feeding sites in the canopy, and come to the ground only when chasing each other in agonistic interactions. Adult males in Kalimantan, however, normally travel terrestrially between feeding sites. How can we explain the geographic differences in male behavior? Three hypotheses for terrestriality and arboreality which are not mutually exclusive, are proposed.

1. Predation Avoidance Hypotheses - PAH
2. Food Dustribution Hypotheses - FDH
3. Habitat Structure Hypotheses - HSH

THE PREDATION AVOIDANCE HYPOTHESES

This hypotheses states that orang-utans in Sumatra must deal with the danger. The basic principle in testing hypothesis is to look for contrary evidence that would reject the hypothesis. The PAH is very hard to reject, we would have to show that tigers do not attempt to prey on orang-utans when they are within striking distance, and that orang-utans are "careless" in the presence of tigers. Showing that wild orang-utans are never eaten by tigers would not test the hypothesis, because this could simply mean that orang-utan defences against tiger predation are very effective. Furthermore, it has been argued that successful predation, eventhough it is a rare event that can occur only once in the life time of prey, has selective consequences which must be immense. In favor to this hypotheses is evidence that orang-utans in Sumatra exhibit behaviors that are reasonably interpreted as responses to the danger of a large and mostly terrestrial predator. Adult females with infants move hinger in the canopy for resting than travelling (Sugardjito, 1988). Another evidence showed that in 1978, several rehabilitant orang-utans were preyed by tiger while some of them are injured when they were foraged to the ground in the surrounding feeding site at the Orang-utans Rehabilitation, Bohorok, Sumatra. This resulted building the feeding platform of orang-utan rehabilitants in 5 metres above the ground.

FOOD DISTRIBUTION HYPOTHESES

The Food Distribution Hypotheses states that the food patches utilized by orang-utans are more widely dispersed in Kalimantan than in Sumatra, so that it is more economic for large adult males to descend to the ground for travel and then ascend the next food tree rather than maneuver through the canopy to the next patch (Rodman, 1979).

To test this hypotheses we would need inter-patch distances for males in each location. Rodman (1984) gives a histogram of combined male and female orang-utans inter-patch distances between food sources which are grouped into two classes, namely longer than 100 meters and shorter than 100 meters. He shows that 75% of the inter-patch distances are less than 100 meters. We did the same method as Rodman for the Sumatran male orang-utans. The result showed that 85% of the inter-patch distances between food sources

are shorter than 100 meters. We can not indicate whether or not the difference is significant because, the data of inter-patch distances between food sources for Kalimantan have been collected from both male and female sexes, whereas the Sumatran data were originated from male only.

Showing that percentage frequencies of inter-patch distances between food sources of Kalimantan orang-utans are farther than Sumatran one would not support the hypothesis, however, because females with infant are assumed to do the same as males to economize their travel between food trees. Kalimantan females descend to the ground for travel are not common (Galdikaas, 1978). This could simply mean that females with infant are more vulnerable to the ground predator like the wild boars (*Sus barbatus*). Furthermore, it has been reported that more infants have been killed and eaten by this predator during in the quarantine at Orang-utan Rehabilitation Center, Tanjung Puting, Central Kalimantan (Galdikas, pers.comm).

HABITAT STRUCTURE HYPOTHESIS

This hypotheses states that canopy is less continuous in Kalimantan than in Sumatra, making it more difficult for heavy adult males to travel above the ground.

We do not have independent measures of canopy structure for different sites, but it has been speculated that at Mentoko study area in Kalimantan the canopy of forest growing on hilly terrain is more discontinuous than forest growing on level terrain (Rodman, pers.comm). If the Habitat Structure Hypothesis is correct, we might predict that at Ketambe, Sumatran adult males would be arboreal in forest on hill sides. Ketambe males, however, are arboreal in both situations (there is implicit assumption that hillside forest at Ketambe at least as discontinuous as level forest at Mentoko).

SEX DIFFERENCES IN POSITIONAL BEHAVIOR

From the perspective of behavioral ecology, the positional behavior of orang-utans is especially interesting because of their very large body size. In those populations where males travel in the trees,

they are the largest habitually arboreal mammals, with adult male weight averaging 84 kg and adult female 38 kg (Rodman, 1984). This great differences in body weight is expected to produce differences in positional behavior and related aspects of foraging and predator avoidance.

STRENGTH TESTS OF LIANAS

We believe that crossing gaps between trees is the most serious problem of habitat structure faced by orang-utans. One of the methods they use is to clamber through vertical lianas. This led us to investigate the strength of lianas relative to the body weights of adult male and female orang-utans. We have performed stress tests of 99 lianas of 30 species in the forest at Ketambe, Sumatra. The lianas varied in size from 1.2 to 3.4 cm diameter. This range of size is realistic because we observed an adult male orang-utan using lianas as small as 2.0 cm, and an adult male orang-utan using lianas as small as 1.8 cm. From each liana, we suspended rocks, humans, and combinations of rocks and humans. We started with 18 kg, and progressed through 40, 50, 66, 80, 100, and 132 kgs until the liana failed. When failure occured, it was by either breaking or pulling free from the canopy.

Table 1. Comparison of locomotion modes between kalimantan and sumatran orang utans

	Kalimantan		Sumatra	
Locomotor modes	Female feeding	Female travel	Female travel	Male travel
Brachiate	10	13	18	21
Clamber=Scramble	47	56	48	38
Vertical climb	31	15	11	9
Quadrupedal walk	12	11	14	8
Tree-sway	0	6	9	24

All entries are column percents, respresenting proportions of bouts.

Not surprisingly, there was a significant positive correlation between the weight required to make the liana fail and the diameter of the liana. Looking at the sample of lianas as a whole, 3% failed at 40 kg, the weight of an adult female orang-utan, and 19% failed at

80 kg, the weight of an adult male (Table 1). The difference in rate of failure is statistically strength of the habitat from the perspective of orang-utans of different sexes; an adult male experiences over 6 times the risk of injury from liana failure as an adult female. We do not have comparative data for males and females on the frequency of use of lianas at Ketambe, but shortly we will discuss locomotor differences that may be related to the problem of liana strength. It may be recalled that the only time Sumatran adult male move on the ground is during dynamic agonistic interactions. We suggest that in these circumstances a heavy animal at substantial risk of habitat failure can not afford to evaluate the strength of its habitat carefully, and the ground is obviously much safer than canopy.

Table 2. Postural behaviour of orangutans and size of utilized substrates

Tree spec. and sex	Substrate size class						G-test
	1	2	3	4	5	(n)	male vs.females
Ficus virens							
Male	2	80	9	9	0	(56)	$p<.01$
Female	40	51	7	2	0	(126)	
Ficus drupacea							
Male	4	45	37	14	0	(78)	$p<.01$
Female	17	52	20	6	6	(90)	

All entries are column percents, respresenting proportions of bouts.

LOCOMOTION

The structure of forest canopy varies markedly from the ground to the tops of tall trees. The understory consists mostly of vertical tree trunks and lianas, whereas the main canopy contains the crowns of most of the relatively large trees in the forest and offers considerable opportunity for crossing between the ends of branches. Due to the problems of branch and liana strength and branch deformation, an animal's ability to move in structurally different strata of the canopy should vary with body weight. Here we discuss Sugardjito's work on sex differences in use of forest strata at Ketambe, Sumatra, and evaluate three hypotheses for the observed patterns.

The study compared an adult male, 3 adult females with infants, 1 adult female without infant, and 3 adolescents (in order of decreasing body weight). The analyses revealed a significant negative rank correlation of height of travelling with estimated body weight. Specifically, the adult male travelled lower (more in the understory), and adult females with infants travelled higher (more in the upper part of the main canopy). No correlation between height of resting and body weight was found. However, adult females with infants rested higher than they travelled; a similar difference was not found for other age-sex classes. The three hypotheses, which are not mutually exclusive, are proposed:

1. Dietary Differences Hypotheses - DDH
2. Vulnerability to Predator Hypotheses - VPH
3. Effectiveness of Locomotion Hypotheses - ELH

DIETARY DIFFERENCES HYPOTHESES

This hypotheses states that foods preferred by adult male are lower, and by adult females are higher. Sugardjito (1988) has noted that the adult male consumed more leaves and bark than the adult females, whereas the females consumed more fruit and insects, and proposes that differences in travel height are related to differences in the height at which the different types of food are consumed. The hypothesis was tested by comparing the distributions of travel heights with the distributions of feeding heights for different food types. Three of four comparations contradict the hypotheses. For fruits, insects and barks, both the adult male and adult females fed significantly higher than they travelled, and there are statistically no difference in the height of feeding for those items. Only for leaves is the comparison of travel and comsumption heights consistent with the hypotheses, both sexes feed on leaves at the same heights that they travel (i.e., the adult male comsumed leaves lower than did the females).

VULNERABILITY TO PREDATOR HYPOTHESES

This hypotheses predicts that the more vulnerable an individual is, the higher it should travel, assuming that danger from tigers and clouded leopards is greater near the ground, and that detection of a predator improves with height. Consistent with this hypotheses is the

fact that the least vulnerable age-sex class, adult male, travels lowest, but Sugardjito has sug-gested that this pattern results from the interaction of weight with habitat structure, which is the third hypotheses, ELH. Next higher are adult females with infants, followed by adolescents which is the most vulnerable class in the life time of orang-utans. The fact that females with infants move higher for resting than travelling does appear to be a response to the danger of predation.

EFFECTIVENESS OF LOCOMOTION HYPOTHESES

This hypotheses states that an animal's weight affects the effectiveness of different locomotor modes in different strata of the forest, resulting in differential use of the canopy. This hypotheses appears to be the most valid, and we explain why, when discussing locomotor modes in the next topic.

LOCOMOTOR MODES

A basic issue in many kinds of studies is whether a species behavior is similar at different sites, that is, how confident can we be generalizing from a single study? We can apply our results to this problem because we used comparable categories for locomotor and postural modes with similar methods. Table 2 below compares the results from Cant's work on adult females at Mentoko in Kalimantan with Sugardjito's study on both sexes at Ketambe in Sumatra.

The first two columns compare locomotion in fedding trees with locomotion during travel of adult females in Kalimantan. The principle differences between the two activities is the much higher frequency of vertical climbing in feeding locomotion.This is expected because the animals tend to feed higher than they travel, and an individual commonly enters a feeding tree relatively low in the canopy and climbs up into the crown.

The second and third columns compare travel locomotion of females in Kalimantan and Sumatra. The major differences are that Sumatran females were observed brachiating and tree swaying more than Kalimantan females. The high value of brachiation is somewhat influenced by the high value of tree-swaying. When animnal used tree-swaying during travel usually it will be continued by brachiation. In addition our impression is that there are fewer lianas at Ketambe than at Mentoko. If so, orang-utans there might need to use tree-

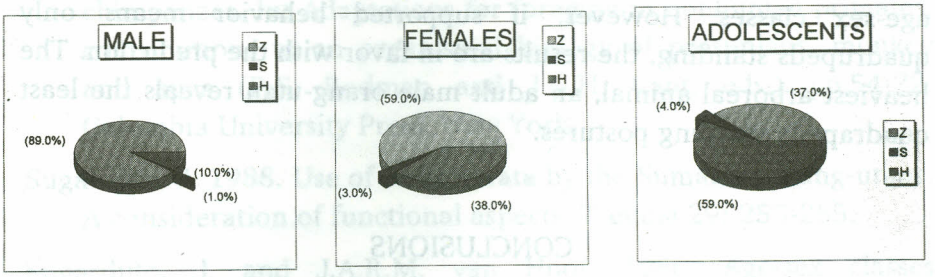
swaying instead of clambering lianas to cross many gaps. However, we still need quantitative data to support this.

The third and fourth columns compare travel locomotion of the two sexes in Sumaatra. The most notable differences are the much higher proportion of tree-swaying by the adult male, and the higher proportion of clambering (scrambling) and quadrupedal walking by the females. These differences appear consistent with interactions of body weight and habitat structure: lighter females usually travelled in the main canopy where broad crowns of tree provide avenues for relatively horizontal movement by walking, and for crossing between the branches of neighboring trees by clambering. In contrast, the heavier male usually travelled lower, in a zone with less continuity of tree branches. Here his greater weight should be an advantage for swaying trees.

POSTURES

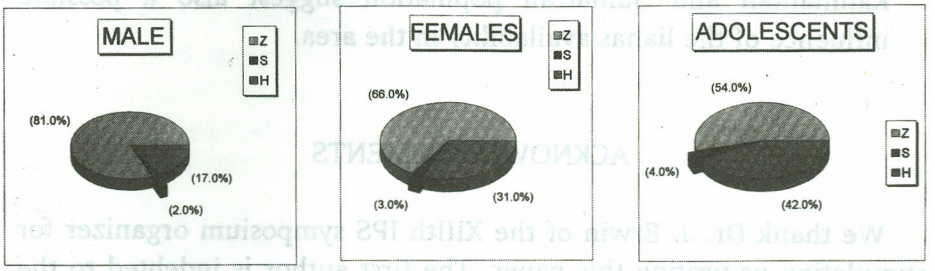
In examining postural behavior, we look first at the size of the arboreal suports (substrates) that orang-utans use. At Ketambe, we observed both male and females feeding in the same large *Ficus* trees, thereby providing a reliable comparison controlling for habitat structure. The simplest prediction about size utilized substrates is that the sexes differ, with the larger male preferring larger branches. This prediction is tested by the results shown in Table 2. Classes of estimated substrate diameter were < 4 cm, 4-10 cm, 10-20 cm, 20-40 cm and > 40 cm. In both species of *Ficus* the sexes differed significantly in substrate use, with the male using larger branches as expected.

It has been suggested by Cartmill and Milton (1977) that we should expect suspensory behaviour, below arboreal structures, to become more important relative to supported behavior (above substrates) as body size increases. They state : a large animal must find it easier to hang below a relatively small branch than to balance atop it. We tested this hypotheses intraspecifically, by comparing three age-sex classes, adult male, adult female, and adolescent during feeding. It can be seen that the adult male hangs or suspended less, contrary to the prediction (Figure 1; 2; and 3).



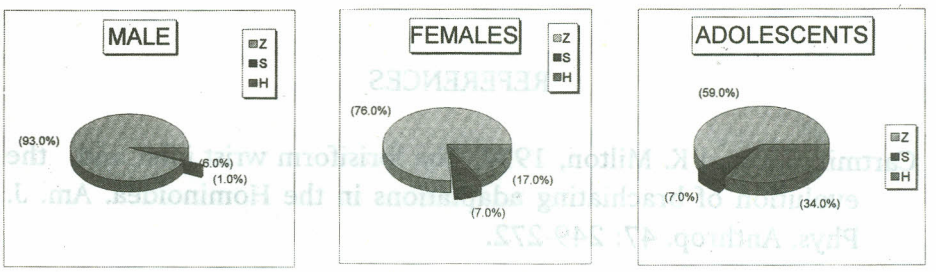
(N = time spent in minutes; 437 for male; 2803 for females; 662 for adolescents)
Z = sit ; S = quadrupeds standing ; H = hang

Figure 1. Feeding postures of Orangutan during feeding fruits



(N = time spent in minutes; 538 for male; 721 for females; 90 for adolescents)
Z = sit ; S = quadrupeds standing ; H = hang

Figure 2. Feeding postures of Orangutan during feeding leaves and shoots



(N = time spent in minutes; 300 for male; 460 for females; 96 for adolescents)
Z = sit ; S = quadrupeds standing ; H = hang

Figure 3. Feeding postures of Orangutan during feeding insects

Instead, the adult male shows sitting posture more than the other two age-sex classes. However, if supported behavior means only quadrupeds standing, the results are in favor with the prediction. The heaviest arboreal animal, an adult male orang-utan reveals the least quadrapeds standing postures.

CONCLUSIONS

1. Adult males travel terrestrialy in Kalimantan can be resulted from the absence of the potential predator (tiger).
2. Differences in locomotor modes are determined by locomotory efficiency in relation to body weight.
3. Differences in freequency of clambering and tree-swaying between Kalimantan and Sumatran population suggest also a possible influence of the lianas availability in the area.

ACKNOWLEDGEMENTS

We thank Dr. J. Erwin of the XIIIth IPS symposium organizer for stimulating us writing this paper. The first author is indebted to the late Mrs. Nina Sulaiman of Universitas Nasional, Jakarta for her continuous support during field data collection. The second author is grateful to Dr. Sampurno Kadarsan of the Indonesian Institute of Sciences (LIPI) for sponsorship of conducting field study in Indonesia.

REFERENCES

Cartmill, M. and K. Milton, 1977. The lorisiform wrist joint and the evolution of brachiating adaptations in the Hominoidea. Am. J. Phys. Anthrop. 47: 249-272.

Rodman, P.S. 1979. Individuaal activity patterns and the solitary nature of orang-utans. In: The great apes (D.A. Hamburg and E.R. McCown, eds.) pp. 234-255. Benjamin/Cumming, Menlo Park,. California.

Rodman, P.S. 1984. Foraging and social systems of orang-utans and chimpanzes. In: Adaptations for foraging in nonhuman primates, contributions to an organismal biology of prosimians, monkey and apes (P.S. Rodman and J.G.H. Cant, eds.) pp.54-72. Columbia University Press, New York.

Sugardjito, J. 1988. Use of forest strata by the Sumatran orang-utans: A consideration of functional aspects. Treubia 29: 255-265.

Sugardjito, J. and J.A.R.M. van Hoof, 1986. Age-sex classes differences in positional behavior of Sumatran orang-utans (*Pongo pygmaeus abelii*) in the Gunung Leuser National Park, Indonesia. Folia Primatol. 74: 14-25.