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The Orangutan Long Call and Snag Crashing at Tanjung Puting Reserve

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ABSTRACT. The long call, which is only given by adult males, is the most frequently uttered orangutan vocalization and the only one which can be heard over long distances. At the Orangutan Research and Conservation Project study area in the Tanjung Puting Reserve, Central Indonesian Borneo, adult males were calling more regularly and frequently than reported from other areas in Borneo. Adult males also exhibited a behavior, not reported elsewhere, sometimes associated with the vocalization of long calls: the pushing over of large snags (branchless dead trees) to the ground. At Tanjung Puting long calls functioned primarily to mediate dominance relationships among adult males who rarely came into direct contact with one another. In addition, long calls may have been helping sexually receptive females locate males.

INTRODUCTION

Wild orangutans are generally quiet, solitary animals who vocalize very little. The "long call" which is only given by adult males is the most frequently uttered of all orangutan vocalizations and the only one which can be consistently heard over great distances. The long call's importance is suggested by anatomy. Orangutan cheekpads, an adult male secondary sexual characteristic, may function as parabolic reflectors (RODMAN, pers. comm., 1976; SHORT, 1981) to help locate the source of long calls.[1)] Although others (BRANDES, 1938; DAVENPORT, 1967; YOSHIBA, 1964) described or mentioned this particular vocalization, MACKINNON (1971) who termed it the "long call" was the first to describe, in any detail, calling behavior in the wild. MACKINNON (1974) also provides sonograms of the call.

The long call is a complex vocalization consisting of a series of grumbles followed by intense bellowing or roaring which gradually subsides into another series of grumbles and sighs. Under optimal conditions, the bellowing can be heard for several kilometers (GALDIKAS, 1978a). Long calls usually vary between 1 or 2 min in duration but have lasted over 4 min. RIJKSEN (1978) suggests that the long call resembles the "pant hoot" display of the chimpanzee and the hoot series in the mountain gorilla.

MACKINNON (1971) argues that the function of this call is to maintain spacing between males with each male defending vocally an area around himself wherever he goes. At his Ulu Segama study sites in North Borneo MACKINNON found that long calls were given irregularly and infrequently, often being triggered by sudden sound cues such as the calls of other males or trees crashing.

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1) Although the acoustic qualities of orangutan cheekpads have not been experimentally tested, removal of similarly shaped facial ruffs in barn owls diminishes their ability to locate the source of sounds (KNUDSEN, 1981). Also, orangutans seem more adept at locating calling males than human observers (GALDIKAS, 1978b).

HORR (1972) also found that males at his Lokan River site, North Borneo, vocalized infrequently, normally "once a day or less." RODMAN (1973) reported even lower frequencies of calling; he mentions that one of two males resident in his Kutai Reserve study area in Kalimantan Timur (Eastern Indonesian Borneo) called an average of twice a month. RODMAN also proposed that calls serve to attract sexually receptive females.

Like MACKINNON, RIJKSEN (1978) found that calls at his Gunung Leuser study area in northern Sumatra were made usually after some disturbance as well as being given spontaneously. In particular, males gave long calls after they had chased "lower ranking" males. RIJKSEN argues that the reaction of an orangutan to a call will depend on the social status of males and sexual receptivity of females.

This paper describes the long calling and snag pushing behavior of orangutan males observed during a four-year period at the Orangutan Research and Conservation Project study area in the Tanjung Puting Reserve of Central Indonesian Borneo (Kalimantan Tengah). At Tanjung Puting males were calling more frequently and more regularly than reported from other areas. In addition, males exhibited a behavior *not* reported elsewhere; the pushing over of large snags to the ground in association with their calling. At Tanjung Puting long calls functioned primarily to mediate dominance relationships among adult males who rarely came into direct contact with one another. In addition, long calls may help sexually receptive females locate males.

THE STUDY

Observation of long calling and snag pushing behavior was made between November 1971 and November 1975 at the 35 km² tropical rain forest Orangutan Research and Conservation Project study site at the Tanjung Puting Reserve, Central Indonesian Borneo. Details of this study are available elsewhere (GALDIKAS, 1978a, b, 1979). Unlike most monkeys and apes, the arboreal orangutans are predominantly solitary; adult males live alone while adult females usually are accompanied only by dependent young.

During four years observations on wild orangutans totalled 6,804.5 hr. Observations on target adult males equalled 2,670 hr and 8 min (39% of total observations). Focal adult males vocalized long calls 907 times. With the exception of one aged and emaciated past prime male who was never observed to call, all individually recognized adult males observed for more than several days vocalized this call. Ten males (either alone or with other orangutans) were observed calling during whole observation days (when the focal animal was followed from the time he left his night nest in the morning to the time he made a nest for the following night).

CONTEXT OF CALLING

The function of the long call at Tanjung Puting was gauged from the circumstances under which it was given, and the reactions of individuals who heard it. Unlike the situation recorded by MACKINNON (1971) at the Ulu Segama where the majority of calls were triggered by "sudden sounds," most calls at Tanjung Puting seemed "spontaneous" in that they did not follow a sound cue. For instance, a habituated adult male who had been observed neither to have heard a long call nor encountered another orangutan in over a week still continued calling daily. At Tanjung Puting only 6.7% of all observed calls were elicited by "sudden sounds" (Table 1). The loud crash made by snags or large trees dropping to the ground was the

Table 1. Spontaneous long calls and calls triggered by "sudden sounds."*

Spontaneous calls:		No. (=846)	Percent (=93.3)
Call as a response to:			
	Sound of something approaching (in trees or on ground)	13	1.4
	Loud bird call	1	.1
	Loud crash of snag or dead branches	27	3.0
	Long call heard in distance	8	.9
	Sounds of gibbons	2	.2
	Sounds of red leaf-eating monkeys	2	.2
	Orangutan sneeze in distance	1	.1
	Swarm of bees	1	.1
	Proboscis movement in trees	3	.3
	Hornbills flying (swish of wings)	2	.2
	Juvenile squealing in distance	1	.1
Subtotal		61	6.7
Total		907	100

*Calls observed vocalized by target males.

most frequent sound cue for triggering calls. Three percent of all observed calls were elicited by such sounds.

However, adult males responded to 60% of loud crashes within approximately 400 m by calling. The fact that adult males reacted strongly to loud crashes may be explained, at least partially, by the fact that, since adult males sometimes pushed over snags, loud crashes, especially on a windless day, frequently indicated the presence of another male.

Ninety-four calls (10%) were initiated while the male was on the ground. Of these, 32 calls (3.5%) were completed in the trees as the male climbed into the canopy. Only in three instances did males call as they came down from the trees. This may have been to alert observers to the males' presence on the ground.

Approximately 10% of calls involved males moving into or from food trees. Another 11% were given from night nests, after the male nested for the night and before or as he left in the morning. Calls were given at any time, night or day, with a slight tendency to call more in the morning. As far as target males observed during whole observation days were concerned, their

Table 2. Frequency of calling during day by target males.*

Time	No. of calls	Percent
5–6:00	3	.5
6–7:00	68	10.4
7–8:00	49	7.5
8–9:00	55	8.4
9–10:00	73	11.1
10–11:00	66	10.1
11–12:00	62	9.4
12–13:00	64	9.7
13–14:00	50	7.6
14–15:00	52	7.9
15–16:00	53	8.1
16–17:00	35	5.3
17–18:00	21	3.2
18–19:00	5	.8
19–20:00	1	.2
Total	657	100

*Calls observed during whole days of observation only.

Table 3. Frequency of calls heard during day.*

Time	No. of calls	Percent
midnight–1:00	14	2.2
1–2:00	14	2.2
2–3:00	9	1.4
3–4:00	18	2.9
4–5:00	36	5.7
5–6:00	56	8.9
6–7:00	71	11.3
7–8:00	68	10.8
8–9:00	40	6.4
9–10:00	38	6.1
10–11:00	20	3.2
11–noon	23	3.7
noon–13:00	16	2.6
13–14:00	21	3.3
14–15:00	23	3.7
15–16:00	22	3.5
16–17:00	46	7.3
17–18:00	32	5.1
18–19:00	17	2.7
19–20:00	6	1.0
20–21:00	16	2.6
21–22:00	11	1.8
22–23:00	5	0.8
23–midnight	6	1.0
Total	628	100

*Calls heard while at camp or while searching for orangutans in forest.

calling rates peaked between 9:00 and 11:00 in the morning (Table 2). This is similar to what MACKINNON (1974) reported for orangutans in North Borneo.

However, since observers usually went back to camp after targets nested and only arrived at the nest the next morning after dawn, the proportion of calls that emanated from night nests was probably far greater than indicated by calls observed vocalized by targets during whole days of observation. Thus, I analyzed the 628 calls heard in the distance from camp or while searching for orangutans in the forest (Table 3). Although numerous calls occurred between 9:00 and 11:00 in the morning, almost one third (31%) were heard in the three hours (5:00 to 8:00 a.m.) that orangutan males were waking for the day. In the afternoon the most calls were heard between 4:00 and 5:00 p.m., the hour that adult male orangutans were likely to be nesting for the night.

On 20 occasions (2%), males were seen breaking and dropping dead or fresh branches while calling. On numerous occasions they shook trees or branches. This was particularly characteristic, but not limited to, elicited calls. MACKINNON (1971) suggested that calling males were "aggressively" motivated because he frequently observed such branch shaking and hair erection. However, at Tanjung Puting during approximately 70% of calls, males sat, stood still or moved in a normal fashion.

Nonetheless, two contexts, in particular, involved calling. One was initiation of contact with another orangutan. Out of 76 instances where adult males contacted individuals not encountered either earlier that day or on the afternoon before, they reacted by calling or pushing snags 43.5% of the time (31.5% long call; 12% snag pushing). However, whenever two adult males actually contacted one another (i.e., both could see the other) invariably at least one of them called.

Adult male-male contacts were very rare. Only four occurred in four years. In two cases where direct aggression took place, once in the form of lengthy combat and once as a long chase, the "winner" called at the conclusion of contact. In another instance, an adult male called as a past prime adult male fled when he moved in the old male's direction.

Another contact was more complicated. A male called after spotting another adult male sitting motionless in the canopy. Soon the sitting male began a call himself but didn't finish it. Then the first male moved rapidly and ostentatiously in the trees towards the sitting male, shaking branches as he went, but when he got within 20 m, the first male seemingly lost his nerve, came down to the ground and ran away. The second male continued sitting.

In addition, observations of one dominant male (one who chased other adult males but was never himself chased) indicate that even when he was totally alone in the forest, his calling rate went up after several other males moved into his home range. Although calls from unseen males did not directly elicit calling behavior on his part, he almost invariably called more on days when calls were heard in the distance.

The social relationships of adult males are almost exclusively limited to consortship with sexually receptive females (GALDIKAS, 1978a, 1979). The second context in which adult males frequently called or at least uttered part of the long call was preceding and/or during copulation. Most (87%) adult male copulations were accompanied by long calling behavior. Thirty copulations were observed. Males called immediately before and/or during 14 copulations. In another two cases, males were silent immediately before mating but had called earlier; the calls were directly followed by proceptive behavior on the part of the female which had led to copulation. In another ten instances males emitted only the grumbling portion of the long call while mating.

During adult male-adolescent female consortships the male's long call played a role in evoking female proceptive behavior. Almost half of observed adolescent female proceptive behavior (43%) directly followed long calls. Adolescent females responded to roughly one third of their consort's calls by immediately moving towards him, if they were some distance away, or by exhibiting proceptive responses, if they were within several trees of him. This percentage of adolescent female response seemed relatively constant over seven consort periods and two different adult male-adolescent female pairs (Table 4). However, adolescent females' rates of success in inducing adult males to begin copulation seemed about the same whether proceptive behavior followed a long call or not. (Adult males responded with copu-

Table 4. Responses of adolescent females to calls of mature male consort.

Date of consortship	No. of calls vocalized in presence of adolescent female consort[1)]	No. of calls to which female consort responded (by approaching closer or by exhibiting proceptive behavior)	Percent of total calls
July 1972	32	12	37.5
October 1974	16	6	37.5
December 1974	15	6	40.0
June 1975	29	11	37.9
July 1975	15	6	40.0
September 1975	11	3	27.3
October 1975	4	0	0
Totals	122	44	36.1

1) The number of long calls vocalized will not necessarily agree with the totals obtained by adding all calls vocalized during consortship days since the adolescent female frequently left her male consort in the late afternoon and did not return to him until the late morning of the following day.

lation only to 39% of adolescent female proceptive responses.) Frequently, the adult male just sat there while the female touched, groomed or mouthed his genitalia. Occasionally, he began the grumbling portion of the long call. But once the female ceased behaving proceptively the adult male often resumed foraging, continued sitting, or even moved away.

SNAG CRASHING

Snag crashing probably represents an orangutan prototradition peculiar to the Tanjung Puting region since manipulation and crashing of snags have not been reported from other areas. Snag crashing was predominantly an adult male activity (Table 5). Among females and immatures, contact with other orangutans seemed to be the primary reason (82%) for snag crashing. In two cases (18%), an adult female pushed snags at the observers.

On 29 occasions (3% of all observed long calls) calling males pushed over large snags as a prelude to the call. Since the crash of the snag as it hit the ground was usually considerably louder than the call itself, this practice alerted those within hearing distance to the possibility of a coming call. The direction of the caller could more easily be pinpointed when he crashed a snag first. That this may have been the function of the snag crash is suggested by the fact that males never pushed snags after calling.

In addition to initiating long calls, adult males attempted to push over large snags without vocalizing 31 times. Snag crashing without calling frequently initiated adult male contact with other orangutans, as well as belligerent moves towards subadult males (35% of total snag crashes). Twice adult males "answered" distant long calls by crashing snags but not calling themselves (6%). Adult males were the only age/sex class that crashed snags, with or without calling, while wandering the forests without meeting other orangutans.

One adult male pushed over snags three times in the course of several hours. This was a daily record and was probably a reaction to another adult male's presence within 500 m.

Snag crashing represented, to a large degree, personal idiosyncrasy. One male, *TP*, was responsible for almost half (48%) of all observed snag pushes. He was dropping snags, usually spontaneously as he moved through the forest alone, at the rate of one for every 18 hr of con-

Table 5. Snag crashing frequencies.

Class of orangutan	Individual	Snags crashed accompanying long call	Snag crashing without long call	Total snags crashed	
				No.	Percent
Adult male	*Nick*	4	8	12	16.9
	TP	18	16	34	47.9
	HH	—	1	1	1.4
	Knobs	1	—	5	7.0
	Fingers	4	1	1	1.4
	Unidentified male	1	—	1	1.4
	Ulysses	1	—	1	1.4
	Ralph	—	4	4	5.6
	Sam	—	1	1	1.4
Subtotal:					
Adult males	9 individuals	29	31	60	84.5
Adult females	2 individuals	—	6	6	8.5
Adolescent female	1 individual	—	1	1	1.4
Subadult male	3 individuals	—	4	4	5.6
Totals	15 individuals	29	42	71	100

servation. Ten percent of his observed calls were accompanied by snag pushing. Another adult male, *Nick*, who later spent much time in the same area of forest, pushed snags at a much lower rate, once during every 111 hr of observation. He was also less skilled than *TP* whose proficiency in manipulating snags was unmatched. Unlike most other orangutans, *TP* did not merely shove snags a few times until they dropped. Rather, he was extremely adept at balancing and rocking them back and forth until they fell in a desired direction. Further, he would sometimes ride the snag down as it began falling, catching himself on terminal branches of another tree with a hand and a foot when the snag was well on its way down. On a windless day, the sound of a snag crashing almost invariably indicated the presence of an adult male. Because of his snag pushing propensity, *TP* was particularly easy to detect. In fact, because only adult males long called and spontaneously crashed snags while alone, they were the most conspicuous orangutan age/sex class in the forest and the easiest to locate.

RESPONSES TO CALLS BY UNSEEN MALES

At Tanjung Puting observers gradually learned to distinguish the calls of four different males, *TP*, *Nick*, *HH* and *Sam*, when these called less than about 400 m away. It is likely, although by no means proven, that orangutans were as skilled, if not more so, at differentiating male calls.

Orangutans were observed 361 times while a long call from an unseen male was heard in the distance. (I assume that orangutans heard calls when observers did.) In the vast majority of cases (84%) targets showed no visible reaction. Nonetheless, age/sex classes were responding differentially to close calls (Table 6). As initially reported by MACKINNON (1971) for the Ulu Segama, adult males at Tanjung Puting were responding at higher rates and more intensely than females and immatures. This difference was significant (Table 7). Adult females did not react very much even when the calling male was within 100 m. However, an adult female once moved away in the trees. Subadult males also moved away in the trees upon hearing nearby calls. This was in sharp contrast to the observed reactions of adult males who descended to the ground and ran away.

Distance of the calling male (HORR, 1975) as well as his relative dominance vis-a-vis the listening male was probably the most important factor in determining adult male response. Generally, at Tanjung Puting the closer the call, the more likely it was to evoke a response of one sort or another from the focal male. The results (Table 8) indicate how effectively adult males were spacing themselves since calls were heard only three times (2%) within 100 m of the target male even when several adult males were in the same general area.

An adult male may need several minutes to travel 100 m arboreally and over half a minute to travel terrestrially. Heard call rates increased considerably (to 18%) if we examine calls which emanated from 100 to 400 m of focal adult males. This suggests that 100 m represents a safety margin. Males obviously felt unocmfortable and fled on the ground when a dominant calling male was close by. When males heard calls from 100 to 400 m away, they reacted more often (67%) than not, but in a variety of ways. However, adult males ignored most calls (55%) over 400 m distant. In fact, males never immediately moved away from a caller when that caller was over 800 m from them. I suspect that even orangutans have difficulty in differentiating callers from that distance. Also, 800 m approximates an orangutan day range so adult males separated by that distance are not in imminent danger of meeting.

Since adult males are virtually never in contact with one another, it is difficult to examine

Table 6. Reactions of target orangutans to long calls by unseen males.

	Distance from caller											
	Very close (less than 100 m)		Close (100–400 m)		Medium far (400–800 m)		Far over (800 m)		Very far (barely audible)		Total	
Response to unseen callers	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
A. Adult male reactions to long calls by unseen males:												
No visible response			10	43.5	11	55.0	65	86.7	5	100	91	72.2
Stopped activity and listened to call			2	8.7	4	20.0	5	6.7			11	8.7
Called			3	13.0	2	10.0	3	4.0			8	6.4
Moved away on ground	3	100	2	8.7	1	5.0					6	4.8
Pushed snag					1	5.0	1	1.3			2	1.6
Kiss-squeaked							1	1.3			1	.8
Moved away in trees			5	21.7	1	5.0					6	4.8
Sat up in night nest and urinated			1	4.4							1	.8
Totals	3	100	23	100	20	100	75	100	5	100	126	100
B. Adult female reactions to calls by unseen males:												
No visible response	7	77.8	34	82.9	47	94.0	57	98.3	17	100	162	92.6
Stopped activity and listened to call	1	11.1	1	2.4	1	2.0					3	1.7
Pushed snag					1	2.0					1	.6
Moved away in trees	1	11.1	3	7.3							4	2.3
Nest shook					1	2.0					1	.6
Dropped branches and kiss-squeaked			1	2.4							1	.6
Left nest							1	1.7			1	.6
Attacked companion female			1	2.4							1	.6
Sat next to companion female			1	2.4							1	.6
Totals	9	100.0	41	100.0	50	100.0	58	100.0	17	100	175	100.0
C. Subadult male reactions to calls by unseen males:												
No visible response			2	50	4	100	3	75	1	100	10	66.7
Vocalized staring in direction of caller and then moved away in trees	1	50									1	6.7
Moved away in trees	1	50	1	25			1	25			3	20.0
Stopped activity and listened to call			1	25							1	6.7
Totals	2	100	4	100	4	100	4	100	1	100	15	100.0
D. Adolescent female reaction to unseen callers:												
No visible response			4	66.7	1	100	26	96.3			31	88.6
Stopped activity and listened to call			2	33.3			1	3.7			3	8.6
Moved towards caller in trees	1	100									1	2.9
Totals	1	100	6	100	1	100	27	100			35	100
E. Juvenile male and adolescent male response to unseen callers:												
No response					2	100	8	100			10	100

Table 7. Comparison of target adult males and adult females regarding presence or absence of visible response to calls from unseen males.*

Distance[1)] from unseen caller	Test used	Level of significance
100 m or less	Fisher's exact	$p \equiv .045$; accept H_a
100–400 m	Chi-square	$p < .01$; accept H_a
400–800 m	Chi-square with rates correction factor	$p < .001$; accept H_a
800+	Fisher's exact	$p \equiv .007$; accept H_a
H_o: $p \geqq .05$ (observed data due to chance)		
H_a: $p < .05$ (observed data not due to chance)		

*The data in Table 6 showed the following problems for statistical analysis: a) differing categories of response to the long call for different age/sex classes and b) very small sample sizes within some categories. To overcome problem a), the types of response were collapsed into two categories: visible response and no visible response. Problem b) was avoided by testing only adult males and adult females over varying distance intervals. 1) Collapsing the adjacent distance variables into as few categories as possible was attempted by comparing the variables to a theoretical medium distribution that lies between them and then testing the distance they differ from this (χ^2 two-tailed test). All categories are somewhat similar in their distribution to adjacent distance but none are similar enough to justify combining any two adjacent intervals. On the other hand, none of the adjacent distance intervals are significantly different. This means that the further an unseen caller is from the target, the less probable is the target's reaction to the call and this loss of response tends to gradual.

directly relationships among them. However, comparison of their differential reactions to long calls, especially calls of known individuals, indicates that males were calling and responding in such a way that long calls mediate spacing in terms of male dominance relationships.

Three adult males, *TP*, *Nick* and *HH*, simultaneously shared at least parts of the same home range and were occasionally observed within 800 m of each other. At that distance given the extremely flat terrain of Tanjung Puting, it is certain that they were not monitoring each other's movements visually but were relying on auditory cues, principally long calls, to avoid or approach one another. Using multiple observers, we were able, on occasion, to follow at least two of these males simultaneously in the same general area.

One of the males, *Nick*, was never in a situation where another adult male called within 100 m of him. In fact, other males in the vicinity seemed to be calling at lesser rates when we observed *Nick* than when we observed either *TP* or *HH* as target.[2)] In 1,336 hr as target *Nick* heard only ten calls from distances less than 800 m away, a rate of less than .01 heard call/hr. This compared with *TP* who heard 15 calls in only 597 hr (a rate of .03 calls heard/hr) and *HH* who heard 16 close calls in only 115 hr (a rate of .14 heard calls/hr). Nor was *Nick* ever observed to move away from a calling male, no matter how close the other male. This contrasts with the two other males who ran away on the ground from callers without making contact. In four of six cases, the identity of the unseen caller was directly verified. *TP* ran away from *Nick* twice, in one case while *Nick* called from over 100 m away. *HH* ran away from *Nick* on the ground once and from *TP* once. On another three occasions, *HH* moved away rapidly in the trees from *Nick*'s call and once, upon hearing *Nick* call, he immediately sat upright in his night nest and urinated. In addition, he was observed sitting motionless[3)] in the canopy for over an hour several times after *TP* or *Nick* called from distances exceeding 100 m.

These incidents took place in different areas of the forest over a period of months so that

2) This was the case even when *TP* or *HH* were not present in the study area.
3) Sitting motionless makes an orangutan inconspicuous.

Table 8. Comparison of *Nick*'s, *TP*'s and *HH*'s responses to unseen callers.

	Distance from Caller											
	Very close (less than 100 m)						Close (100–400 m)					
	Nick		*TP*		*HH*		*Nick*		*TP*		*HH*	
Response to distant call	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
No visible reaction							3	50	2	40	4	40
Stopped activity and listened to call							1	17	1	20		
Called, moving in caller's direction							2	33				
Moved away on ground			1	100	2	100			2	40		
Crashed snag and moved in caller's direction												
Kiss-squeaked												
Moved away in trees											5	50
Sat up in night nest and urinated											1	10
Total			1	100	2	100	6	100	5	100	10	100

(continued)

territorial impulses or varying emotional states cannot explain individual male reactions. Further, while both *Nick* and *TP* called, crashed snags, and moved in the direction of other males who were in the vicinity, this was not observed in *HH*'s case. It appears a dominance hierarchy existed with *HH* avoiding contact with both *Nick* and *TP*, and *TP* avoiding contact only with *Nick* (Table 9).

Since calling makes a male conspicuous, a frequently calling male runs a higher risk of being located and chased by a more dominant male than a male who calls infrequently. Thus, it could be argued that higher ranking males would call more than lower ranking ones. Indeed, daily call rates were very different for different individuals. *Nick* called the most frequently, *TP* less, and *HH* called about half of *Nick*'s rate. Most significantly, on days when *Nick*, *TP* or *HH* were known to be within 800 m of each other, *Nick* continued calling but *TP* and *HH* called at very low rates.

Thus, long calls mediated the adult male hierarchy in such a way that even when two or more males were within several hundred meters of each other, contact rarely took place since the less dominant males called much less and moved out of the paths of the higher ranking males. In several cases of "no response" to a dominant's nearby calling (between 100 and 800 m), analysis of travel directions as the silent males foraged showed a distance-increasing effect (MARLER, 1965).

As noted earlier, females generally did not respond to long calls. Most adult females in the study area were either pregnant or lactating during the study period while large adolescent females were not regularly followed as focal animals. When not pregnant or not lactating, adult females are in estrus only a few days each month. Thus, it is not surprising that observers never witnessed a non-consorting focal female move directly towards a distant calling male, locate him and initiate consortship. Nonetheless, there is evidence that sexually receptive females, particularly adolescents, were locating dominant adult males by their long calls. During the series of consortships witnessed between *Nick* and an adolescent female, *Noisey*, over a one-year period, *Noisey* contacted *Nick* five times while he was the

Table 8. (continued)

Medium far (400–800 m)						Far (800 m plus)						Very far (barely audible)			
Nick		*TP*		*HH*		*Nick*		*TP*		*HH*		All		Total	
No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
2	50	3	33	4	100	5	83	37	93	5	100	3	100	68	71.6
1	25	3	33			1	17	2	5					9	9.5
1	25													3	3.2
		1	11											6	6.3
		1	11											1	1.1
								1	2					1	1.1
		1	11											6	6.3
														1	1.1
4	100	9	100	4	100	6	100	40	100	5	100	3	100	95	100

Table 9. Mean daily call rate for individual adult males.*

Name of male	Daily call rate: calls/whole day	No. of whole days observed
PP(past prime)	0	7
Nick	4.3	101
TP	3.1	36
Sam	2.3	16
HH	2.2	5
Ulysses	4.0	3

*Observed over three whole days or more.

focal animal to initiate consortship (despite the presence of several other adult males in her home range).

In addition, while *Noisey* usually followed *Nick*, she also frequently moved away from him during the late afternoons to forage on her own. The next morning she would locate *Nick* using his long call(s), sometimes moving from as far away as 200–300 m to join him.

The evidence is more ambiguous concerning adult pairs. The initiation of two adult male-female consortships was observed. In one case the adult male clearly approached the adult female while in the second instance, the adult female moved towards the calling male.

DISCUSSION

At Tanjung Puting adult males were calling more frequently and regularly than reported from other areas. MACKINNON (1974) noted that in his Ulu Segama study areas A and B he respectively heard 0.7 and 0.2 calls per day spent in the field. At Tanjung Puting 1.5 calls per day[4] were heard. Direct observations of calling males indicated that prime adult males usu-

4) A total of 1,896 calls were heard during approximately 1,300 days spent in the study area. These calls consisted of 628 heard in the distance while I was in the forest or at camp, 907 vocalized by target males and 361 heard in the distance while observing orangutans.

ally called at least twice daily with dominant males calling more frequently than less dominant ones. One dominant male called an average of four times per day.

The differences in adult male call rates between various regions of Borneo may simply reflect regional variation, differences in population density, or may be due to differential sampling. Since dominant males at Tanjung Puting called the most, perhaps adult males sampled extensively in other areas were not the most dominant or were calling at lower rates for other reasons. For instance, GALDIKAS (1978a) suggests that one of two frequently observed adult males at Kutai Reserve (RODMAN, 1973) was actually a past prime male. (At Tanjung Puting the one observed past prime male never called at all.) Even if observed males in other areas were dominant, they may have been calling less frequently because no subordinate males were in the same general vicinity. Thus, at the same site in Kutai only two adult males were observed during 15 months. MACKINNON (1971) noticed that call rates went up when orangutans were "overcrowded." He notes that the presence of other nearby males intensified calling behavior. However, at Tanjung Puting this was only true for dominant males. In addition, at Tanjung Puting males occasionally pushed over snags to the forest floor as a prelude to the long call, thus enhancing the call's loudness. Males also crashed snags without vocalizing in contexts where calling might have been expected. Since this practice has not been reported from other areas where orangutans have been studied, it probably represents an orangutan proto-tradition peculiar to the Tanjung Puting region. How widespread this practice actually is, however, will not be known until orangutans are studied in other parts of Central Kalimantan and also West Kalimantan.

At Tanjung Puting long calls function to mediate spacing among adult males in terms of their dominance relationships. This was documented with three adult males who simultaneously ranged through the same general area of forest without once encountering one another. Long calls probably serve the same function among orangutan populations in other regions as well.

At Tanjung Puting long calls help sexually receptive females locate males. Since females are much less conspicuous than adult males [females are smaller, have no loud vocalizations, rarely crash snags and move less far during the course of a day (GALDIKAS, 1978a)], it seems much easier for females to locate adult males than vice versa. Nonetheless, the data for long calls serving to attract estrous females are always likely to be more ambiguous than the data concerning long calls mediating spacing among males for the following reason: the reproductive stakes regarding the initiation of consortship are ultimately much higher for individual males than for females. Whether or not an estrous female consorts with a male of her choice or with someone else, she is more than likely to mate with someone and produce offspring. For her, the question is selection of the best possible partner under the circumstances. For a male, the question is more urgent.

Since females are a scarce resource and male-male competition for this resource very severe, an unsuccessful male may not mate at all (TRIVERS, 1972). Since orangutans generally do not congregate and males are more mobile than females, an adult male who is locating estrous females (and overriding female selection in cases disadvantageous to himself) at the same time that he is trying to attract females with his long call will probably be more successful reproductively than one who only attracts females (or one who only tries to locate them). The two strategies are not mutually incompatible but complement each other. Thus, it is not surprising that calling males initiate consortships with seemingly indifferent females who exhibit no obvious proceptive behaviors at the same time that females are eagerly locating adult males.

As mentioned, the evidence for female selection of sexual partners, in terms of male calling behavior, will probably always be relative and somewhat ambivalent. Nonetheless, it is clear that females are selecting males whenever it is possible for them to do so (GALDIKAS, 1981). The fact that even subordinate adult males continue advertising their presence by long calling, albeit at relatively low rates, suggests that there must be a pay-off for them (in terms of attracting females) that more than makes up for the heightened possibility of being located and attacked by dominant males. There can be no doubt that the long call is crucial to an understanding of male-male competition and female sexual selection in this species.

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