

## Associations among wild orang-utans: sociality, passive aggregations or chance?

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**Abstract.** Encounters and associations between adult male, adult female and subadult male orang-utans, *Pongo pygmaeus*, were examined at the Kutai National Park and Gunung Palung Nature Reserve, Indonesia. Observed rates of encounters, durations of associations and proportions of time spent in associations of two members of each age–sex class from each population were compared with expected values generated from null models of associations. Encounter rates, durations of associations and proportions of time spent in associations were greater than expected by chance. Two factors appear to generate these non-random patterns: subjects at both sites met conspecifics at food sources more often than expected, and associations frequently involved social behaviour. Three differences in association patterns existed between populations. Orang-utans at Kutai encountered each other more frequently, engaged in longer associations, and spent a greater proportion of time together than conspecifics at Gunung Palung. Variations in association patterns between populations reflected age–sex class differences in behaviour. In contrast to adult and subadult males at Kutai, males at Gunung Palung avoided conspecifics. Similarly, adult females and subadult males at Gunung Palung spent less time with others than did their Kutai counterparts. An analysis of the nature of associations revealed two additional behavioural differences between populations. Mating did not occur at Gunung Palung, but was observed frequently at Kutai, and subadult males at Kutai received aggression, while those at Gunung Palung did not. These data support the hypothesis that variations in the reproductive states of adult females account for differences in the patterns of association between orang-utans. Sociality among orang-utans appears primarily the result of aggregation at common resources, either food or mates.

The description and the analysis of social systems are two major areas of ethological research. Animals of many species form non-random associations, ranging from breeding pairs to large hunting parties, but individuals of several other species are found both alone and in aggregations (see reviews in Wilson 1975). For highly gregarious species, the description of social patterns is relatively straightforward. In contrast, progress in understanding the social systems of animals that form only temporary groups has been hindered by the lack of a standard against which to measure the degree of sociality. Recent models developed to examine mixed-species associations of primates,

however, provide such a standard, and an appropriate test with which to assess the cohesiveness among animals (Waser 1982, 1984, 1987; Whitesides 1989). These models generate null hypotheses of the expected encounter frequencies, durations of associations and proportions of time spent in associations based on the assumption that individuals move independently and randomly. In this paper we employ these models to investigate associations between orang-utans, *Pongo pygmaeus*, an apparent exception to the near universal pattern of sociality among higher primates (see reviews in Smuts et al. 1987).

George Schaller (1961) initiated modern field studies of orang-utans with brief observations in Borneo. Schaller was able to discern little about

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the social organization of orang-utans, but later speculated that these animals lived in 'open groups' like those said to characterize chimpanzees, *Pan troglodytes* (Schaller 1965). MacKinnon (1971, 1974) reported results of the first long-term study of orang-utans; his observations appeared to confirm Schaller's suggestion. He described a large community in Borneo consisting of females with young, which were loosely associated with high-ranking adult males. These animals formed constantly varying subgroups as they ranged nomadically over a large shared range. MacKinnon's description and terminology indicated a strong similarity with chimpanzees.

Subsequent research on orang-utans provided a somewhat different picture. Studies by Horr (1975), Rodman (1973), Galdikas (1979) and Mitani (1985) in Borneo and by Rijksen (1978), Schurmann & van Hooff (1986), Sugardjito et al. (1987) and teBoekhorst et al. (1990) in Sumatra produced, as Galdikas (1985) wrote '... a portrait of a pongid that ... is unusually consistent in its social organization over the entire range in which it is found'. All of these populations consisted of a stable set of resident adult females with dependent and older immature offspring. These females occupied overlapping but non-identical ranges. There were adult and subadult males in each population that lived within a fixed area; the home ranges of males overlapped those of one or more females. In addition to these resident animals, all populations included a set of non-resident individuals, which appeared to wander over larger regions. These patterns were consistent between studies and revealed that associations outside the maternal family were ephemeral.

Despite the consistency of social patterns revealed by field studies of orang-utans, opinion varies widely with respect to how 'social' they are (e.g. compare Rodman 1973; Galdikas 1985; Sugardjito et al. 1987). Here we attempt to resolve this issue by applying the null models of associations to data from studies of orang-utans at two sites in Borneo. First, we compare the observed patterns of associations with those expected under the null models, and examine differences between the study sites. Second, we investigate the sites of encounters and the behavioural interactions during associations, to determine the causal factors accounting for differences in the observed patterns. Third, we provide a comparison with other study sites to examine the variation in patterns of associ-

ations among populations of orang-utans. We conclude with comments on the relevance of our findings to current hypotheses that propose a functional link between the intellectual abilities of animals and complex social systems.

## METHODS

### Study Sites and Subjects

Observations of orang-utans were made in Indonesia by J.C.M. and field assistants for 16 months from July 1981 to October 1982 at Mentoko camp in the Kutai National Park, East Kalimantan, and by J.C.M., D.P. and field assistants for 14 months from April to May 1988 and August 1988 to July 1989 at the Cabang Panti Research Station in the Gunung Palung Nature Reserve, West Kalimantan. The 3-km<sup>2</sup> Kutai study site comprised mixed, lowland dipterocarp forest. The Gunung Palung study area covered 5 km<sup>2</sup> and a mosaic of habitats including lowland dipterocarp and peat swamp forests.

The study populations at each site consisted of resident and non-resident animals. Individuals encountered regularly during each study formed the resident populations. Animals seen during short periods (<6 months) were considered non-residents. Residents at the Kutai study site included one adult male, three adult females with their offspring and two subadult males. Two adult males, four adult females with their offspring, two subadult males and three adolescent females were residents at Gunung Palung. Non-resident populations consisted of nine animals at Kutai and five individuals at Gunung Palung. Observations were not distributed evenly between animals in the study population, and only individuals that were observed for over 135 h are included in the following analyses. The study subjects were two adult males, two adult females and two subadult males from each population (Table I). With the exception of one adult male (LU) at the Kutai study site, all of these individuals were residents.

### Observational Methods

Orang-utans range over large areas and are usually separated from one another, thus making it difficult to find and follow individuals regularly. Target animals were therefore located and followed opportunistically. These individuals were

**Table I.** Observation time and mean travel rates of orang-utan study subjects

Study site	Animal	Age-sex class*	N days	Travel rate (m/h)	Observation hours
Kutai	BC	AM	90	24	507
	LU	AM	18	32	138
	SI	AF	214	65	2035
	SO	AF	44	38	329
	DU	SM	91	46	794
	LE	SM	84	57	758
Gunung Palung	HE	AM	40	43	309
	MA	AM	61	31	355
	KA	AF	55	64	479
	SU	AF	32	53	289
	CR	SM	20	65	168
	PE	SM	58	72	463

\*Age-sex classes abbreviations: AM: adult male; AF: adult female; SM: subadult male.

usually followed continuously from dawn to dusk. The activity states of target individuals during observations were recorded to the nearest minute. Associations between targets and conspecifics were noted ad libitum. When animals associated with each other, the activity of targets was recorded continuously, while the behaviour of conspecifics was checked ad libitum.

Positions of animals were recorded continuously and mapped with respect to the trail system. Travel distances were recorded whenever subjects moved, and the daily path lengths traversed by animals were calculated from these movements. Travel velocities of individuals were estimated by dividing path lengths by the amounts of time the animals were active. Mean travel speeds of individuals and for each age-sex class were derived from these data.

#### Methods of Sampling Encounters, Associations and Durations of Associations

Spatial and behavioural criteria defined encounters and associations between animals. Encounters and associations took place if animals initially approached to within 30 m of each other. At this distance tree foliage density at both sites permitted animals to make visual contact. Once contact was made, animals occasionally drifted more than 30 m apart, but maintained association by continuing to follow each other actively. In these situations, orang-utans stayed within a 30-m radius of each other most of the time, and the additional behavioural criterion of following from a distance was invoked to define associations.

Encounters between animals were scored only for target animals. Instances in which the observer initiated observations by finding two or more orang-utans together were not recorded as encounters. Thus, observed encounter rates ( $Z_{obs}$ , see below) are estimates of the rates of formations of associations between target individuals and others. Observed durations of associations ( $T_{obs}$ , see below) were tabulated for those between target animals and conspecifics. A few associations (7%) were not observed entirely. For these truncated data, we calculated the theoretical distribution of durations based on a log-normal density function (Lee 1980). The parameters of the log-normal distribution provided an estimate of the mean durations of associations. Estimates of the proportions of time individuals spent in association with conspecifics were computed by multiplying estimates of observed encounter rates ( $Z_{obs}$ , see below) and durations of associations ( $T_{obs}$ , see below).

#### Null Models of Rates, Durations and the Proportion of Total Time of Associations

Expected rates, durations and proportions of total time of associations between individual orang-utans were calculated by adapting null models developed to examine mixed species associations of primates (Waser 1982, 1984, 1987). Following Waser (1982), a group of species  $i$  with radius  $r_i$  and average velocity  $v_i$  moving randomly in two dimensional space will encounter groups of species  $j$  with

radius  $r_j$  and average velocity  $v_j$  at a rate

$$Z_{\text{exp}} = 2 r p_j (v_i^2 + v_j^2)^{1/2} \quad (1)$$

where  $r = r_i + r_j + d$ ,  $p_j$  = the density of groups of species  $j$ , and  $d$  = a distance criterion applied by the investigator to define associations. This equation assumes that the distribution of travel velocities is approximated by a Maxwell-Boltzmann function (Waser 1982). For purposes of the following analyses, subscript  $i$  refers to a target orang-utan and subscript  $j$  is either all other conspecifics or age-sex class of individuals. When individuals rather than groups are the units of interest,  $r_i = r_j = 0$ ,  $r = d$ ,  $p_j$  = the density of individuals in the study population,  $v_i$  = the mean travel velocity of individual  $i$ , and  $v_j$  = the velocity of all other conspecifics or age-sex class of individuals. The average duration of these associations expected by chance is

$$T_{\text{exp}} = 2.467 r (v_i^2 + v_j^2)^{-1/2} \quad (2)$$

where  $r$ ,  $v_i$  and  $v_j$  are defined as above (Waser 1984).

An estimate of the expected proportion of the time each individual spends in association with conspecifics ( $P_{\text{exp}}$ ) is easily derived by multiplying values of  $Z_{\text{exp}}$  and  $T_{\text{exp}}$  (Waser 1987)

$$P_{\text{exp}} = Z_{\text{exp}} \times T_{\text{exp}} = 4.934 r^2 p_j \quad (3)$$

To simplify the graphical presentation of results, we compare the logarithms of the ratios of observed to expected frequencies of encounters, durations of associations and proportions of time spent in associations. Values greater than zero indicate that observed frequencies, durations and proportions exceeded those expected by chance.

### Encounter Sites

The sites where animals met were mapped with respect to the locations of food sources. Encounters were defined as taking place at food trees or elsewhere. The average feeding bout length for orang-utans at the Kutai site was 36 min (Rodman 1977). A conservative approach was adopted for the purposes of this classification, and food trees were operationally defined as those trees where animals fed for over 1 h. To examine whether the location of food affected the rate with which orang-utans encountered each other, we compared the observed proportion of encounters near food sites with a null expectation based on the proportion of time animals spent at food. We calculated expected values for each animal by dividing the number of hours it was observed at food sources, as defined above, by the total number of observation hours.

### Definition of Association Types

Associations were classified as either passive or social, based on the behavioural interactions between orang-utans. Passive associations were aggregations in which animals showed no overt interaction with each other. Social associations were those in which orang-utans interacted actively. We defined two types of passive associations and four kinds of social associations according to the following behavioural criteria.

#### Passive associations

(1) Associations at a food tree ('food'): the animals met at a food tree, fed without overtly interacting with each other, and departed separately. (2) Associations while both animals travelled ('travel'): orang-utans travelled past each other during their normal foraging movements. During these associations, animals did not interact overtly.

#### Social associations

(1) Aggressive associations ('aggressive'): the animals chased or fought each other. (2) Mating associations ('mating'): the orang-utans mated. (3) Associations in which animals avoided each other ('avoidance'): orang-utans avoided the presence of conspecifics by travelling in an opposite direction immediately upon encounter or by increasing the distance between themselves. (4) Other social associations ('other'): animals travelled and foraged with each other.

### Statistical Tests

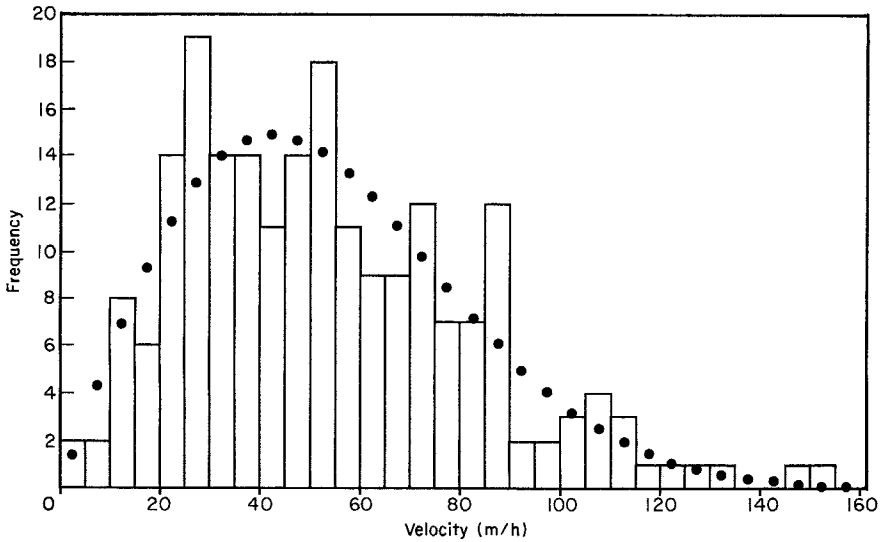
Standard parametric and non-parametric statistical procedures were employed in the following analyses (Sokal & Rohlf 1981). All statistical tests were two-tailed with the criterion for significance set at  $P < 0.05$ .

## RESULTS

### Null Models of Association

#### Assumptions of the models

Table I shows the mean travel velocities recorded for individual orang-utans from both populations. From these data we constructed a frequency histogram of observed travel velocities (m/h) and the



**Figure 1.** Frequency distribution of 209 travel velocities of orang-utans from the Kutai and Gunung Palung study populations ( $\square$ ) compared with expected frequencies of velocities under the Maxwell-Boltzmann probability function ( $\bullet$ ) with mean velocity = sample mean velocity = 53 m/h. The Maxwell-Boltzmann probability function is

$$f(v) = \pi(2\bar{v}^2)^{-1} v \exp(-\pi v^2/4\bar{v}^2)$$

in which  $v$  = velocity and  $\bar{v}$  = average velocity. Expected frequencies are calculated from the integral as follows:

$$n \int_{v_1}^{v_2} f(v) = n[\exp(-\pi/4v_1^2) - \exp(-\pi/4v_2^2)]$$

in which  $v_1$  and  $v_2$  are the lower and upper limits of the interval and  $n$  is the sample size.

theoretical Maxwell-Boltzmann distribution of travel speeds (Fig. 1). For a two-dimensional Maxwell-Boltzmann distribution

$$v/s_v \approx 1.9$$

where  $v$  = the mean travel velocity and  $s_v$  = the standard deviation of speeds (Waser 1984). The value calculated from the travel speeds in Fig. 1 is 1.84, and a goodness-of-fit test indicated that the observations match the theoretical distribution remarkably well ( $\chi^2 = 21.17$ ,  $df = 20$ ,  $P > 0.30$ ). Thus, a primary assumption of the null models of encounters and associations is not violated.

#### Encounter rates

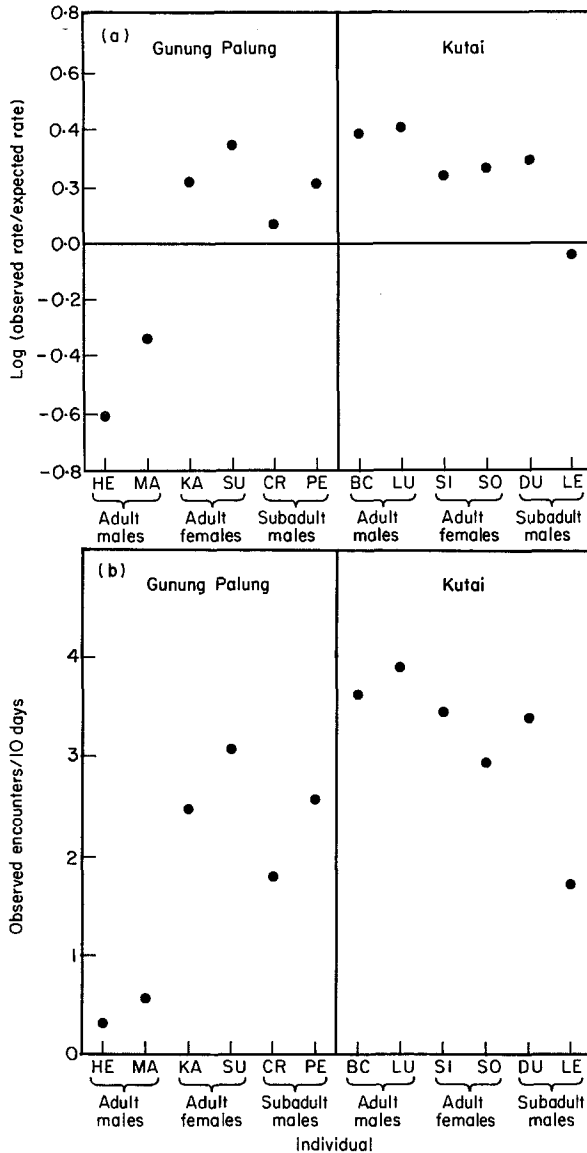
Observed rates of encounter between orang-utans were significantly greater than those expected by chance in a comparison using animals at both study sites (Wilcoxon matched-pairs signed-ranks test,  $N = 12$ ,  $P < 0.02$ ; Fig. 2a), but this pattern did not hold for all individuals. Both adult males at the Gunung Palung site and one subadult male at Kutai encountered other individuals less often than

expected by chance. Observed encounter rates differed between animals living in the two populations. Orang-utans at Kutai encountered each other more frequently than those at Gunung Palung (Mann-Whitney  $U$ -test,  $N_1 = N_2 = 6$ ,  $P < 0.05$ ; Fig. 2b).

#### Durations of associations

Observed durations of associations between target individuals and other conspecifics were significantly longer than those expected based on the null model when the data from the two populations were pooled (Wilcoxon test,  $N = 12$ ,  $P < 0.05$ ; Fig. 3a). The age-sex class of individuals affected association durations. Adult males were intolerant of each other, and associated for periods shorter than expected by chance (Table II). Adult females stayed with subadult males longer than predicted by the null model (Table II).

Observed durations of associations between orang-utans living in the different populations showed substantial differences (Fig. 3b). Associations at the Kutai study site were significantly



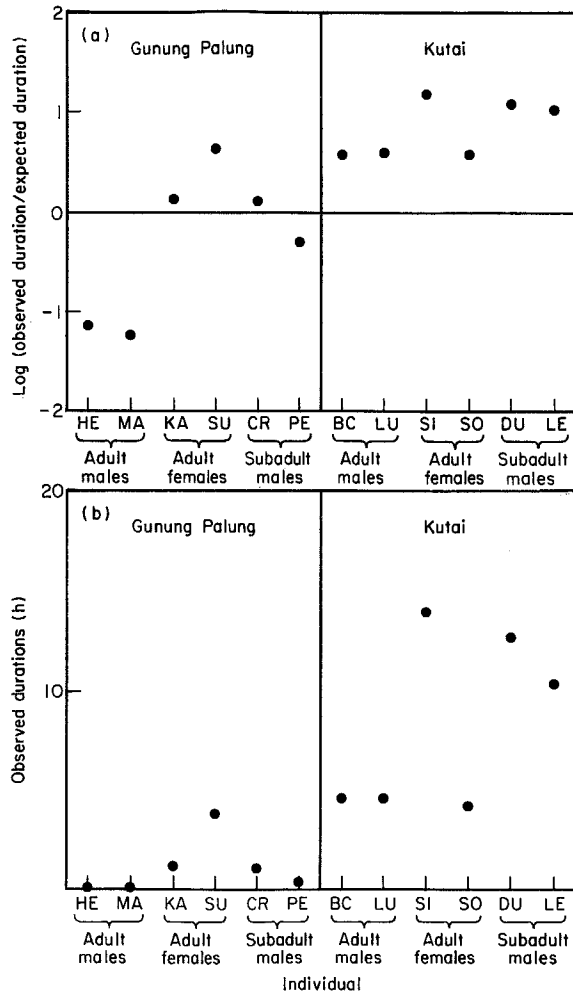
**Figure 2.** Encounter rates between orang-utans. (a) Observed and expected encounter rates. The null model specified by equation (1) in the text generated the expected rates. The logarithms of the ratios of observed to expected rates are shown. Values greater than zero indicate that observed rates exceeded those expected by chance. (b) Observed encounter rates with all orang-utans.

longer than those at Gunung Palung (Mann-Whitney  $U$ -test,  $P < 0.01$ ,  $N_1 = 6$ ,  $N_2 = 6$ ). Associations with females lasted longer at Kutai than those at Gunung Palung (Mann-Whitney  $U$ -test,  $P < 0.05$ ,  $N_1 = 6$ ,  $N_2 = 6$ ; Table III); adult and subadult males of the Kutai population accompanied females for considerably longer during each association than did the males of the Gunung Palung

population. The durations of associations involving adult and subadult males did not show any differences between study sites (Mann-Whitney  $U$ -test,  $P > 0.05$  for both comparisons; Table III).

#### *Proportions of time in associations*

Observed values of the total proportion of time target orang-utans spent in association were



**Figure 3.** Durations of associations between orang-utans. (a) Observed and expected durations with all orang-utans. The null model specified by equation (2) in the text generated the expected durations. The logarithms of the ratios of observed to expected durations are shown. Values greater than zero indicate that observed durations exceeded those expected by chance. (b) Observed durations with all orang-utans.

significantly greater than those expected by chance (Wilcoxon test,  $P < 0.01$ ,  $N = 12$ ; Fig. 4a). As in the case with encounter rates, male orang-utans at Gunung Palung were notable exceptions to this general rule; the two adult males were the only individuals that spent less time with conspecifics than expected on the basis of the null model (Fig. 4a).

The two study populations differed in their observed proportions of time spent in associations. Kutai orang-utans associated with conspecifics more than animals at Gunung Palung (Mann-Whitney  $U$ -test,  $P < 0.01$ ,  $N_1 = 6$ ,  $N_2 = 6$ ; Fig. 4b).

Since males at the Kutai study site spent a considerable amount of time with females, the proportion of time adult females at Kutai spent in associations with others exceeded that of Gunung Palung females (Mann-Whitney  $U$ -test,  $P < 0.01$ ; Table III). Similarly, subadult males at Kutai associated with females and other subadults frequently, and Kutai subadults spent more time with conspecifics than subadults at Gunung Palung (Mann-Whitney  $U$ -test,  $P < 0.05$ ; Table III). The observed proportions of time adult males spent in associations did not differ between populations (Mann-Whitney  $U$ -test,  $P > 0.05$ ; Table III).

**Table II.** Observed and expected durations of associations with orang-utans of different age-sex classes\*

Study site	Individual	Age-sex class	Log (observed/expected) durations with		
			Adult males	Adult females	Subadult males
Kutai	BC	AM	-1.93	0.81	-0.05
	LU	AM	-1.63	1.35	X
	SI	AF	1.19	1.80	1.25
	SO	AF	-0.23	-0.13	1.16
	DU	SM	-0.16	1.61	0.77
	LE	SM	0.56	1.60	0.99
Gunung Palung	HE	AM	-1.28	X	X
	MA	AM	-1.42	X	-1.11
	KA	AF	-0.17	X	0.30
	SU	AF	0.27	X	0.16
	CR	SM	-0.06	0.27	X
	PE	SM	-0.26	-0.23	-0.90

\*Logarithms of the ratios of observed to expected durations are shown. Values greater than zero indicate that observed durations exceeded those expected by chance. X refer to individuals that were not observed in associations with members of the indicated age-sex class. Age-sex class abbreviations as in Table I.

**Table III.** Observed durations and proportions of time spent in associations\*

Study site	Individual	Age-sex class	Observed durations (h) of associations with			Observed % of time in association with		
			AM	AF	SM	AM	AF	SM
Kutai	BC	AM	0.02	7.07	1.13	0.00	0.14	0.01
	LU	AM	0.04	23.04	0.00	0.01	0.17	0.00
	SI	AF	15.42	5.85	15.03	0.22	0.03	0.20
	SO	AF	0.89	0.69	16.18	0.01	0.00	0.10
	DU	SM	0.91	38.22	5.62	0.01	0.34	0.05
	LE	SM	4.02	33.66	9.40	0.04	0.09	0.04
Gunung Palung	HE	AM	0.07	0.00	0.00	0.00	0.00	0.00
	MA	AM	0.05	0.00	0.07	0.00	0.00	0.00
	KA	AF	0.64	0.00	1.48	0.01	0.00	0.02
	SU	AF	1.97	0.00	1.16	0.03	0.00	0.01
	CR	SM	0.81	1.50	0.00	0.01	0.01	0.00
	PE	SM	0.47	0.44	0.09	0.01	0.00	0.00

\*Mean values of association durations are shown. Sample sizes for associations are given in Table V. Age-sex class abbreviations as in Table I.

### The Nature of Encounters and Associations

#### Encounter sites

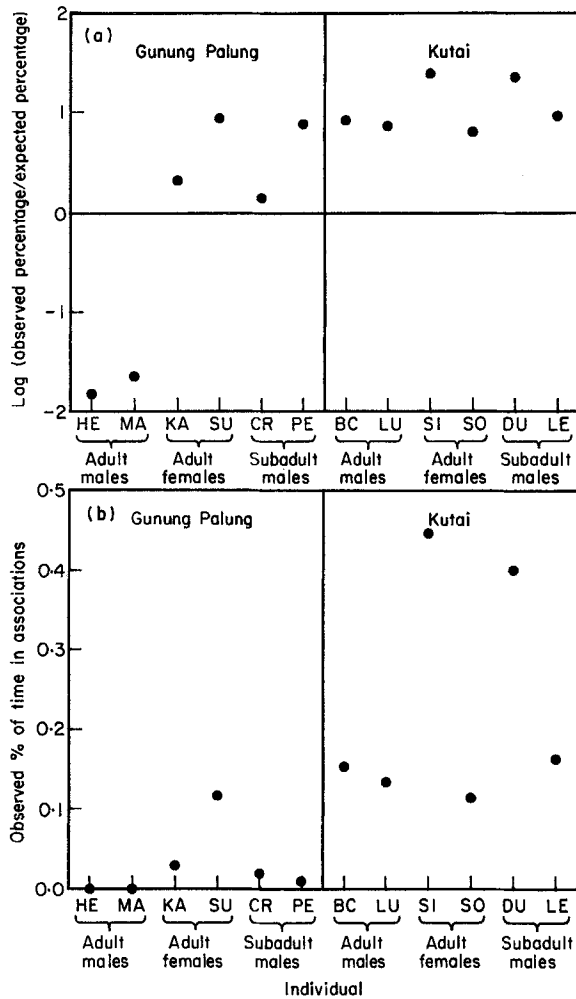
Orang-utans did not encounter each other randomly with respect to the location of food sources (Table IV). All animals encountered conspecifics more frequently near food sources than expected

on the basis of chance (Wilcoxon test,  $N=12$ ,  $P<0.01$ ).

#### Association types

While food served as a common meeting ground, orang-utans frequently interacted socially after a





**Figure 4.** Percentage of time spent in associations between orang-utans. (a) Observed and expected percentages. The null model specified by equation (3) in the text generated the expected percentages. The logarithms of the ratios of observed to expected percentages are shown. Values greater than zero indicate that observed percentages exceeded those expected by chance. (b) Observed percentages of time spent in associations with all orang-utans.

food encounter. Social associations occurred more often than passive associations (sign test,  $P < 0.05$ ,  $N = 12$ ; Table V). The age-sex class of animals affected their participation in social associations. Adult males engaged in higher proportions of aggressive interactions than adult females, and subadult males avoided conspecifics more frequently than did adult females.

The nature of associations differed between study sites in three ways (Table V). First, mating was not observed at Gunung Palung, but occurred frequently at the Kutai study site. Second, aggressive

interactions involving subadult males did not take place at Gunung Palung, but were not uncommon at Kutai. Third, orang-utans at the Kutai study site travelled and foraged together ('other' social associations) more frequently than animals at Gunung Palung.

#### *Durations as a function of association type*

The durations of associations varied as a function of type (Table VI). Passive associations at food trees and while travelling usually lasted about 1 h.

Table IV. Observed and expected proportions of encounters near food sources\*

Study site	Individual	Age-sex class	Observed proportion of encounters near food sources	Expected proportion of encounters near food sources
Kutai	BC	AM	0.76	0.07
	LU	AM	0.33	0.21
	SI	AF	0.52	0.08
	SO	AF	0.89	0.08
	DU	SM	0.52	0.16
	LE	SM	0.42	0.20
Gunung Palung	HE	AM	1.00	0.14
	MA	AM	1.00	0.23
	KA	AF	0.75	0.19
	SU	AF	0.56	0.18
	CR	SM	1.00	0.23
	PE	SM	0.75	0.22

\*Expected values for each animal were calculated by dividing the number of hours it was observed at food sources by the total number of observation hours. Age-sex class abbreviations as in Table I.

Associations in which animals behaved aggressively or avoided each other were also relatively short. In contrast, interactions involving mating or animals following each other ('other' associations) were prolonged, and generally lasted several hours. Observed durations showed significant heterogeneity among association types (two-way repeated-measures ANOVA,  $P < 0.001$ ), but not among age-sex classes of individuals ( $P > 0.50$ ). Small sample sizes precluded making pairwise comparisons of durations between association types. Visual inspection of these data, however, revealed that mating associations were longer than associations of all other types (Table VI).

## DISCUSSION

### The Null Models

Results of the preceding analyses show that in two populations of orang-utans the rates of encounters, durations of associations and proportions of time spent in associations were greater than those predicted by chance. An examination of the locations of encounters and nature of associations suggests two causal factors that account for these patterns. First, orang-utans encounter each other more often than expected by chance because of a bias towards meeting at food sources. Second, animals interacted socially during most associations. Social associations were longer than passive

aggregations in which animals travelled past each other or fed together without interacting. As a consequence, associations between orang-utans were longer than expected on the basis of the null model. The observed proportions of time orang-utans spend together are a logical by-product of these two factors.

### Comparisons between Study Sites

Despite these common patterns in encounters and associations, striking differences between the populations at Gunung Palung and Kutai existed. Orang-utans at Kutai encountered each other more frequently, engaged in longer associations, and spent a greater proportion of the time together than conspecifics at Gunung Palung. Differences between the study sites reflected three underlying sex differences in association patterns. First, in contrast to males at Kutai, adult males at Gunung Palung avoided others; these animals encountered and associated with conspecifics less frequently than expected by chance. Second, associations with adult females lasted longer at Kutai than Gunung Palung, and as a result, Kutai females spent more time with conspecifics than did Gunung Palung females. Third, subadult males at Kutai associated with other orang-utans more than subadult males at Gunung Palung.

These results appear to reveal a fundamental difference in association patterns between the

Table V. Participation in types of associations\*

Study site	Individual	Age-sex class*	N Associations	Passive			Social			Total		
				Food	Travel	Total	Aggressive	Mating	Avoidance		Other	
Kutai	BC	AM	17	47	0	47	24	6	18	6	54	
	LU	AM	4	0	0	0	100	0	0	0	100	
	SI	AF	65	18	18	36	0	22	0	42	64	
	SO	AF	9	78	0	78	0	11	0	11	22	
	DU	SM	25	0	4	4	28	12	48	8	96	
	LE	SM	12	0	0	0	33	8	42	17	100	
	Gunung Palung	HE	AM	1	0	0	0	100	0	0	0	100
		MA	AM	2	0	0	0	50	0	50	0	100
		KA	AF	12	17	17	34	0	0	17	8	25
		SU	AF	9	11	11	22	22	0	33	0	55
		CR	SM	3	33	0	33	0	0	66	0	66
		PE	SM	12	42	0	42	0	0	58	0	58

\*The percentages of associations are shown for each individual. Age-sex class abbreviations as in Table I.

**Table VI.** Durations of associations between orang-utans as a function of association type\*

Passive		Social			
Food	Travel	Aggressive	Mating	Avoidance	Other
1.2 ± 0.2 (43)	0.7 ± 0.2 (16)	4.2 ± 1.3 (22)	60.6 ± 18.6 (18)	1.0 ± 0.4 (35)	13.8 ± 2.7 (26)

\*Means ± SE (h) are shown with sample sizes below in parentheses. See text for further explanation of association types.

two populations. Nevertheless, the patterns of associations among orang-utans at Kutai during Rodman's (1973) earlier study resembled those of Gunung Palung more than those at the same site described here, which suggests that the differences may be related to a temporally varying factor. An examination of the nature of associations is again informative, and points to two major differences between the two populations: (1) mating was not observed at Gunung Palung, while mating occurred frequently at Kutai; and (2) subadult males at Gunung Palung were not involved in aggression, while at Kutai the subadults experienced aggression. These differences can be related to the reproductive conditions of the females at the two sites. Females at Gunung Palung were not sexually active because they carried small, clinging offspring during observations (J. C. Mitani, unpublished data). In contrast, Kutai females were followed by older, independent juveniles (Mitani 1985). Female SI at Kutai was often observed in prolonged intersexual associations during which mating occurred. Female SO mated, but did so infrequently; this animal gave birth during the penultimate month of observations, and with an 8-month gestation period (Martin 1981), was pregnant during most of the 16-month study. Aggressive interactions involving subadult males took place at Kutai largely in the context of mating competition for females (Mitani 1985).

Differences in the reproductive status of females may account for much of the variation in observed patterns of associations among populations of orang-utans (cf. Mitani 1985; teBoekhorst et al. 1990). Encounters occurred more often at Kutai than at Gunung Palung because males sought females for mating. Males followed females at Kutai primarily to mate, and associations between orang-utans lasted longer at Kutai compared to

those at Gunung Palung since interactions involving mating were, in general, significantly longer than all other associations. Finally, as a result of a common attraction to females, males at Kutai met each other more frequently than males at Gunung Palung; more aggression took place between males over females at Kutai than at Gunung Palung.

#### Comparisons with Other Studies

Orang-utans have been the subjects of several independent field studies (see review in Rodman 1988). What are the predicted patterns of encounters and associations between animals in these other studies? The null models employed here require information on the velocity of animals, their population density, and a measure of distance at which two animals are 'in association'. Using data from other field reports and a general form of the null models (see Waser 1987), it is possible to rank various studies with respect to predicted encounter rates, durations of associations and proportions of time in associations (Table VII). Three studies may be compared: Rodman's (1973, 1977) 15-month study at Kutai in 1970–1971; Galdikas' (1979, 1985) first 4 years of research at Tanjung Puting in Central Borneo; and Rijksen's (1978) 3-year study at Gunung Leuser in North Sumatra. Expected rates of encounters are lowest at Kutai, where density is intermediate and travel speeds are lowest; highest at Gunung Leuser, where densities are highest and travel speeds are intermediate; and intermediate at Tanjung Puting, where density is low, but travel speeds are high. The expected durations of associations are high at Kutai and low at Tanjung Puting and Gunung Leuser, while the expected proportions of time spent in associations are low at the two Bornean sites and high at the Sumatran study area. Based on these results, one a

**Table VII.** Expected rates of encounters, durations of associations and percentage time spent in associations among orang-utans at three sites\*

Study site	$p$ (animals/km <sup>2</sup> )	$v$ (km/day)	$r$ (km)	Encounters per day	Durations (days)	% Time in associations	Reference
Kutai	3	0.305	0.03	0.070	0.121	0.008	Rodman 1977
Tanjung Puting	2	0.792	0.03	0.121	0.047	0.006	Galdikas 1988
Gunung Leuser	5	0.640	0.03	0.244	0.058	0.014	Rijksen 1978

\*Expected rates, durations and percentages were calculated using the following formulas: encounters per day =  $2.546 pvr$ , durations =  $1.234 r/v$ , % time in associations =  $3.14 pr^2$  (Waser 1987).  $r = 30$  m, the distance at which associations between animals are defined.

priori prediction is that the orang-utans of Gunung Leuser would be more 'social' than the animals at Tanjung Puting and those during the earlier study at Kutai. Seen in this light, it is perhaps not surprising that Rijksen (1978), as well as Sugardjito and co-workers (Sugardjito et al. 1987) described more associations between orang-utans in Sumatra than either Galdikas (1985) or Rodman (1973), who worked at two areas in Borneo. The remaining information needed to assess whether observed rates of encounters, durations of associations and proportions of time in associations were higher or lower than those predicted from the null models are not available from published reports.

Galdikas (1985) has noted that independent young orang-utans, particularly nulliparous females, are more sociable than others, and these animals are not part of the analysis presented here. Thus, it may be argued that we have overlooked some aspects of association patterns among orang-utans. For example, one might expect young animals to be gregarious given the life-history characteristics of orang-utans; young dispersing individuals may associate with conspecifics frequently to learn the locations of food sources in new environments. Apart from these considerations, the preceding analyses make clear that even for young orang-utans, it is important to evaluate the observed patterns of associations of orang-utans against a null expectation rather than to simply conclude that individuals are more or less sociable than others.

### Concluding Comments

Results of the present study indicate that encounters and associations between orang-utans

in two populations occur more frequently than expected by chance. The locations of encounters and the nature of associations suggest that these non-random patterns are attributable to the attraction of orang-utans to common resources, either to food trees, or among males, to potential mates. Associations often include social behaviour, but compared with most diurnal primates, which live in long-lasting groups, associations among orang-utans are ephemeral.

Recent research has suggested that the higher intellectual abilities of primates are linked to social complexity (Cheney et al. 1986). Consequently, it may be puzzling that an animal with the well developed intelligence of an orang-utan lives in what appears to be a relatively simple social system. Field research of other 'solitary' primates reveals clear patterns of associations among individuals (e.g. Clark 1985), and a more complex social network linking individual orang-utans may emerge through longer study. If true, a 'social system' will be detected in which some animals interact regularly over periods spanning several years. The Tanjung Puting study (Galdikas 1979, 1985, 1988), now in its twenty-first year, promises to reveal whether long-term social relationships among orang-utans exist. Until these data are forthcoming, however, the present picture of the social life of orang-utans will continue to contradict the proposed functional relationship between social complexity and intelligence.

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## REFERENCES

- Cheney, D., Seyfarth, R. & Smuts, B. 1986. Social relationships and social cognition in nonhuman primates. *Science*, **234**, 1361–1366.
- Clark, A. 1985. Sociality in a nocturnal 'solitary' primate: *Galago crassicaudatus*. *Int. J. Primatol.*, **6**, 581–600.
- Galdikas, B. 1979. Orangutan adaptation at Tanjung Puting Reserve: mating and ecology. In: *The Great Apes* (Ed. by D. Hamburg & E. McCown), pp. 194–233. Menlo Park, California: Benjamin Cummings.
- Galdikas, B. 1985. Orangutan sociality at Tanjung Puting. *Am. J. Primatol.*, **9**, 101–119.
- Galdikas, B. 1988. Orangutan diet, range and activity at Tanjung Puting, Central Borneo. *Int. J. Primatol.*, **9**, 1–31.
- Horr, D. 1975. The Borneo orang-utan: population structure and dynamics in relationship to ecology and reproductive strategy. In: *Primate Behaviour. Vol. 4*. (Ed. by L. Rosenblum), pp. 307–323. New York: Academic Press.
- Lee, E. 1980. *Statistical Methods for Survival Data Analysis*. Belmont, California: Lifetime Learning Publications.
- MacKinnon, J. 1971. The orang-utan in Sabah today. *Oryx*, **11**, 141–191.
- MacKinnon, J. 1974. The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Anim. Behav.*, **22**, 3–74.
- Martin, D. 1981. Breeding great apes in captivity. In: *Reproductive Biology of the Great Apes* (Ed. by C. Graham), pp. 343–373. New York: Academic Press.
- Mitani, J. 1985. Mating behaviour of male orangutans in the Kutai Game Reserve, Indonesia. *Anim. Behav.*, **33**, 391–402.
- Rijksen, H. 1978. *A Field Study on Sumatran Orangutans (Pongo pygmaeus abelii Lesson, 1827)*. Wageningen: H. Veenman and Zonen.
- Rodman, P. 1973. Population composition and adaptive organisation among orangutans of the Kutai Reserve. In: *Comparative Ecology and Behaviour of Primates* (Ed. by R. Michael & J. Crook), pp. 171–209. New York: Academic Press.
- Rodman, P. 1977. Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In: *Primate Ecology* (Ed. by T. H. Clutton-Brock), pp. 384–414. London: Academic Press.
- Rodman, P. 1988. Diversity and consistency in ecology and behaviour. In: *The Orangutan* (Ed. by J. Schwarz), pp. 31–51. Oxford: Oxford University Press.
- Schaller, G. 1961. The orangutan in Sarawak. *Zoologica*, **46**, 73–82.
- Schaller, G. 1965. Behavioural comparisons of the apes. In: *Primate Behaviour* (Ed. by I. DeVore), pp. 474–483. New York: Holt, Rinehart, Winston.
- Schurmann, C. & van Hooff, J. 1986. Reproductive strategies of the orang-utan: new data and a reconsideration of the existing sociosexual models. *Int. J. Primatol.*, **7**, 265–288.
- Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R. & Struhsaker, T. 1987. *Primate Societies*. Chicago: University of Chicago Press.
- Sokal, R. & Rohlf, F. J. 1981. *Biometry*. San Francisco: W. H. Freeman.
- Sugardjito, J., teBoekhorst, I. & van Hooff, J. 1987. Ecological constraints on the grouping of wild orangutans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra. *Int. J. Primatol.*, **8**, 17–42.
- teBoekhorst, I., Schurmann, C. & Sugardjito, J. 1990. Residential status and seasonal movements of wild orang-utans in the Gunung Leuser Reserve (Sumatera, Indonesia). *Anim. Behav.*, **39**, 1098–1109.
- Waser, P. 1982. Primate polyspecific associations: do they occur by chance? *Anim. Behav.*, **30**, 1–8.
- Waser, P. 1984. Chance and mixed-species associations. *Behav. Ecol. Sociobiol.*, **15**, 197–202.
- Waser, P. 1987. Interactions among primate species. In: *Primate Societies* (Ed. by B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker), pp. 210–226. Chicago: University of Chicago Press.
- Whitesides, G. 1989. Interspecific associations of Diana monkeys, *Cercopithecus diana*, in Sierra Leone, West Africa: biological significance or chance? *Anim. Behav.*, **37**, 760–776.
- Wilson, E. O. 1975. *Sociobiology*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.