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Circadian long call distribution in wild orangutans

Distribution circadienne des cris longs (long calls) chez l'orang-outan en milieu naturel

MARINA DAVILA ROSS AND THOMAS GEISSMANN

Résumés

We present first data on circadian long call distribution of wild orangutans in Northwest Borneo. Data were collected during two months in Batang Ai National Park. A total of 151 male long calls were heard, exhibiting a bimodal distribution pattern with peaks at 05:00-06:00 hours and 18:00-19:00 hours. An earlier study found pronounced differences between the calling rates of Bornean orangutans, which showed an almost unimodal call distribution with its peak at mid-morning, and those of Sumatran orangutans, which showed a bimodal call distribution with a distinct calling peak at predawn and a more moderate peak near dusk (MacKinnon 1974). Our findings from Batang Ai resemble more closely the pattern reported for Sumatra than those reported for other Bornean localities and, therefore, contradict earlier reports suggesting a Sumatra-Borneo dichotomy in orangutan call distribution. In addition, orangutans in Batang Ai were heard to regularly emit long calls throughout the night. This behaviour is unusual for a diurnal species.

Distribution circadienne des cris longs (long calls) chez l'orang-outan en milieu naturel

Nous présentons les premières données sur la distribution circadienne des cris longs (*long calls*) chez les mâles orangs-outans vivant en milieu naturel au nord-ouest de Bornéo. Les données ont été récoltées lors d'une étude de terrain de deux mois au Parc National de Batang Ai. Les 151 cris longs entendus montraient une distribution bimodale, caractérisée par des pics à 05:00-06:00 et 18:00-19:00 heures. Une étude précédente avait révélé des différences profondes entre les taux de cris longs des orangs-outans de Bornéo et de Sumatra. Alors que la distribution des cris longs à Bornéo était presque unimodale et montrait un pic en milieu d'avant-midi, la distribution à Sumatra était bimodale et montrait un pic distinct avant l'aube et un second pic plus modéré au crépuscule (MacKinnon 1974). Nos résultats à Batang Ai ressemblent davantage au schéma rapporté précédemment à Sumatra qu'à ceux rapportés pour les autres localités de la région de Bornéo. En conséquence, ils contredisent les résultats précédents qui suggèrent une dichotomie Sumatra-Bornéo dans la distribution des cris longs chez l'orang-outan. De plus, nous avons noté que les orangs-outans de Batang Ai émettent des cris longs pendant la nuit, comportement inhabituel pour une espèce diurne.

Entrées d'index

Keywords: orangutans, *Pongo* spp., long call, calling time, circadian rhythms, interspecific competition, population differences

Mots-clés: orangs-outans, *Pongo* spp., cris longs, distribution temporelle des cris, rythmes circadiens, compétition interspécifique, différences entre populations

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Texte intégral

1 Introduction

Animals that produce long-distance acoustic signals often emit these at specific times during their active period (e.g. Chivers 1973; Dabelsteen and Mathevon 2002; Geissmann and Mutschler 2006; Keast 1994; MacKinnon 1974; Staicer et al. 1996). Many primate species, for instance, produce so called loud calls (excluding alarm calls) with a circadian distribution typically peaking near the beginning and, less often, near the end of their periods of activity (reviewed by Seyfarth 1987). Various functions have been proposed for primate loud calls, including territorial advertisement, maintenance of inter-group spacing and intra-group cohesion, and mate-attraction (reviewed by Hohmann and Fruth 1995). Loud calls in many primate species share traits such as being loud, stereotypical, and mainly produced by high ranking males (Geissmann 2000; Waser 1982). At least in Old World monkeys and apes (but possibly in other primates as well), loud calls are believed to be phylogenetically homologous characteristics (Geissmann 2000).

Of all orangutan (genus Pongo) vocalisations, the long call is the loudest, with its idiosyncratic acoustic traits carried for 300 meters and more (Lameira and Wich 2008), and one of the most frequently uttered (Galdikas 1983; MacKinnon 1971, 1974; Mitani 1985). They are only made by orangutan males and mainly by flanged males (Delgado et al. 2009; Galdikas and Insley 1988; MacKinnon 1971; Mitani 1985). Long calls may last up to three minutes (MacKinnon 1971; Davila Ross and Geissmann 2007).

It has been proposed that orangutan long calls may have evolved as part of the male-to-male competition over resources, such as females (e.g. Galdikas 1983; MacKinnon 1974; Mitani 1985). Several functions have been suggested for the long calls, including keeping males apart over long distances (e.g. Galdikas 1983; MacKinnon 1971, 1974; Mitani 1985; Rijksen 1978), attracting sexually receptive females over far distances (Galdikas 1983; Horr 1972, 1975; MacKinnon 1969; Rodman 1973), and signalling nulliparous females to initiate mating with flanged males (Galdikas 1983, 1995; Schürmann 1982).

The circadian distribution of orangutan long calls has first been systematically monitored by MacKinnon (1973, 1974, p. 35) during an etho-ecological study carried out at two field sites (Ulu Segama, Northeast Borneo, and Ranun, Sumatra, respectively). He found marked differences between his study sites: Bornean orangutans exhibited an almost unimodal call distribution with its peak at mid-morning (09:00-10:00 hours), whereas Sumatran orangutans showed a bimodal call distribution with a distinct calling preference at predawn (04:00-05:00 hours) and a more moderate peak near dusk (17:00-18:00 hours). MacKinnon (1974) assumed that these two completely different calling patterns were typical for orangutans of the respective islands, and that orangutans compete acoustically with several other animals for calling time. Specifically, MacKinnon (1974) presented the following explanation for these differences in calling patterns, which we term the “calling time competition hypothesis”. The hypothesis claims that the lower primate density in Borneo than in Sumatra and the absence of the particularly loud and vocal siamangs and Thomas’s leaf monkeys in Borneo result in different competition levels for a calling time window between the islands. Whereas Bornean orangutans may call at their preferred time (according to MacKinnon, it is mid-morning), Sumatran orangutans are forced to call at suboptimal times in the periphery of their active period (predawn, near-dusk).

In accordance with this hypothesis, one should expect that orangutans of other localities on Borneo would also exhibit a unimodal call distribution with a clear morning peak rather than a bimodal call distribution. In order to test this prediction, we collected the first data on circadian call distribution of orangutans in Northwest Borneo. According to Groves (2001), orangutans of this area are identified as *Pongo pygmaeus pygmaeus*. In order to facilitate comparisons, we compile published data on orangutan calling distribution that have been collected since MacKinnon’s pioneering study.

2 Methods

The occurrences of orangutan long calls were recorded by MDR at all hours of the day and night (318 hours total) from 6th of August to 1st ofOctober 2001, in the Batang Ai National Park, Sarawak, Malaysia (Figure 1). Hereby, date, time, location, direction, and distance from the observer, was noted for all calls, as well as the weather condition. The distribution of data collection time is shown in Table 1.

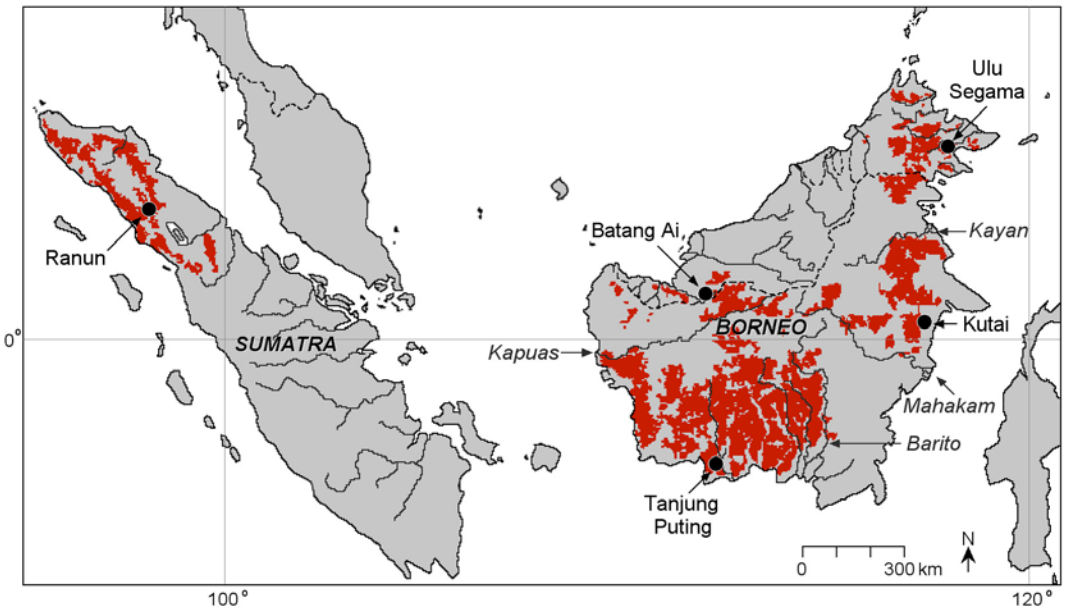

Figure 1

Orangutan long call study sites (dots) on Sumatra and Borneo, with current orangutan distribution (red shaded areas) and main rivers (map adapted from Rijksen and Meijaard 1999).

Sites d'étude des cris longs d'orangs-outans (points) à Sumatra et Bornéo, ainsi que distribution actuelle des orangs-outans (zones rouge sombre) et des principales rivières (carte adaptée d'après Rijksen et Meijaard 1999).

Table I

Distribution of long call monitoring time in Batang Ai

Distribution des durées d'observation des cris longs à Batang Ai

Time of day and night *Heures (jour et nuit)*	Number of calls *Nombre de cris*	Hours of survey *Durée observation*	Calls per survey hour *Fréquence horaire*
00:00-01:00	0	4.00	0.000
01:00-02:00	2	4.17	0.480
02:00-03:00	1	5.00	0.200
03:00-04:00	1	4.00	0.250
04:00-05:00	4	5.00	0.800
05:00-06:00	6	6.67	0.900
06:00-07:00	9	14.83	0.607
07:00-08:00	16	22.00	0.727
08:00-09:00	8	24.33	0.329
09:00-10:00	8	23.00	0.348
10:00-11:00	4	20.50	0.195
11:00-12:00	7	19.83	0.353
12:00-13:00	9	20.25	0.444
13:00-14:00	10	18.75	0.533
14:00-15:00	6	19.00	0.316
15:00-16:00	9	18.00	0.500
16:00-17:00	13	21.17	0.614
17:00-18:00	15	16.25	0.923
18:00-19:00	11	11.33	0.971
19:00-20:00	4	10.50	0.381
20:00-21:00	2	10.50	0.190
21:00-22:00	4	9.00	0.444
22:00-23:00	1	5.75	0.174
23:00-00:00	1	4.25	0.235
Total	151	318.08	

The Batang Ai National Park(24,040 ha) is mainly a dipterocarp primary forest located in the southern portion of the state Sarawak, Malaysia, close to the Lanjak-Entimau Wildlife Sanctuary (Sarawak) and the Bentuang Karimun National Park (West Kalimantan) (Meredith 1995). It has been reported to support the highest orangutan density in the state (Bennett 1998).

Within the park, Kota Enggam (N 01°18.156-201', E 112°05.883-910', elevation 290-348 m; N 01°18.086-155', E 112°06.327-516', elevation 326-386 m), Bukit Spantu (N 01°14.518-996', E 112°05.500-769', elevation 397-525 m), and Nanga Rirong (N 01°19.036-195', E 112°05.097-916', elevation 320-440 m) were chosen as study locations because of their strong presence of orangutans and absence of loud rivers nearby which might have reduced audibility of orangutan calls.

Astronomically defined average sunrise time was at 06:27 hours (standard deviation sd = 4 minutes), sunset was at 18:34 hours (sd = 6 minutes).

For a direct comparison with orangutan long call temporal distributions collected in previous studies, Batang Ai data on orangutans were represented by the relative number of calls per day (Figure 2a).

3 Results

During the field study in Batang Ai, an average of 4.3 calls per day and an average of 0.45 calls per survey hour were heard (N = 151 long calls). The circadian distribution of the calls revealed a bimodal pattern (Figure 2a). Call rates peaked from 05:00 to 06:00 hours and from 18:00 to 19:00 hours. In order to facilitate comparison with published data of other studies, Figure 2 shows the circadian distribution of the absolute number of calls heard. If we divide the number of calls in each interval by the amount of time spent surveying this time slot (in order to correct for the uneven survey time distribution), the distribution pattern for Batang Ai remains the same. No long calls were heard between 00:00 and 01:00 hours. Batang Ai hourly call rates of the 24-hour cycle were not found to be significantly different using the chi-square test (chi square = 31.04; df = 23, $p > 0.05$). However, this may be the result of the small number of calls per hour. If the compared data sets are condensed to blocks of 4 hours each, the call distribution differs significantly from a random distribution (chi square = 11.82; df = 5, $p = 0.0363$).

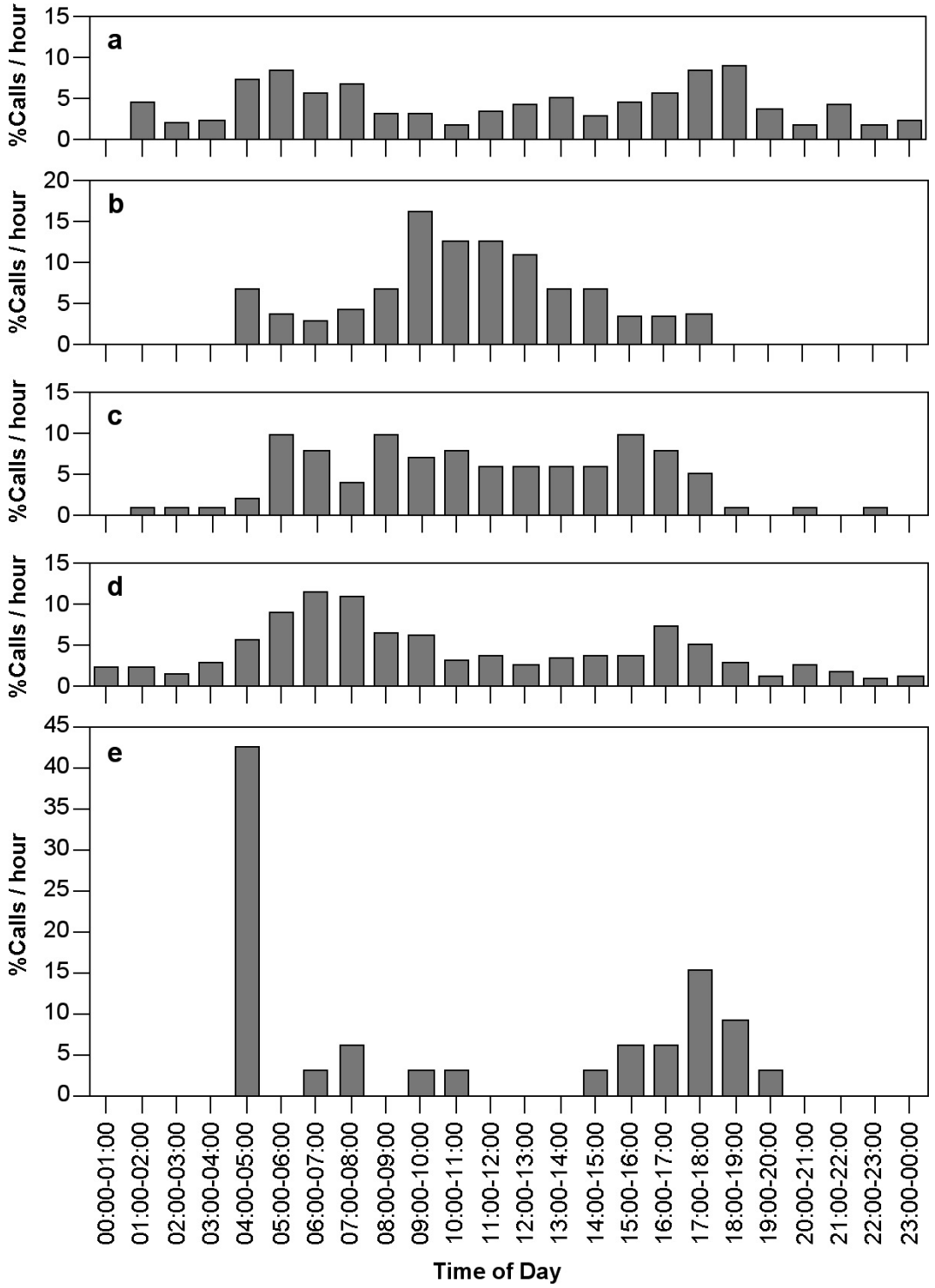

Figure 2

Circadian orangutan long call distribution of (a) Northwest (present study; *N*=151), (b) Northeast (MacKinnon 1974; *N*=240), (c) East (Mitani 1985; *N*=157), and (d) Southwest Borneo (Galdikas 1983; *N*=628) and (e) Sumatra (MacKinnon 1974; *N*=33). Original values for (b), (c), and (e) were not published and were derived for this figure by measuring column lengths of the circadian long call histograms represented in the respective publications.

Distribution circadienne des cris longs d'orangs-outans dans les zones géographiquement isolées du (a) nord-ouest (présente étude; N=151), (b) nord-est (MacKinnon 1974; N=240), (c) est (Mitani 1985; N=157) et (d) sud-ouest de Bornéo (Galdikas 1983; N=628), et à (e) Sumatra (MacKinnon 1974; N=33). Les valeurs originales pour (b), (c) et (e) ne sont pas publiées et ont donc dû être dérivées pour cette figure, en mesurant la longueur des colonnes sur les histogrammes de cris longs représentés dans les publications respectives.

In Batang Ai, orangutans regularly emitted nocturnal long calls, and calls appeared to be more evenly distributed during all hours of the day and the night than previously reported from other populations (Ulu Segama in Northeast Borneo: MacKinnon 1974; Kutai in East Borneo: Mitani 1985; Tanjung Puting in Southwest Borneo: Galdikas 1983; Ranun in Sumatra: MacKinnon 1974) (Figure 2).

Numerous calls of Batang Ai were heard from close proximity but coming from different directions within short time frames. This was particularly the case for the long calls emitted from the orangutan sleeping nests at night, i.e. calls were heard to come from four different directions no more than 100 meters away from the observer's tent, suggesting that there were four adult males in a relatively small area.

4 Discussion

The circadian distribution of orangutan long calls has been described from five localities: Northwest Borneo (Batang Ai: present study), Northeast Borneo (Ulu Segama: MacKinnon 1974), East Borneo (Kutai: Mitani 1985), Southwest Borneo (Tanjung Puting: Galdikas 1983), and Sumatra (Ranun: MacKinnon 1974) (Figure 2). A comparison of the circadian call rate contour across localities does not support a Sumatra-Borneo dichotomy: Whereas Northwest and Southwest Bornean data resemble Sumatran data in exhibiting two distinct peaks in calling activity (one at predawn and one at dusk), the pattern of Northeast Borneo shows only one distinct peak (at mid-morning), and the call distribution of East Borneo has an intermediate shape. This suggests that (1) MacKinnon's (1974) postulation on differences between Bornean and Sumatran long call distributions needed data based on more than his two study locations and that (2) the "calling time competition hypothesis" (specifically, the absence of siamangs and Thomas's leaf monkeys from Borneo) cannot explain intra-island differences and inter-island commonalities in the orangutan call time preferences. To our knowledge, loud vocalising species of gibbons, leaf-monkeys, pheasants, or hornbills, that potentially represent vocal competitors to orangutans, are common at each of these sites.

In Batang Ai, orangutan long calls are emitted within virtually every hour of the night (Figure 2, Table 1). Nocturnal calling, albeit at lower rates, has also been reported from two other Bornean localities (Galdikas 1983; Mitani 1985), whereas the evidence for nocturnal calling of Sumatran orangutans is limited to predawn (MacKinnon 1974). However, night calls may be underrepresented in these studies since some researchers might have collected vocal data almost entirely throughout the diurnal periods.

Factors other than inter-species competition for the calling time may play a role in reported local differences of orangutan calling time. These may include environmental variables (i.e. resource availability and abundance), social influences (i.e. male-male competition), demographics, and methodologies.

Orangutan long calls vary in rates from less than once a month (Meredith 1995) to 1.5 calls per day (Galdikas 1983). With 4.3 calls per day, the vocal rate of Batang Ai is 287% higher than the highest measured values reported so far. This rate was derived by a simple division of the total of calls heard and the total of full days spent in the forest, identical to the calculation carried out for the

second highest call rate reported prior to our study (Galdikas 1983). As an alternative method to calculate the daily calling rate, we summed up the calling rates (calls per hour) for every hour of the day and night. Carrying out the latter procedure, which appeared to be scientifically more correct to us, we determined 5.6 calls per day. However, previous authors may have recorded lesser numbers of calls because they concentrated more on behavioural contexts rather than on monitoring sounds (Galdikas 1983; MacKinnon 1974; Mitani 1985).

Although orangutan density in Batang Ai was not quantified, the high calling rate of orangutans, the numerous orangutan sightings, their visible nests, and evidence that sleeping sites of adult males were sometimes very close to one another suggest a high orangutan population density in this Northwest Bornean region. It is unknown, however, whether the Batang Ai population density remained high throughout the year. During the time of the field study, it may have been influenced by the profusion of ripe empili (*Lithocarpus* spp.) fruit, which appear to play an important part in the diet of Batang Ai orangutans. Easy access to food (as during a must-fruiting event), but also habitat destruction due to logging, among other factors, may facilitate orangutan accumulation or lead to overcrowding and, therefore, necessitate an elevated calling rate (Delgado and van Schaik 2000; MacKinnon 1971). In addition, calling rates also tend to increase during periods of male contests and reproductive activity (Utami and Mitra Setia 1995).

There may be considerable seasonal variation in calling by orangutans in the wild that cannot be accounted by a study of short duration. A long-term study combining ethological data with those on the circadian long call distribution would be desirable.

Furthermore, our observation that orangutans call almost consistently throughout all hours of the night is not in accordance with the behaviour of diurnal primates. The reasons for nocturnal calling in orangutans are unknown. This phenomenon would seem to be of high interest and significance in future research on this diurnal and socially flexible species.

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