Title of paper: New evidence from observations of progressions of mandrills (*Mandrillus sphinx*): a multilevel or non-nested society?

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Abstract

African papionins are well known for the diversity of their social systems, ranging from multilevel societies based on the one-male-multifemale units (OMUs), to non-nested societies. However, the nature of *Mandrillus* societies is still unclear due to difficult observational conditions in the dense forests of central Africa. To discuss characteristics of mandrill societies and their social systems, I analysed the age-sex compositions, behaviours, and progression patterns of their horde/subgroups using video images of them crossing open places. The progressions were very cohesive, and the very large aggregations (169–442 individuals) had only 3–6 adult males (1.4–1.8% of all individuals) and 11–32 subadult males (6.5–7.2%). No herding behaviours were observed in the males and most of small clusters within the progressions were not analogous to OMUs of a multilevel society, but consisted of only adult females and immatures. Their progressions under alerting circumstances showed patterns similar to those in a non-nested social system: females with dependent infants concentrated toward the rear part, while adult and subadult males did so toward the front. These results suggest that cohesive aggregations and female-biased sex ratio are common characteristics of the mandrill species. Mandrills might form female-bonded and non-nested societies, although their fission-fusion dynamics may be different from those typical in 'savannah baboons'.

Keywords

Mandrill, Social system, Age-sex composition, Progression, Moukalaba-Doudou

Introduction

Primates exhibit tremendous diversity in their social systems. Although many researchers have discussed the evolutionary history of social systems for more than five decades, it is still one of the central arguments in primatology (Crook and Gartlan 1966; Itani 1977; Kappeler and van Schaik 2002; Shultz et al. 2011), specifically in relation to the African papionins (subtribe Papionina). Their social systems vary among species (Swedell 2011). Hamadryas baboons (*Papio hamadryas*) and geladas (*Theropithecus gelada*) form multilevel societies, in which a number of one-male-multifemale units (OMUs) are nested within a social unit termed 'band'; other *Papio* species, often referred to as the 'savannah baboons' (*P. anubis*, *cynocephalus* and *ursinus*), live in non-nested societies, in which multiple females and typically multiple males form a cohesive female-bonded group. This variety has been explained as reflections of past selection pressures on different populations. For example, Henzi and Barrett (2003) hypothesized that hamadryas baboons developed the multilevel society for adaptations to both the high predation risk and the scarce resources and shelters, whilst savannah baboons in the less harsh area remained non-nested. Nevertheless, most of these discussions have been focused only on the species in the arid areas, and mandrills (*Mandrillus sphinx*) nor drills (*M. leucophaeus*) have not been included in these arguments. It is essential to explore the nature of *Mandrillus* societies, though they are not the sister taxon of *Papio*-*Theropithecus* but of eye-lid mangabeys (*Cercocebus* spp.) (Harris 2000), to develop a comprehensive understanding of the social evolution of African papionins.

Their large home range (81 km^2 by MCP method based on a 6-year-study, White et al. 2010) and poor visibility in the dense rainforest make it difficult for field researchers to observe the behaviours of wild *Mandrillus* populations and the nature of their societies is still unclear. Besides, there are some conflicting arguments about their social systems. Their large aggregations, termed 'hordes', have originally been considered as multilevel societies and fully-matured males were believed to be leaders of each OMU, mainly because of the various sizes of aggregations, from several tens to hundreds, and frequent fission-fusion (mandrills, Hoshino et al. 1984; Rogers et al. 1996; drills, Gartlan 1970). More recently, Abernethy et al. (2002) reported a considerably different view of mandrill society. They argued that mandrills form a stable social unit and rarely divide into small subgroups. In addition, the hordes had only 1–17 adult males and the number of mature males in the hordes fluctuated seasonally according to the number of females with sexual tumescence. Based on the results, they hypothesized that mandrills live in a female-led society, where males are not resident members but migrators, who enter hordes at the onset of seasonal cycles in the females. Studies on vocal communications (Kudo 1987) and social network analysis of a small captive group of 19 individuals (Bret et al. 2013) also suggested the important role of females on group cohesion. In this paper, the term 'horde' is used for a large group of mandrills around which any other group is not observed nor heard, 'subgroup' is used for a group that has evidently divided from a horde, and 'aggregation' includes both 'horde' and 'subgroup'.

Several key differences in their behaviours between multilevel and non-nested society allow us to consider *Mandrillus* social system. On the one hand, in OMU-based multilevel societies, leader males herd their females by exhibiting aggressions, like neck bites, and through soliciting behaviours, such as looking back and gazing (Kummer 1968; Mori 1979; Swedell and Schreier 2009). As a consequence, members of the same OMU, which consists of 2–28 individuals (Grüter and Zinner 2004), always stay together and rarely intermingle with other OMUs, and no females are found outside the OMUs (Kummer 1968; Snyder-Mackler et al. 2012). On the other hand, based on studies on non-nested societies of the savannah baboons, they were found to travel in consistent patterns of progression. Subadult males tend to be in the front part of the march (Rhine et al. 1979). Adult males, which are the most robust animals to external threats, tend to concentrate toward the side of potentially danger, such as the front part when entering open waterholes (Rhine 1975; Rhine and Tilson 1987). On the contrary, females with a dependant infant, which are the most sensitive to threats, tend to remain in the rear part of the march when they enter the waterholes (Rhine 1975). Additionally, related females form the core of their group, and strong bonds between males and females do not always exist (Altmann 1980; Silk et al. 2006).

Thus, if mandrills form an OMU-based multilevel social system, 1) adult and subadult males may display herding behaviours toward females, 2) several small OMU-like clusters of 2 to 30 individuals, which have one or two males and several females, could be found within one aggregation, and 3) all females would be near at least one male. On the contrary, if mandrills live in a non-nested society, 1) adult and subadult males may occur mainly in the front part of the progressions, especially when they are on the alert, 2) females with infants may aggregate in the rear part when they proceed with caution, and 3) small clusters without males may be observed. The aim of this study is to examine these predictions by observations on their progressions.

Methods

I conducted the study over 25 months, between August 2009 and September 2013, in the northeastern part (approximately 280 km²) of the Moukalaba-Doudou National Park, Gabon. The annual rainfall in the study area was 1,583–2,163 mm (2002–2006, Takenoshita et al. 2008), and the minimum and maximum temperatures were 19.4–25.0 °C and 27.6–34.1 °C (2006–2009, PROCOBHA researchers team, unpublished data). There are two distinct seasons in this region, a rainy season from October to April, and a dry season from May to September. A more detailed description of this site has been provided in Takenoshita et al. (2008).

I searched for mandrill hordes and followed them for as long a time as possible. Whenever a horde came near an open place, such as a logging road or a river, I tried to record the progression of all members crossing the area using a video camera. When the horde divided into several subgroups, one of them was focused for the recording. In order to ensure that all the members of one horde or subgroup were recorded, I confirmed the absence of a preceding or remnant individual by auditory information and observation from the beginning of the passage to at least 5 min after the last individual had crossed. After the recording, I also confirmed the absence of other traces within 100 m of each side from the crossing point.

I carried out four types of analysis using the video images. First, I categorized each animal into 6 age-sex classes as shown in Table 1. Females with sexual swellings could not be counted precisely because of the long distances from the focal aggregations. When the individuals repassed reversely, I counted them and subtracted their number from that of the crossed individuals to ensure a precise count. Pubescent males (PMs) and adult females that were not holding infants (non-FIs) were indistinguishable from each other until their genital parts were displayed, because their body sizes and morphological features are very similar (Abernethy et al. 2002). Therefore, these unidentified individuals were classified into the two classes in a ratio of the identified ones. In Case 1, however, it was impossible to sort them since none had clearly displayed its genital parts. Socionomic sex ratio (SSR, the number of adult females per adult and subadult males) was also calculated in each case, other than in Case 1. Secondly, behaviours related to herding, in other words, *aggression* (bite, grab, approach, and bark), *look-back* (look at another behind the performer), and *facing* (gaze at each other), were recorded with their directions and the age-sex class of the individuals involved. Further, in order to evaluate degree of alertness against human observers in each case, I noted the number of individuals looking at the observers. I also noted appearance time from the bushes and arrival time at the other side of the open place for each individual to an accuracy of one-tenth of a second, and calculated their crossing speeds. When the vigilance levels of individuals are high, their crossing speeds should be fast to avoid potential risk. Therefore, I compared them among cases using the Mood’s median test with the

Bonferroni correction. Lastly, randomization tests of 100,000 iterations were performed by case in the progression orders, in order to evaluate the concentration of animals belonging to several age-sex classes towards the fore or rear of a progression. Medians of the order in adult males (mAM), subadult males (mSM), and females holding an infant (mFI) were used for the test statistic. Then I divided each progression into clusters when an inter-arrival time between individuals was more than 10 s, and the age-sex class compositions of them were noted only when they contained 30 or less individuals to facilitate their comparison with the OMUs. All statistical tests in this paper were two-tailed and conducted using R 3.0.0 software (R Core Team 2013). A p value of 0.05 or lower was considered significant and that of 0.08 or lower was treated as a tendency towards significance.

Results

Description of each passage case

I searched for mandrill hordes for 432 days, and located them 47 times. I also observed 11 solitary males and one bachelor group of two adult males. I was able to record full members of a mandrill large aggregation three times in total. I could not confirm if they were the same ones, because I did not find any identical individual among cases. I have described the circumstances in each case below.

Case 1 (3 May 2010, 11:02–11:06, Online Resource 1): A field assistant and I found a horde and followed it from 10:09. It fissioned into several subgroups and, after a few minutes, crossed fallen trees over a river approximately 10 m wide. We focused on one subgroup and recorded it during the crossing. Distance between the focal subgroup and us was approximately 50 m and it was at least 300 m apart from the other subgroups. A total of 169 individuals passed on the same tree during the 4 min 20 s period. About 10 min after they arrived at the other bank, they fused with the other subgroups, which had also apparently gone over other fallen trees.

Case 2 (27 November 2011, 9:47–9:51, Online Resource 2): When two assistants and I walked on a logging road that was 2 m wide, we heard female mandrills' long-distant calls in the bush at a distance of approximately 20 m. We receded approximately 10 m and waited in hiding for 5 minutes. Then a horde began to cross the road. The distance between the horde and us was approximately 30 m. A total of 352 individuals passed during the 3 min 50 s period, and two of them repassed once reversely. Thus, the total number of members in the horde was 350. We did not hear any other noise or call from outside the focal horde. Width of the progression was about 10 m.

Case 3 (25 October 2012, 13:00–13:11): I was driving a buggy car with an assistant on a logging road and heard long-distance calls and alert calls of mandrills in the bush from one side of the road. Then three individuals (the age-sex class could not be identified) crossed the road and video recording was started from the fourth individual crossing. We knew this was a subgroup because we heard other individuals at a distance of at least 200–300 m away from the focal subgroup. The crossing was at a distance of approximately 30 m away from us. A total of 451 members passed during the 11 min 7 s period, and nine repassed once reversely. Thus, the total number in the subgroup was 442. Width of the progression was approximately 5 m.

Age-sex class composition

Horde/subgroup sizes and age-sex class compositions of each case with those of mandrills in other sites and other terrestrial African papionin species are shown in Table 2. All three aggregations, which included two subgroups, contained at least 169–442 individuals. They were larger than the bands and groups of other African papionins. In the aggregations that I observed, adult males accounted for only 1.4–1.8%, which were much lower than the other

African papionins, and subadult males for 6.5–7.2%. Then the SSR was 4.45 and 4.51 in Case 2 and 3, respectively. These tended to be higher when compared with the other species.

Herding behaviour

I observed 3 instances of grab and 11 of look-backs, but no facing was observed. Two out of the three grabs were by adult or subadult males towards juveniles who overtook them, and 8 out of the 11 look-backs were performed by adult females towards juveniles or their infants. None of these behaviours was observed between adult or subadult males and adult females.

Alertness during crossing

Only 12 (7.1%) individuals gazed at the observers during the passage in Case 1, while 141 (40.3%) and 349 (79.5%) animals did so in Case 2 and 3, respectively.

The crossing speeds were significantly higher in Case 2 (median [min–max] = 3.33 [0.22–6.67] m/sec) than in Case 3 (1.33 [0.16–5.00] m/sec) and Case 1 (0.53 [0.06–1.91] m/sec). Further, those in Case 3 were higher than in Case 1 (Mood's median test with Bonferroni correlation, Case 1 vs. Case 2, $p < 0.01$; Case 2 vs. Case 3, $p < 0.01$; Case 3 vs. Case 1, $p < 0.01$). Thirteen individuals paused on the tree for an average of 15.5 s in Case 1, whereas none did so in the other cases. These results indicate that the mandrills of Case 2, and subsequently of Case 3, were on a high alert due to the presence of the observers, and they crossed the open places with caution, whereas those of Case 1 were at a relatively lower degree of alertness.

Patterns of progression order

Patterns of progression orders are presented in Fig. 1. In Case 1 (Fig. 1a), subadult males (SMs) were significantly concentrated towards the front of the progression (randomization test, mSM = 36, $p = 0.03$), but the patterns of the concentration of adult males (AMs) and females holding an infant (FIs) were not statistically significant (mAM = 66, p = n.s; mFI = 114.5, p = n.s). In Case 2 (Fig. 1b), both AMs and SMs were concentrated towards the front (mAM = 17, $p < 0.01$; mSM = 69, $p < 0.01$) and FIs were towards the back (mFI = 225, $p < 0.01$). In Case 3 (Fig. 1c), FIs were concentrated towards the back (mFI = 303, $p < 0.01$) and SMs showed a tendency of concentration towards the front (mSM = 143, $p = 0.076$), though the pattern of AMs was not statistically significant (mAM = 164, p = n.s).

Six small clusters were detected in the progressions. Their compositions were as follows: (1AM + 2 [PM/non-FI] + 1J) and (2AF + 3 [PM/non-FI] + 3J + 2I) in Case 1; (1AF + 1 [PM/non-FI]) and (7AF + 11J) in Case 3; (2AF + 1 [PM/non-FI] + 2J) and (1AF + 2J) in the reversely repassed animals of Case 3. Although the first one can be identical to a OMU, most of the clusters did not represent a clear analogy for the OMU of a multilevel society. Indeed, 5 out of the 6 clusters did not include adult nor subadult males.

Discussion

The mandrills recorded in this study formed very cohesive progressions when they crossed an open area. Every aggregation of more than a hundred was in the form of long queue with a width of 10 m or less. Cohesive aggregations of mandrills were also reported in Campo and Lopé (Hoshino et al. 1984; Rogers et al. 1996; Abernethy et al. 2002). In terms of age-sex compositions, all three cases included only a few adult males and the SSR were more biased towards females than those in the other African papionins, as is the case in the other mandrill studies (Table 2). Thus, cohesive aggregation and female-biased sex ratio could be common characteristics in mandrills. Fluctuation in the proportion of adult males was not observed in this study probably due to the limited sample size. The days that I observed the progressions correspond with the season of low or moderate number of adult males within a horde in Lopé, where the fruiting phenology is similar to Moukalaba (Abernethy et al. 2002). I also observed solitary males and, just for once, a bachelor group within the study site. Possibly high proportion of males wandering outside hordes, as well as higher mortality of males (Setchell et al. 2005), may cause the extremely low proportion of adult males in the hordes. Since bachelor mandrill groups have not been observed in the other sites (Hoshino et al. 1984; Rogers et al. 1996; Abernethy et al. 2002), more information on wandering males is needed.

No aggressive or soliciting behaviour was observed between adult or subadult males and adult females within the progressions. Most of the look-backs, by which animals monitor the identity of their followers (Sueur and Petit 2010), were observed between adult females and their putative offspring. Moreover, most observed clusters did not have compositions analogous to the OMUs but included only adult females and immatures. These results suggest the bonds among females and immatures, which is analogous to female-bonded non-nested societies of savannah baboons (Altmann 1980; Silk et al. 2006). Abernethy et al. (2002) also mentioned the absence of OMUs in the hordes, and Bret et al. (2013) suggested the central role of females on mandrill group cohesion.

Adult females holding infants were concentrated towards the back of the progression in Case 2 and 3, when the animals were on a high alert. This pattern was not observed in the less cautious Case 1 (Fig. 1). On the contrary, adult males in Case 2 (but not in Case 3) were significantly concentrated towards the front, and this was not true in Case 1. Further, subadult males were significantly or nearly significantly concentrated towards the front in all cases.

In conclusion, the behaviours and the progression patterns of mandrills in Moukalaba were not analogous to those in the OMU-based multilevel societies but to those in savannah baboons. Although the results should be interpreted carefully due to limited sample size, they indicate that mandrills may form non-nested societies with strong bonds among females. In the terms of the subgrouping, however, it remains possible that mandrill hordes are different from the cohesive savannah baboon groups. Indeed, subgroupings were observed in two out of the three cases in the present study, as well as in several previous studies on both two *Mandrillus* species (Hoshino et al. 1984; Astaras et al. 2008) and in *Cercocebus* mangabeys (Mitani 1989; Range and Fischer 2004). Abernethy et al. (2002) also observed the short-term subgrouping for at least a few days just after their passage of open places, and White et al. (2010) observed regular subgrouping of the same horde. We should consider the social organization and fission-fusion dynamics separately (Aurelli et al., 2008; Grueter et al. 2012), and take into account the possibility that mandrills have more fluid fission-fusion dynamics than typical savannah baboons, as reported in the Guinea baboons (*P. papio*) (Patzelt et al. 2011). Further observations are required in relation to the duration, scale, and membership of subgrouping to examine the hypothesis.

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Table 1 Age-sex classes and references on physical and social development.

Age-sex class[*1]	Estimated age	Definition / Physical and social development
Infant (I)	0-12 months	Smallest individual which hangs onto its mother
Juvenile (J)	1-3 years	Small animal which travels independently
Adult female (AF)	≥4 years	Fully grown female. There are two categories of AF in the progressions: FI (judged as AF because it has an infant) and non-FI (judged as AF only when genital was observed, else indistinguishable from PM) / Average females give the first birth at 4.6 yrs in captivity (Setchell et al. 2002)
Pubescent male (PM)	4-5 years	Body size is similar to adult female and testes are small / Testes descend at 3.8 yrs and canines appear at 4.8 yrs (Setchell and Dixson 2002; Setchell and Wickings 2003)
Subadult male (SM)	6-9 years	Body size larger than female and testes volume increased / Testes volume and testosterone level increase, second sexual adornment emerge, and most males become peripheral at 6-7 yrs (Setchell and Dixson 2002)
Adult male (AM)	≥10 years	Fully grown male / Attain full body length and mass at 10 yrs and some males associate with group (Setchell and Dixson 2002)

I was capable of conducting the age-sex classification because I had undergone training at the Centre International de Recherches Médicales de Franceville (CIRMF), Gabon and Kyoto City Zoo, Japan.

*1: Abernethy et al. (2002) used a little different categorization from this study: *infant* was 0-12 months old, *juvenile* was 1-2 years old, *adult female* was >3 years old, and *males* were divided into four classes (3-4 years, 5 years, 6-9 years and >10 years old).

Table 2 Age-sex class compositions of *Mandrillus sphinx* and other African papionins. Parentheses mean the percentage of individuals in the group.

Species	Study sites	Horde/group size	I	J	AF	PM	(AF or PM)	SM	AM	UN	SSR	References
M. sphinx	Moukalaba/Case 1	169 (subgroup)	10 (5.9%)	67 (39.6%)	10 (5.9%)[*1]	-	68 (40.2%)[*1]	11(6.5%)	3 (1.8%)	0	-	This study
M. sphinx	Moukalaba/Case 2	350	33 (9.4)	129 (36.9)	124.7 (35.6)	35.3 (10.1)		23 (6.6)	5 (1.4)	0	4.5	This study
M. sphinx	Moukalaba/Case 3	442 (subgroup)	47 (10.6)	141 (31.9)	171.5 (38.8)	41.5 (9.4)		32 (7.2)	6 (1.4)	3 (0.7)	4.5	This study
M. sphinx	Lopé (n = 20)	338-845	9-175 (1.4-25.7)	100-340 (19.0-51.2)	94-288 (22.9-44.6)	59-171 (11.5-24.7)		6-32 (0.8-5.9)	1-17 (0.1-3.8)		3.0-33.1	Abernethy et al. 2002
M. sphinx	Lopé (n = 3)	449-625	38-86 (8.1-13.8)	73-200 (16.3-45.8)	-	-	247-312 (39.5-57.0)	56-83 (11.4-14.3)	21-30 (3.4-5.2)		-	Rogers et al. 1996
M. sphinx	Campo (n = 4)	15-80	-	-	-	-		-	1-6 (6.5-8.3)		6.5-8.3[*2]	Hoshino et al. 1984
P. hamadryas	Eritrea (n = 6)	139.2	12.8 (8.6)	39.8 (26.8)	58.3 (42.8)	-		7.8 (6.2)	20.3 (15.7)		2.4	Zinner et al. 2001
P. hamadryas	Various sites[*3]	38–146			28.5–58				9–30		1.1–2.8[*2]	Swedell 2011
T. gelada	Gich Plateau (n = 3)	103.0	13.0 (18.7)	31.3 (22.9)	37.7 (37.0)	2.3 (1.7)		3.3 (4.4)	15.3 (15.2)		2.0	Ohsawa 1979
T. gelada	Various sites[*3]	60–271			59				16		3.7[*2]	Swedell 2011
P. cynocephalus	Amboseli (n = 3)	34.3	1.7 (4.9)	7.7 (22.3)	15.7 (45.6)	3.3 (9.7)		1.0 (2.9)	5.0 (14.6)		2.7	Altmann et al. 1985
P. cynocephalus	Various sites[*3]	31–80			11.5–22				5–12		1.3–4.4[*2]	Swedell 2011
P. anubis	Various sites[*3]	15–115			3.9–38				2.3–17		1.1–9.5[*2]	Swedell 2011
P. ursinus	Various sites[*3]	20.5–79			11–31				2–13.3		2.1–10.3[*2]	Swedell 2011
Cercocebus spp.	Various sites[*3]	10.5-89			2.2-23				1-9		1.75-4.0[*2]	Swedell 2011
C. agilis	Bai Hokou (n = 4)	135.5	10.8 (7.9)	52.3 (38.5)	48.3 (35.6)	-		-	24.3 (17.9) (SM included)		2.0	Devresse et al. 2013

The mean values are shown except mandrills. The comparison must be conducted roughly because the age-sex classifications are slightly different among studies and species.

-: Not available. UN: Unknown. *1: In Case 1, numbers of adult females without an infant and pubescent males were not calculated because all the individuals of these classes were indistinguishable from each other (see text). *2: Subadult males are not included for calculations because their numbers are not available. *3: These data are based on Fig. 15.4 in Swedell (2011). Ranges of mean value are shown in the table.

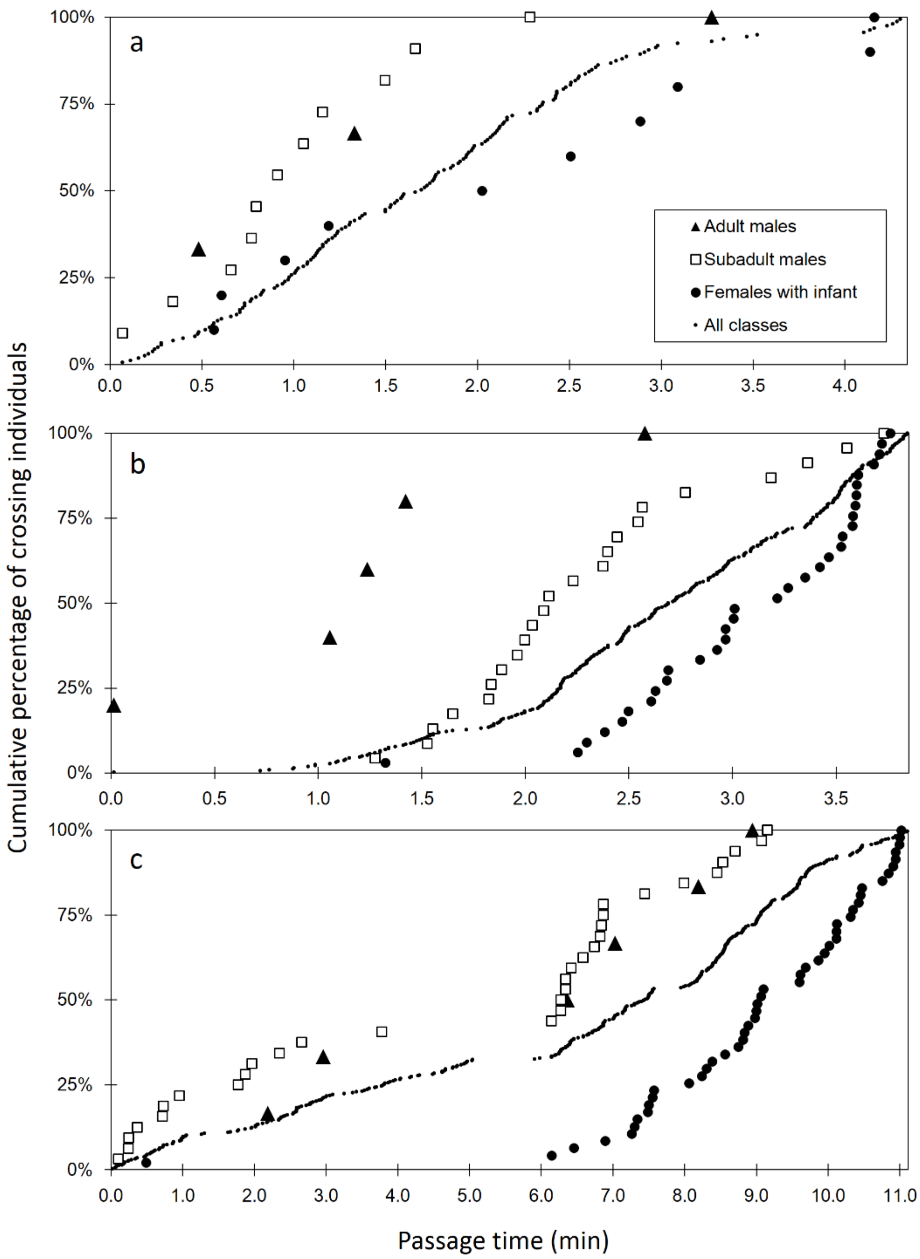

Fig. 1 Cumulative percentage of individuals in each age-sex class over the passage time. **1a** Case 1. **1b** Case 2. **1c** Case 3. Individuals who repassed reversely have not been included. Small dots (all classes) mean all individuals that passed the open place other than the dependant infants; thus, the classes whose points are located above them tend to concentrate in the front part of the progression, and ones below the small dots tend to be in the rear.

Online Resource 1 Video image of a progression of mandrills in Case 1. A subgroup crossed a fallen tree over a river.

Online Resource 2 Video image of a progression of mandrills in Case 2. A horde crossed a logging road 2 m wide.