Bonobo habituation in a forest–savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context

Article *in* Primates · July 2015

DOI: 10.1007/s10329-015-0476-0 · Source: PubMed

Victor Narat
CNRS- MNHN

Flora Pennec
Muséum National d'Histoire Naturelle

Bruno Simmen
French National Centre for Scientific Research

Sabrina Krief
Muséum National d'Histoire Naturelle

Primates
DOI 10.1007/s10329-015-0476-0

ORIGINAL ARTICLE

Bonobo habituation in a forest–savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context

Victor Narat[1] · Flora Pennec[1] · Bruno Simmen[2] · Jean Christophe Bokika Ngawolo[3] · Sabrina Krief[1,4]

Received: 16 September 2014 / Accepted: 27 June 2015

Abstract Habituation is the term used to describe acceptance by wild animals of a human observer as a neutral element in their environment. Among primates, the process takes from a few days for *Galago* spp. to several years for African apes. There are also intraspecies differences reflecting differences in habitat, home range, and ape–human relationship history. Here, we present the first study of the process of bonobo habituation in a fragmented habitat, a forest–savanna mosaic in the community-based conservation area led by the Congolese nongovernmental organization Mbou-Mon-Tour, Democratic Republic of the Congo. In this area, local people use the forest almost every day for traditional activities but avoid bonobos because of a traditional taboo. Because very few flight reactions were observed during habituation, we focused on quantitative parameters to assess the development of ape tolerance and of the tracking efficiency of observer teams. During the 18-month study period (May 2012–October 2013), 4043 h (319 days) were spent in the forest and bonobos were observed for a total of 405 h (196 contacts on 134 days). The average contact duration was stable over time (124 min), but the minimal distance during a contact decreased with habituation effort. Moreover, bonobo location and tracking efficiency, daily ratio of contact time to habituation effort, and the number of observations at ground level were positively correlated with habituation effort. Our observations suggest that bonobos become habituated relatively rapidly. These results are discussed in relation to the habitat type, ape species, and the local sociocultural context of villagers. The habituation process involves changes in ape behavior toward observers and also more complex interactions concerning the ecosystem, including the building of an efficient local team. Before starting a habituation process, knowledge of the human sociocultural context is essential to assess the balance between risks and benefits.

Keywords Ape habituation · Bonobo · Forest–savanna mosaic · Sociocultural context · DRC

✉ Victor Narat
victor.narat@gmail.com

1 Muséum National d'Histoire Naturelle, UMR7206 (MNHN-CNRS-Paris7) Eco-anthropologie et Ethnobiologie, Site du Musée de l'Homme, 17 Place du Trocadéro, 75016 Paris Cedex, France

2 Muséum National d'Histoire Naturelle, UMR7206 (MNHN-CNRS-Paris7) Eco-anthropologie et Ethnobiologie, 1 Avenue du Petit Château, 91800 Brunoy, France

3 NGO Mbou-Mon-Tour, Nkala, Territoire de Bolobo, Province du Bandundu, Democratic Republic of the Congo

4 Projet Pour la Conservation des Grands Singes, 3 Rue Titien, 75013 Paris, France

Introduction

Primate studies carried out in captivity complement those performed in the wild for many aspects of their biology, including tool use, self-medicating behavior, physiology, and locomotion (e.g., Matsuzawa 1994, 1996; Krief et al. 2006a, 2006b; Gustafsson et al. 2011; Vereecke and D'Août 2011; Zimbler-DeLorenzo and Stone 2011). In the wild, such studies may require the primates to be observed at close distance for long periods, with individual identification. Habituation is the term used to describe "acceptance by wild animals of a human observer as a neutral element in their environment" (Tutin and Fernandez 1991). Among primates, habituation may take from a few days (*Galago* spp.) to several years in the case of chimpanzees

Published online: 11 July 2015

Pan troglodytes and bonobos *Pan paniscus* (Johns 1996; Van Krunkelsven et al. 1999; Williamson and Feistner 2003; Sommer et al. 2004; Bertolani and Boesch 2008). These differences between species are related to social organization, diet, density and visibility in the habitat, and the local history of human–primate relationships (Johns 1996; Van Krunkelsven et al. 1999; Williamson and Feistner 2003; Sommer et al. 2004; Goldsmith 2005). Habituation is easier for animals/primates/apes living in areas where they are not targeted by hunters. The human context (behavior toward the apes and presence or absence of an eating taboo) has an influence on the habituation process. It is more risky to perform habituation on apes where local people hunt and eat them. Therefore, good knowledge of the local context for primate habituation is essential before starting the process.

Habituation is a powerful tool in the study of wild primates but involves risks because of the increased possibility of transmitting disease and of causing stress (Goodall 1986; Woodford et al. 2002; Williamson and Feistner 2003; Goldsmith 2005; Boesch 2008; Köndgen et al. 2008; Sak et al. 2013; Shutt et al. 2014). Moreover, as the fear of humans decreases, the risk of poaching increases (Williamson and Feistner 2003). Nevertheless, the continuous presence of researchers or field assistants might limit the incursion of poachers and promote primate conservation. Additionally, there is debate among conservationists concerning the use of habituation in ape-watching ecotourism ventures (Macfie and Williamson 2010). In the first wild-ape studies, habituation was performed by artificial feeding, exacerbating changes in behavior toward humans and other species, and even between individuals within the same party. In a well-known long-term study of apes at Gombe, Tanzania, where artificial feeding began in 1963, chimpanzees were observed to be aggressive toward baboons because of the increased stress generated by competition for food (Goodall 1971, 1986). They were also aggressive toward humans, and some diseases (pneumonia, polio, mange) were transmitted by humans to chimpanzees; 42 chimpanzees died of human diseases over 32 years (Butynski 2001). Primate provisioning also affects body mass and physiology, and may cause deformities (Asquith 1989; Pusey et al. 2005; Turner et al. 2008). The Gombe chimpanzees were free-living animals, but artificial food provisioning led to their "wildness" being questioned (Reynolds 1975). At Wamba, the oldest bonobo study site, food provisioning was performed from 1976 to 1996. The validity of the results obtained on gregariousness and party size were questioned (Wrangham 2008). However, Mulavwa et al. (2008) showed that, under natural conditions, they found the same results regarding party size as they did during food provisioning. At Wamba, there is a lack of information about the effect of food provisioning on health status, physiology or behavior. Transmission of zoonotic diseases is also a risk when habituation is performed without provisioning (Woodford et al. 2002; Goldsmith 2005). Consequently, habituation must be performed knowing the risks and assuming that the cost–benefit balance is positive for the species.

Primate habituation is often viewed only as a methodological issue, but it is also of interest to analyze the process itself relative to the local socioecosystem and primate–human relationships. Most studies dealing with ape habituation have focused on changes in behavioral responses toward observers during the first steps of the process (Tutin and Fernandez 1991; Van Krunkelsven et al. 1999; Blom et al. 2004; Bertolani and Boesch 2008), whereas few investigators have analyzed the development of habituation or tracked its efficiency after the initial stages. Among great apes, the bonobo (*Pan paniscus* Schwartz, 1929) is endemic to the Democratic Republic of the Congo (DRC) and is an endangered species (IUCN and ICCN 2012). There are relatively few long-term bonobo study sites with habituated groups (e.g., Wamba, Lomako, and LuiKotale). In the only study that reported the development of bonobo habituation (Van Krunkelsven et al. 1999 at Lomako), the bonobos exhibited fewer flight reactions in response to observers, and increased curiosity. During the first 7 months of habituation of a human-naïve group of bonobos, the frequency of display of no discernible response to humans (termed "ignorance") increased (Van Krunkelsven et al. 1999). There is no published information on the duration of bonobo habituation. Herein, we report on the process of development of habituation in bonobos of the Manzano Forest. Manzano is a new study site with long-term perspectives for data collection (i.e., several years of observation; Kappeler et al. 2012) located in a forest–savanna mosaic, relatively infrequently encountered as a habitat for bonobos (Inogwabini et al. 2008; IUCN and ICCN 2012; Thompson 2002). The site is also original because it is located outside official protected areas but is nevertheless protected by local people. The context is thus of interest because of the conservation approach led by the villagers and the traditional human activities occurring in both forest and savanna.

While local people are often considered to be primarily a source of disturbance for apes ("let them live the best possible life in highly protected areas free of human disturbance," Goldsmith 2005), they may also be a driver of protection. Moreover, highly protected areas are not always the best solution where they do not take into account the needs of local people and potentially result in extensive human–wildlife conflicts (Madden 2004). This project began because of a local initiative for community-based conservation led by the Congolese nongovernmental organization (NGO) Mbou-Mon-Tour, with an initial motive to support bonobo habituation for ecotourism (V. Narat, unpublished data). In this context, we argued that the habituation should be carried out under the best conditions and fully validated by scientists. Here we focus on an 18-month period of continuous habituation and report quantitative parameters used to evaluate the habituation process and the efficiency of tracking by observers (tracking efficiency). Methods are proposed to evaluate the course of habituation through simple parameters associated with the characteristics of observation, the habituation effort, and the composition of the teams of observers. We hypothesized that, during the habituation process, bonobo tolerance and tracking efficiency would increase with habituation effort.

Methods

Study site

This research was conducted in an area of about 20 km^2 in the Manzano Forest (2°38′S, 16°23′E), Embirima, Bolobo Territory, DRC (Fig. 1), in the community-based conservation area (official formalization in progress) led by the Congolese NGO Mbou-Mon-Tour (MMT). This study site represents the most southwestern extent of the geographic range of bonobos and is the closest to Kinshasa (Inogwabini et al. 2008; Narat et al. 2012) (Fig. 1). The habitat within Bolobo Territory is composed of a forest–savanna mosaic with 60 % lowland tropical rainforest and 40 % savanna (survey block of 1993 km^2 in the Territoire de Bolobo; Inogwabini et al. 2008). The rainforests comprise Marantaceae forest, mixed mature forest, disturbed forest, and periodically inundated forest. The savannas are composed of herbaceous and woodland savannas. The annual rainfall from May 2012 to May 2013 was 2387 mm, with a dry season (<100 mm of rainfall per month, Dupain et al. 2002) lasting 3 months (June–August).

The human density in the area was lower than 5 inhabitants/km^2 (B. Perrodeau 2010, pers. com.), and all settlements were located in savanna. Five traditional farms, the homes of one or two families (2–15 people), were established at the edge of the Manzano Forest (Fig. 1). Local people, a Teke ethnic group, respect a traditional taboo on bonobos, which are considered as almost human (Kano 1992; Inogwabini et al. 2008; Narat 2011). Moreover, the Teke avoid bonobos, which are considered to be a bad omen when encountered in the forest, and also avoid contact with bonobo feces (V. Narat, unpublished data).

The Teke people are highly dependent on the forest, which they enter almost every day for shifting cultivation (mostly cassava, corn, sugarcane, and bananas), hunting (using rifles, snares, and nets), fishing, and gathering (Narat et al. 2012). After 3 days at work, the fourth day is called *Mpika* and implies a prohibition on entering the forest, although it is possible to overcome this restriction for specific rituals.

Since 2001, Nkala Village has decided to preserve a forested area for bonobo conservation, the decision being made by community councils. Subsequently, several other villages have followed this example. In the patches of forest under study, some human activities are strictly

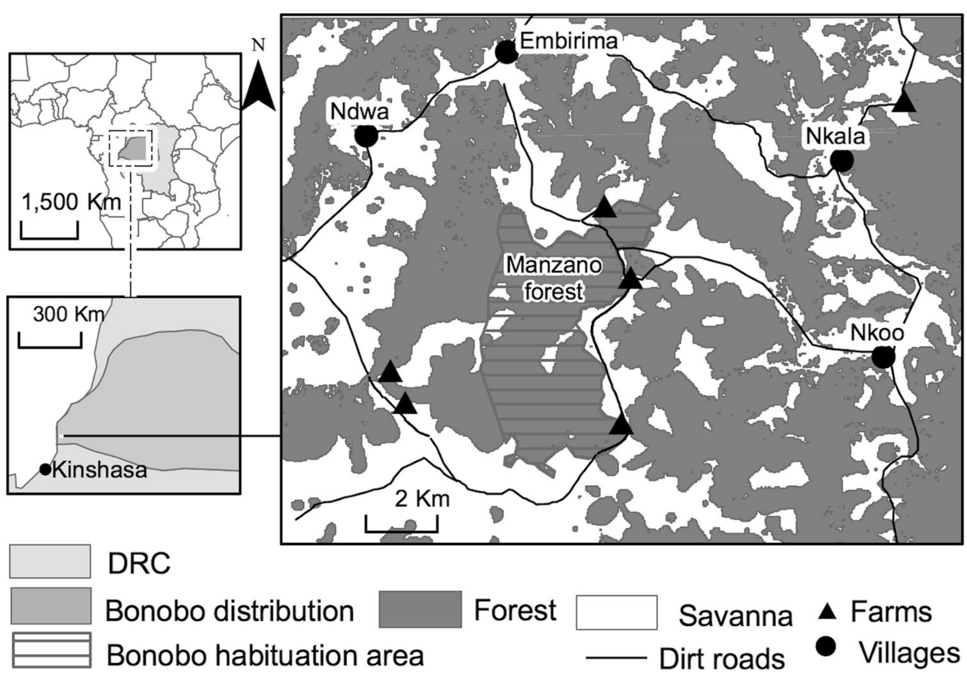

Fig. 1 Study site location and bonobo habituation area in the Manzano Forest

forbidden (hunting and shifting cultivation) but human presence is allowed (V. Narat, unpublished data).

From the creation of the community conservation forest in 2007 until 2010, local trackers entered the Manzano Forest twice a week to begin a trail network and to search for bonobos (J.C. Bokika 2010, pers. com.). These trackers did not receive any training from conservation or research teams until a pilot study was started by V.N. in 2010. During this pilot study, very few flight reactions were observed (Narat 2011).

Study period and team patrols

Data were collected for 18 months from May 2012 to October 2013. The pilot study was performed for 6 months over 2010–2011 and led to permission to carry out the study presented here. The pilot study results are not presented here (see Narat 2011).

A continuous habituation process (6 days per week) was started in May 2012 with four local field assistants and two researchers from the research program supervised by MMT and the French National Museum of Natural History. Researchers were present for three periods during the 18 months of the study: 12 weeks at the beginning (May–July 2012), 12 weeks in the middle (February–April 2013), and 3 weeks at the end (October 2013). Over the first year, four local field assistants participated in the study, and five during the second period when researchers were present; then, because of budget restrictions, only two of them worked for the last 6 months. Between one and four teams composed of one to four observers patrolled the forest during the 18-month period. The results include data collected by researchers and field assistants.

Methodology

Teams patrolled the forest between 6:00 am and 6:00 pm. Each team recorded the forest entry and exit times and the timing of encounters and separation between two patrol teams. Thus, the habituation effort for 1 day was the sum of the time spent patrolling by all teams. However, the duration of encounters among several teams was counted for only one team for the day. Patrol teams were generally composed of two individuals but could comprise up to six people during bonobo observation because of the fusion of patrol teams. Bonobos were located by vocalizations and fresh signs (food remains, feces, footprints, and nests). Because it was in the context of work, and after agreements were obtained from the traditional chief for each team member, field assistants and nonlocal team members were authorized to enter the forest on *Mpika* days, and to collect bonobo feces (used for another study, see Narat et al. 2014, in review).

The initial priority was to find night nest sites of bonobos to follow them from the nest on the following morning. When vocalizations were heard after 4:00 pm, the observers located the nest site without approaching the bonobos for direct observation to avoid disturbing them, and kept at least 60 m from the nest site.

A contact was deemed to begin when at least one bonobo and one observer saw each other at an estimated distance of less than 60 m, a threshold determined during the pilot study according to the distance where both species can detect each other without resulting in immediate flight of the bonobos. The end of the contact was considered to be when no further visual or audible sign of the presence of a bonobo was recorded at less than 60 m for 30 min after the last presence sign was recorded. During contacts, observers spoke and moved quietly, staying in a single group, and adapting their reactions according to the bonobos' behavior. Leaf-tearing and tongue-clacking were considered as signs that bonobos were aware of observer presence (Williamson and Feistner 2003). A minimum distance of 8 m was maintained between the closest individual and the observers to decrease the risk of disease transmission (Macfie and Williamson 2010).

During each contact, the observers identified as many individuals as possible, based on morphological features (sex and age class, body size, face color, hair on the head, anogenital area shape, and particular features such as mutilations). Four age classes were distinguished: infant (estimated age 0–2.9 years), juvenile (3–9.9 years), subadult (10–14.9 years), and adult ($\geq$15 years) (Van Krunkelsven et al. 1999; Pontzer and Wrangham 2006). Individual identifications were performed and confirmed by V.N. and F.P. during their presence in the field, by observations and photographs.

For this study, the following parameters were used: (1) duration (min), (2) minimal distance (m), (3) party size (all age classes, Van Krunkelsven et al. 1999), and (4) ground-level observations. During forest patrols, the group sizes of all fresh nests (Ogawa et al. 2007) were recorded to study changes in bonobo party size over the study period.

Bonobo habituation level was tested over the 18 months of the study with the following parameters: (1) contact duration, (2) daily contact time ratio (daily contact time divided by daily habituation effort), (3) minimal distance, (4) monthly ratio of numbers of contacts at ground level weighted by monthly habituation effort, and (5) changes in party size and nest party size. Location efficiency was evaluated from the monthly contact ratio (monthly number of contacts weighted by monthly habituation effort), i.e., the efficiency of teams at finding bonobos during 1 month of habituation effort, and tracking efficiency was determined from the number of contacts per day (only days with at least one contact), i.e. the efficiency of teams to follow bonobos after one contact.

Data for the 18-month study period were analyzed to examine habituation and the development of tracking efficiency over time. The 18-month study period was also divided into two—according to the total time spent in the forest—in order to compare parameters between the first half and the second half of the study period. Moreover, periods of researcher presence (RP) and absence (RA) in the observer teams were compared to evaluate the differences in the habituation effort and contact parameters.

Statistical analyses

Correlation tests (Spearman or Pearson depending on the normality of variables tested with a Shapiro test) were used to test correlation between parameters and total habituation effort. The significance threshold used by default for the interpretation of p values was 0.05, with Bonferroni correction for multiple tests. Median comparisons (Mann–Whitney U test) were used to test differences between RP and RA periods. All statistical analyses were performed using R software (R core team, 2012) (http://www.r-project.org).

Results

Over the 18 months of the study period, 319 days (out of 535 days) totaling 4043 h were spent in the forest for bonobo tracking; 196 contacts occurred (on 134 days) for a total of 405 h. The average cumulative research effort per month was 225 h (range 141–318 h; standard deviation (SD) = 46.8 h). Over the 18 months, the average daily number of observers in the forest was 2.7 (range 1–7; SD = 1.4), with more observers (Mann–Whitney test, $p < 0.001$, $U = 19128$) and greater maximal daily numbers of patrol teams in the RP periods (Mann–Whitney test, $p < 0.001$, $U = 13735$) compared with RA periods. The average number of observers during contacts was 2.3 (1–6; SD = 1.09). Most contacts were made by a team composed of two observers (1, 23 %; 2, 36 %; 3, 28.5 %; 4, 8 %; 5, 2.5 %; 6, 2 %), with more observers per contact during RP periods (mean = 2.7; SD = 1.2) compared with RA periods (mean = 1.9; SD = 0.8) (Mann–Whitney test, $p < 0.001$, $U = 6613$). These data are detailed in Table 1.

Bonobo habituation level

There was no significant correlation between contact duration and habituation effort; the average contact duration over the 18-month period was 124 min ($n = 196$, range 1–494 min, SD = 97.0 min), and there was no difference in contact duration between RP and RA periods.

With increasing habituation effort, the daily contact time ratio increased significantly ($n = 319$, Spearman test, $p = 0.01$, $r = 0.14$, range 0–56 min/h) and the minimal distance decreased significantly ($n = 195$, Spearman test, $p < 0.001$, $r = -0.46$, range 8–60 m; Fig. 2a). Over the first half of the study period, the average of the daily contact time ratio was 5.5 min/h ($n = 152$, range 0–56.2 min/h, SD = 11.5 min/h) with an average minimal distance of 31 m ($n = 56$, range 10–60 m, SD = 12.4 m); in the second half of the study, the corresponding values were 8.6 min/h ($n = 167$, range 0–42.7 min/h, SD = 11.1 min/h) and 21 m ($n = 139$, range 8–50 m, SD = 10.5 m).

The daily contact time ratio in RA periods was low compared with RP periods (Mann–Whitney test, $p < 0.001$, $U = 14244$). Because of a difference in the number of field assistants between the two RA periods (four in the first, two in the second), a comparison was also performed between those periods. The daily contact time ratio was lower over the first RA period (3.0 min/h) compared with the second RA period (8.9 min/h) (Mann–Whitney test, $p < 0.001$, $U = 3974$); there was no significant difference in daily contact time ratio between the RP periods and the second RA period. The minimal distance was shorter during RA periods (Mann–Whitney test, $p = 0.007$, $U = 54255$). See Table 1 for details.

The monthly number of ground-level observations, weighted by monthly habituation effort, was significantly positively correlated with the total habituation effort ($n = 18$, Spearman test, $p = 0.04$, $r = 0.48$; Fig. 2c). Three ground contacts were recorded over the first half of the study period, and ten over the second half.

The observed bonobo party size increased over the study period ($n = 190$, Spearman test, $p < 0.001$, $r = 0.29$, range 1–19), in contrast to the fresh-nest party size, which was stable over time ($n = 114$, mean = 6.3, range 1–20, SD = 3.9) (Fig. 2b). The average observed party size increased from 6.5 individuals ($n = 54$, 1–16, SD = 3.6) during the first half of the period, to 8.4 individuals ($n = 136$, 1–19, SD = 4.7) over the second half. The average fresh nest party size was stable at 5.6 over the first half period ($n = 44$ nest groups) and 6.6 over the second half ($n = 70$ nest groups). Because the observed party size could be biased by the habituation process (the observed party size is not the real one), the effects of party size on contact duration and minimal distance were not tested. There was no difference in the observed party size between RA and RP periods.

Bonobo location and tracking efficiency

There was a significant positive correlation between the monthly contact ratio and the habituation effort ($n = 18$, Pearson's test $p = 0.01$; $r = 0.58$; Fig. 2d). Over the first half of the study period, 57 contacts occurred, and 139 over

Table 1 Changes in habituation parameters over the study period and comparison between researcher presence (RP) and absence (RA)

	n	First half of study period, 0–2021 h		Second half of study period, 2022–4043 h		Correlation test with total habituation effort	Comparison between team compositions				
							RP, 1465 h		RA, 2578 h		Mann–Whitney test
		n	Mean min–max; SD	*n*	Mean min–max; SD		*n*	Mean min–max; SD	*n*	Mean min–max; SD	
Daily habituation effort (h)	319	152	13.3 1.3–26.1; 5.5	167	12.1 1.6–24.5; 4.8	**$p = 0.006$, $r = -0.15$** Spearman's test	106	13.8 1.3–26.5; 5.2	213	12.1 1.6–25.9; 5.0	**$p = 0.009$** **$U = 13307$**
Number of observers	–	–	–	–	–	–	106	3.8 2–7; 1.4	213	2.1 1–4; 0.9	**$p < 0.001$** **$U = 19128$**
Maximum daily number of patrol teams	–	–	–	–	–	–	106	2.0 1–4; 0.7	213	1.7 1–4; 0.7	**$p < 0.001$** **$U = 13735$**
Number of observers/contact	–	–	–	–	–	–	103	2.7 1–6; 1.2	93	1.9 1–4; 0.8	**$p < 0.001$** **$U = 6613$**
Contact duration (min)	196	57	151 1–494; 124	139	113 1–405; 81	$p = 0.32$, $r = -0.07$ Spearman's test	103	120 1–494; 100.0	93	129 1–475; 93.9	$p = 0.26$ $U = 4338$
Daily contact time ratio	319	152	5.5 0–56; 11.5	167	8.6 0–42.7; 11.1	**$p = 0.01$, $r = 0.14$** Spearman's test	106	10.5 0–56; 13.1	213	5.5 0–42.6; 10.0	**$p < 0.001$** **$U = 14244$**
Minimal distance (m)	195	56	31 10–60; 12.4	139	21 8–50; 10.5	**$p < 0.001$, $r = -0.46$** Spearman's test	103	25.9 8–60; 12.2	92	21.6 8–60; 11.4	**$p = 0.007$** **$U = 5425$**
Monthly ground-level contact/monthly habituation effort*	18	3	–	10	–	**$p = 0.04$, $r = 0.48$** Spearman's test	–	–	–	–	–
Party size	190	54	6.5 1–16; 3.6	136	8.4 1–19; 4.7	**$p < 0.001$, $r = 0.29$** Spearman's test	100	7.5 1–19; 4.4	89	8.3 1–19; 4.5	$p = 0.23$ $U = 4005$
Fresh nest party size	114	44	5.6 1–14; 3.5	70	6.6 1–20; 4.1	$p = 0.98$, $r = -0.002$ Spearman's test	–	–	–	–	–
Monthly number of contacts/monthly habituation effort*	18	57	–	139	–	**$p = 0.01$, $r = 0.58$** Pearson's test	–	–	–	–	–
Daily tracking efficiency	134	47	1.2 1–4; 0.5	87	1.6 1–6; 0.9	**$p = 0.004$, $r = 0.25$** Spearman's test	62	1.7 1–6; 1.04	72	1.3 1–3; 0.5	**$p = 0.03$** **$U = 2633$**

* For the monthly analyses, the number of contacts and ground contacts are given without weighting for habituation effort in the first and second halves of the study period. Significant p values are shown in bold

the second half. Likewise, the daily tracking efficiency (number of contacts during days with at least one contact) was significantly and positively correlated with the habituation effort ($n = 134$, Spearman's test $p = 0.004$, $r = 0.25$). Over the first half of the study period, the average number of contacts per contact day was 1.2 ($n = 47$, range 1–4, SD = 0.5), and 1.6 over the second half ($n = 87$, range 1–6, SD = 0.9) (Mann–Whitney test, $p = 0.003$, $U = 1508$).

Identification

Over the 18 months of the study, 18 individuals were clearly identified: 13 females (nine adults, two subadults,

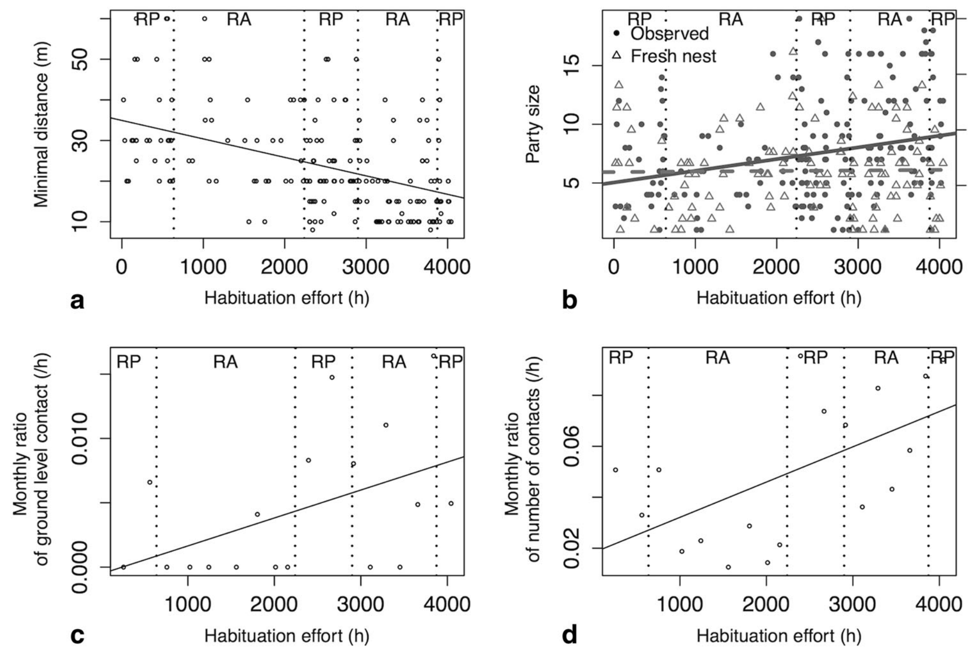

Fig. 2 Changes in (**a**) minimal distance, (**b**) observed (*solid line*) and fresh nest (*dashed line*) party size, (**c**) monthly ratio of ground-level contact, and (**d**) monthly ratio of contact to habituation effort. *Vertical dotted lines* separate researcher presence (RP) and absence (RA) periods

two juveniles) and five males (two adults, two juveniles, and one infant). Five individuals were identified during the first half of the study period and 13 in the second half.

Discussion

This is the first study to document the process of habituation of bonobos in a forest–savanna mosaic area with traditional human activities and is the second study of bonobo habituation (Van Krunkelsven et al. 1999). The decrease in the minimal distance, and the increases in the daily contact time ratio and in the monthly ratio of ground contact, are consistent with an increase in the habituation level of bonobos over the 18-month study period.

Bonobo location and tracking efficiency also increased over the study period. This aspect is important because a long-term study site requires the permanent presence of field assistants/researchers in the forest. Improving the team's knowledge of bonobo ecology and bonobo tracking is essential to build a long-term study site (Doran-Sheehy et al. 2007). During the periods of researcher absence, the daily contact time ratio was lower but the field assistants were closer during contacts, presumably because they were more accustomed to the forest and less noisy than the researchers when they were moving in the forest. Moreover, the daily contact time ratio in the first period without researchers (four field assistants) was about one-third less than in the second period (two field assistants), indicating increased field assistant efficiency.

These results highlight the importance of local team training, motivation, and knowledge. The two field assistants retained in this project were the most motivated and the most efficient ones, and they achieved the same daily contact time ratio as that in RP periods. Even if the field assistants were less efficient during the first RA periods, the continuous habituation effort based on building a local team allowed an improvement in bonobo habituation level and tracking efficiency.

Unexpectedly, contact duration was not correlated with habituation effort. Also, there was no difference in contact duration between RA and RP periods. Over the study period, bonobo tracking improved. These results indicate good tolerance by bonobos at the beginning of the study and little disturbance by human presence. When a contact ended, it was probably not caused by observer presence. After the termination of a contact by the bonobos climbing or traveling on the ground, they were frequently found later in the day, resulting in an increase in the number of recorded contacts but not in contact duration (i.e., the contacts were of similar total duration but were interrupted by traveling).

The party size was observed to increase over time, in contrast to the nest party size, which remained the same. This could be an artifact caused by the decrease of the minimal distance, which allowed better observation and visual counting, and potentially also by an improvement in the habituation of some individuals. Indeed, it is possible that, during a contact, some bonobos remained out of the observers' field of view on the ground or at the party periphery. The increase in bonobo party size observed through the study period is probably a bias due to the habituation process rather than a real increase in the party size. Thus, party size used during the habituation process has to be considered carefully because of the bias of habituation level and the difficulty of characterizing parties (Van Elsacker et al. 1995).

The results of this study cannot be closely compared with those of Van Krunkelsven et al. (1999) at Lomako, which focused on behavioral responses toward observers over the first 7 months of habituation effort on a human-naïve bonobo group. Comparisons can only be made with respect to minimal distance and contact duration. At Lomako, the average minimal distance was lower (15 m, range 4.5–40 m) than at Manzano but the average contact duration was also shorter (51 min, range 0–246 min) (Van Krunkelsven et al. 1999). The longer contact duration at Manzano could be associated with the frequent human activities in the forest without aggressiveness toward bonobos (and avoidance of them). It could also reflect a difference in habitat; at Lomako, where the forest is probably denser, observers have to be closer to observe bonobos, with more risk of disturbance resulting from closer contacts. Differences in methodology and the absence of a definition of contact in the Lomako study may also hinder comparison between these studies.

The habituation of bonobos at Manzano was more rapid, or the baseline level of habituation was higher, than for chimpanzees in a savanna woodland habitat (Tutin et al. 1983; Sommer et al. 2004) and in continuous rainforest (Taï Forest; Bertolani and Boesch 2008; Table 2). The daily contact time ratio—daily time in minutes in contact with apes divided by daily habituation effort—was compared for these studies. For chimpanzees, the average daily contact time ratio in the last year of the study period was 5.9 min/h at Assirik after 4 years of continuous habituation effort, 0.6 min/h at Gashaka after 2 years of continuous habituation effort, and 8.3 min/h at Taï after 5 years of continuous habituation effort; in contrast, it was 6.3 min/h in our study after only 6 months of discontinuous habituation effort (2010–2011) and 18 months of continuous habituation effort (2012–2013). Several aspects of the local socioecosystems influence the development of habituation and might explain these differences.

Ape species

During the habituation process, the more cohesive bonobo social organization compared with chimpanzees (Furuichi 2009) is likely to favor the habituation level for each individual because the probability of observing the same individual in several contacts is higher for bonobos. Moreover, bonobos are more arboreal than chimpanzees (Doran 1993; Doran and Hunt 1996), which is likely to promote tolerance toward observers because they can see observers arriving more easily and feel in a safer position in trees than on the ground.

Habitat

The forest–savanna habitat conformation allows observers to travel rapidly in the savanna so they are able to reach the desired area quickly, for example, in response to vocalizations. Moreover, in contrast to savanna chimpanzees, which have a large home range (from 60 to 300 km^2; Baldwin et al. 1982; Tutin et al. 1983; Pruetz 2006) and low densities, the forest–savanna mosaic bonobos spend almost all of the time in the forest areas (V. Narat, unpublished data). Thus, the search area is reduced to about 20 km^2 (including 1 km^2 of savanna), which is the estimated home range of the Manzano community based on Global Positioning System tracking (V. Narat, unpublished data). In this context, the bonobo habituation process may be easier because the survey area is mainly reduced to the forest part. When bonobos are close to the forest border or in savanna (traveling on the ground), the bonobo vocalizations can be heard from very far away (more than 600 m), allowing more accurate location.

Human–ape relationship history

The local status of chimpanzees or bonobos varies among their respective distribution areas from an eating taboo to traditional hunting and consumption (Peterson 2003; Thompson et al. 2008; Lingomo and Kimura 2009). Their sociocultural context within different human populations influences the behavior of apes toward humans (Goldsmith 2005; Hart et al. 2008; Thompson et al. 2008; McLennan and Hill 2010). In the region studied, several human contextual factors may favor habituation: (1) an eating taboo, (2) avoidance of bonobos in the forest, (3) low human density, and (4) relatively few crops cultivated near the border of the forest, limiting human–wildlife conflicts. Moreover, from 2007, when the local community forest for bonobo conservation was established at Manzano, MMT trackers entered the forest twice a week searching for bonobos. Although they did not perform "active habituation" (they did not follow bonobos), the community conservation dynamics might have promoted the bonobo habituation process. Unfortunately, this historical context could not be quantified to evaluate its effects on the development of bonobo habituation. The sociocultural context must be studied to understand the development of ape tolerance toward observers. Furthermore, in our case, the local field assistants had a taboo toward bonobos and it was critical to share our objectives with them and to adapt our work to their traditions. During the first RA period, the

Table 2 Comparison of local context, habituation effort, and ratio of daily contact time to habituation effort during the last year of habituation in this study and in three studies on chimpanzees

Study site, country, species	Habitat	Conservation status (year commenced)	Human presence	Local ape status	Habituation effort	Daily contact time/habituation effort (min/h)	References
Manzano, DRC, bonobo (*P. paniscus*)	Forest–savanna mosaic	Community-based conservation (Mbou-Mon-Tour, formalization in progress)	Yes (settlement in savanna) <5/km^2	Taboo	6 months, discontinuous (2010–2011); 18 months, continuous (2012–2013)	6.3	This study
Assirik, Senegal, chimpanzee (*P. t. verus*)	Savanna	National Park (Niokolo Koba 1954)	No (since 1950)	Unknown	4 years, continuous (1976–1979)	5.9	Tutin et al. 1983
Gashaka, Nigeria, chimpanzee (*P. t. vellerosus*)	Woodland savanna	National Park (Gashaka Gumti 1991)	Yes, declining	Eating taboo	2 years, continuous (2000–2001)	0.6	Sommer et al. 2004; Dunn 1995
Taï forest, Côte d'Ivoire, chimpanzee (*P. t. verus*)	Forest	National Park (Taï, 1972)	Yes ~100/km^2	Hunting	5 years, continuous (1989–1994)	8.3*	Bertolani and Boesch 2008; Herbinger et al. 2003

* More than half of the time spent with Zora, a female adult chimpanzee habituated since the beginning (1989)

relatively low efficiency of field assistants might have been caused by a fear of "folk metaphysics" related to bonobos.

Finally, this study contributes to the advance of knowledge of the development of habituation in bonobos and of *Pan* habituation in general. The process of habituation of apes should be studied by their reaction toward observers during the first habituation steps and also by using quantitative parameters that allow the evaluation of ape tolerance toward observers during later habituation steps, and of improvements in bonobo tracking. Observations must be interpreted by taking into account the habitat type and the human context, particularly outside officially protected areas. Because our preliminary study showed a good baseline tolerance of bonobos toward observers, we did not analyze the evolution of their reaction toward observers. In other contexts, the first bonobo reactions toward observers must be analyzed during the habituation process. Moreover, the habituation effort and efficiency must be quantified and qualified according to the composition of the team (presence or absence of researchers). The quality of team building is a critical factor to improve ape habituation. We argue that, when possible, it is important to employ local field assistants to ensure longitudinal data collection, to encourage the involvement of local people in ape research and conservation, and to promote economic outcomes. Indeed, the employment of local rather than nonlocal field assistants is probably more efficient. Their presence in the forest almost daily ensures monitoring for poaching activities, and the relationship with local field assistants allows researchers to better understand the local sociocultural context. The definition of habituation relates to a change in ape tolerance toward observers but must also take into account the way in which teams of observers themselves habituate to locate, track, and observe apes. The present results are encouraging and give us reason to believe that this new long-term study site will facilitate future understanding of bonobo flexibility in the forest–savanna mosaic, an infrequent habitat type within the bonobo distribution area. Overall, in this case, the traditional taboo on bonobos and the community-based conservation project favored the habituation process because bonobos had a good tolerance toward observers from the very start, probably limiting the stress due to bonobo tracking. Moreover, the scientific and ecotourism projects (with employment and promotion of this region) may strengthen local involvement in the community-based conservation project. However, the human–bonobo proximity, increasing with the improvement of habituation, implies the need to carefully monitor their health status to limit as much as possible the risk of zoonotic diseases inherent to this process. Thanks to good habituation and ongoing individual identification (to date, all 24 individuals have been identified), future studies should help to elucidate important questions in bonobo ecology, behavior, zoopharmacognosy, conservation, and evolution.

Acknowledgments We thank the Ministère de l'Environnement, Conservation de la Nature et Tourisme for research permission, the Mbou-Mon-Tour NGO and traditional chiefs for authorization to conduct this work. Acknowledgments for funding are due to the Action Transversale du Muséum "Relations Sociétés-Nature dans le long terme" and the UMR7206 Eco-anthropology and Ethnobiology. This study would not have been possible without the field assistants Blanchard Bongwana, Osa Otsiu Epany, Mozungo Ngofuna, and Debaba Munziu. We also thank all members of Mbou-Mon-Tour for their support and contribution to bonobo conservation.

References

Asquith PJ (1989) Provisioning and the study of free-ranging primates: history, effects and prospects. Am J Phys Anthropol 32S10:129–158

Baldwin PJ, McGrew WC, Tutin CE (1982) Wide-ranging chimpanzees at Mt. Assirik, Senegal. Int J Primatol 3:367–385

Bertolani P, Boesch C (2008) Habituation of Wild Chimpanzees (*Pan troglodytes*) of the South Group at Taï Forest, Côte d'Ivoire: empirical measure of progress. Folia Primatol 79:162–171

Blom A, Cipolletta C, Brunsting AM, Prins HH (2004) Behavioral responses of gorillas to habituation in the Dzanga-Ndoki National Park, Central African Republic. Int J Primatol 25:179–196

Boesch C (2008) Why do chimpanzees die in the forest? The challenges of understanding and controlling for wild ape health. Am J Primatol 70:722–726

Butynski TM (2001) Africa's great apes. In: Beck BB, Stoinski TS, Hutchins M, Mapple TL, Norton B, Rowan A, Stevens EF, Arluke A (eds) Great apes and humans. The ethics of coexistence. Smithsonian Institution Press, Washington, pp 3–56

Doran DM (1993) Comparative locomotor behavior of chimpanzees and bonobos: the influence of morphology on locomotion. Am J Phys Anthropol 91:83–98

Doran DM, Hunt K (1996) Comparative locomotor behavior of chimpanzees and bonobos. In: Wrangham RW, McGrew WC, de Waal FBM, Heltone PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, pp 93–108

Doran-Sheehy DM, Derby AM, Greer D, Mongo P (2007) Habituation of western gorillas: the process and factors that influence it. Am J Primatol 69:1354–1369

Dunn A (1995) Gashaka Gumti, Nigeria-From Game Reserve to National Park. RDFN 18:20–22

Dupain J, Van Elsacker L, Nell C, Garcia P, Ponce F, Huffman MA (2002) New evidence for leaf swallowing and Oesophagostomum infection in bonobos (*Pan paniscus*). Int J Primatol 23:1053–1062

Furuichi T (2009) Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates 50:197–209

Goldsmith ML (2005) Habituating primates for field study: ethical considerations for African great apes. In: Turner TR (ed) Biological anthropology and ethics. State University of New York Press, Albany, pp 49–64

Goodall J (1971) Some aspects of aggressive behaviour in a group of free-living chimpanzees. Rev Int Soc Sci 23:89–97

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge

Gustafsson E, Krief S, Saint Jalme M (2011) Neophobia and learning mechanisms: how captive orangutans discover medicinal plants. Folia Primatol 82:45–55

Hart JA, Grossmann F, Vosper A, Ilanga J (2008) Human hunting and its impact on bonobos in the Salonga National Park, Democratic Republic of Congo. In: Furuichi T, Thompson JM (eds) The bonobos: behavior, ecology and conservation. Springer, New York, pp 245–271

Herbinger I, Boesch C, Tondossama A (2003) Côte d'Ivoire. In: Kormos R, Boesch C, Bakaar MI, Butynski TM (eds) West African Chimpanzees. Status survey and conservation action plan. IUCN, Gland and Cambridge, pp 99–109

Inogwabini B-I, Bewa M, Longwango M, Abokome M, Vuvu M (2008) the bonobos of the Lake Tumba–Lake Maindombe hinterland: threats and opportunities for population conservation. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology and conservation. Springer, New York, pp 273–290

IUCN and ICCN (2012) Bonobo (*Pan paniscus*): conservation strategy 2012-2022. IUCN/ICCN, Gland

Johns BG (1996) Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. Biol Cons 78:257–262

Kano T (1992) The last ape: pygmy chimpanzee behavior and ecology. Stanford University Press, Stanford

Kappeler PM, van Schaik CP, Watts DP (2012) The values and challenges of long-term field studies. In: Kappeler PM, Watts DP (eds) Long-term field studies of primates. Springer, Heidelberg, pp 3–18

Köndgen S, Kühl H, N'Goran PK, Walsh PD, Schenk S, Ernst N, Biek R, Formenty P, Mätz-Rensing K, Schweiger B, Junglen S, Ellerbrok H, Nitsche A, Briese T, Lipkin WI, Pauli G, Boesch C, Leendertz FH (2008) Pandemic human viruses cause decline of endangered great apes. Curr Biol 18:260–264

Krief S, Huffman MA, Sévenet T, Hladik C-M, Grellier P, Loiseau PM, Wrangham RW (2006a) Bioactive properties of plant species ingested by chimpanzees (*Pan troglodytes schweinfurthii*) in the Kibale National Park, Uganda. Am J Primatol 68:51–71

Krief S, Wrangham R, Lestel D (2006b) Diversity of items of low nutritional value ingested by chimpanzees from Kanyawara, Kibale National Park, Uganda: an example of the etho-ethnology of chimpanzees. Soc Sci Inform 45:227–263

Lingomo B, Kimura D (2009) Taboo of eating bonobos among the Bongando people in the Wamba region, Democratic Republic of Congo. Afr Stud Monogr 30:209–225

Macfie EJ, Williamson EA (2010) Best practice guidelines for great ape tourism. IUCN, Gland, Switzerland

Madden F (2004) Creating coexistence between humans and wildlife: global perspectives on local efforts to address human-wildlife conflict. Hum Dimens Wildl 9:247–257

Matsuzawa T (1994) Field experiments on use of stone tools in the wild. In: Wrangham RW, McGrew WC, de Waal FBM, Heltone PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, pp 351–370

Matsuzawa T (1996) Chimpanzee intelligence in nature and in captivity: isomorphism of symbol use and tool use. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp 196–209

McLennan MR, Hill CM (2010) Chimpanzee responses to researchers in a disturbed forest-farm mosaic at Bulindi, Western Uganda. Am J Primatol 72:907–991

Mulavwa M, Furuichi T, Yangozene K, Yamba-Yamba M, Motema-Salo B, Idani GI, Ihobe H, Hashimoto C, Tashiro Y, Mwanza N (2008) Seasonal changes in fruit production and party size of bonobos at Wamba. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology and conservation. Springer, New York, pp 121–134

Narat V (2011) Résilience des bonobos (*Pan paniscus*) à la fragmentation de l'habitat et à la pression anthropique. Etude préliminaire lors de deux missions dans le Territoire de Bolobo en République Démocratique du Congo. Veterinarian thesis, École Nationale Vétérinaire de Nantes

Narat V, Cibot M, Bokika Ngawolo JC, Dumez R, Krief S (2012) Etude préliminaire de l'influence des disponibilités alimentaires et des activités humaines sur l'utilisation spatiale de l'habitat par les chimpanzés et les bonobos. Rev Primatol. doi:10.4000/primatologie.1121

Narat V, Guillot J, Pennec F, Lafosse S, Grüner AC, Simmen B, Bokika Ngawolo JC, Krief S (2014) Intestinal helminths of wild bonobos in forest-savanna mosaic: risk assessment of cross-species transmission with local people in the Democratic Republic of the Congo. *EcoHealth*, in review
Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A (2007) Sleeping parties and nest distribution of chimpanzees in the savanna Woodland, Ugalla, Tanzania. Int J Primatol 28:1397–1412
Peterson D (2003) Great apes as food. Gastronomica 3:64–70
Pontzer H, Wrangham RW (2006) Ontogeny of ranging in wild chimpanzees. Int J Primatol 27:295–309
Pruetz JD (2006) Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: G Hohmann, MM Robbins, C Boesch (eds) Feeding ecology in apes and other primates. Ecological, physiological and behavioural aspects. Cambridge University Press, New York, pp 161–182
Pusey AE, Oehlert GW, Williams JM, Goodall J (2005) Influence of ecological and social factors on body mass of wild chimpanzees. Int J Primatol 26:3–31
Reynolds V (1975) How wild are the Gombe chimpanzees? Man 10:123–125
Sak B, Petrzelkova KJ, Kvetonova D, Mynarova A, Shutt KA, Pomajbikova K, Kalousova B, Modry D, Benavides J, Todd A (2013) Long-term monitoring of microsporidia, cryptosporidium and giardia infections in Western Lowland gorillas (*Gorilla gorilla gorilla*) at different stages of habituation in dzanga sangha protected areas Central African Republic. PloS One 8:e71840. doi:10.1371/journal.pone.0071840
Shutt K, Heistermann M, Kasim A, Todd A, Kalousova B, Profosouva I, Petrzelkova K, Fuh T, Dicky J-F, Bopalanzognako J-B, Setchell JM (2014) Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. Biol Cons 172:72–79
Sommer V, Adanu J, Faucher I, Fowler A (2004) Nigerian chimpanzees (*Pan troglodytes vellerosus*) at Gashaka: two years of habituation efforts. Folia Primatol 75:295–316
Thompson JM (2002) Bonobos of the Lukuru Wildlife Research Project. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 61–70
Thompson JM, Nestor LM, Kabanda RB (2008) Traditional land-use practices for bonobo conservation. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology and conservation. Springer, New York, pp 227–244
Turner SE, Fedigan LM, Nobuhara H, Nobuhara T, Matthews HD, Nakamichi M (2008) Monkeys with disabilities: prevalence and severity of congenital limb malformations in *Macaca fuscata* on Awaji Island. Primates 49:223–226
Tutin CEG, Fernandez M (1991) Responses of wild chimpanzees and gorillas to the arrival of primatologists: behaviour observed during habituation. In: Box HO (ed) Primate responses to environmental change. Springer, New York, pp 187–197
Tutin CE, McGrew WC, Baldwin PJ (1983) Social organization of savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Senegal. Primates 24:154–173
Van Elsacker L, Vervaecke H, Verheyen RF (1995) A review of terminology on aggregation patterns in bonobos (*Pan paniscus*). Int J Primatol 16:37–52
Van Krunkelsven E, Dupain J, van Elsacker L, Verheyen R (1999) Habituation of bonobos (*Pan paniscus*): first reactions to the presence of observers and the evolution of response over time. Folia Primatol 70:365–368
Vereecke EE, D'Août K (2011) Introduction. primate locomotion: toward a synergy of laboratory and field research. In: D'Août K, Vereecke EE (eds) Primate locomotion: linking field and laboratory research. Springer, New York, pp 1–6
Williamson EA, Feistner AT (2003) Habituating primates: processes, techniques, variables and ethics. In: Setchell JM, Curtis DJ (eds) Field and laboratory methods in primatology: a practical guide. Cambridge University Press, Cambridge, pp 25–39
Woodford MH, Butynski TM, Karesh WB (2002) Habituating the great apes: the disease risks. Oryx 36:153–160
Wrangham RW (2008) Foreward to ecological study section. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology and conservation. Springer, New York, pp 97–100
Zimbler-DeLorenzo HS, Stone AI (2011) Integration of field and captive studies for understanding the behavioral ecology of the squirrel monkey (*Saimiri* sp.). Am J Primatol 73:607–622