



## Why do wild bonobos not use tools like chimpanzees do?

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### Abstract

One of the most conspicuous behavioural differences among great apes is the paucity of tool use among wild bonobos (*Pan paniscus*) in comparison to chimpanzees (*Pan troglodytes*) who are one of the most prolific and skilled tool users in the animal kingdom. This is in spite of the fact that bonobo tool use repertoires are as large and diverse as chimpanzees' in captive settings. In this study, we compared tool using behaviours and potential drivers of these behaviours in the Wamba bonobo population located in central Democratic Republic of Congo with the Goualougo chimpanzee population of northern Republic of Congo. The tool use repertoire of wild bonobos was comprised of only 13 behaviours, compared to 42 for chimpanzees. However, the number of tool behaviours observed in each study site was similar between bonobos and chimpanzees, and many types of tool use for social, self-grooming/stimulation, and comfort/protection functions were commonly used by both species. A marked difference is that 25 of 42 tool behaviours exhibited by chimpanzees are performed for feeding, in contrast to a single report of bonobos using a leaf sponge to drink water. We examined whether the differences in tool use repertoires can be explained by the necessity, opportunity, relative profitability, or invention hypotheses. We found that habitat composition and fluctuation of fruit production at these two sites were similar, particularly when compared with variation observed between sites within each species. Thus it was unlikely that the necessity hypothesis explains the lack of tool use for feeding in bonobos. Though

further study at Wamba is needed, we did not identify any obvious differences in prey availability that would indicate differences in tool using opportunities between the sites. This study could not test the relative profitability hypothesis, and further research is needed on whether tool use is the most efficient means of calorie or protein intake for wild apes. Bonobos at Wamba formed much larger and stable parties than chimpanzees at Goulougo, which was contrary to the prediction by the invention hypothesis. Another explanation is that differences in tool use behaviour between bonobos and chimpanzees might not be explained by the current ecological or social conditions, but rather by circumstances during the Pleistocene Epoch. The observed species differences might also reflect divergent behavioural predispositions, rather than actual differences in cognitive abilities.

### Keywords

bonobo, chimpanzee, *Pan paniscus*, *Pan troglodytes*, tool use, environmental condition.

## 1. Introduction

Comparisons of bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*) lifestyles have revealed several intriguing differences between these closely related apes (Kano, 1992; Fruth et al., 1999). These allopatric species reside in the equatorial forests of Africa, separated by the Congo River. They both live in multi-male multi-female groups with male philopatry and a fission-fusion social structure (Kano, 1982a). One of the most conspicuous behavioural differences between these apes is the rarity of tool use among wild bonobos in comparison to chimpanzees who are one of the most prolific and skilled tool users in the animal kingdom (McGrew, 1992; Sanz & Morgan, 2007; Shumaker et al., 2011). An increased knowledge of the ecology and sociality of wild bonobos and the central subspecies of chimpanzee (*P. t. troglodytes*) now makes it possible to examine the specific environmental and social factors which may elicit tool use among chimpanzees and bonobos. Such a comparison is particularly informative because chimpanzees inhabiting the Congo Basin exist within habitat types that are more similar to bonobos than other chimpanzee subspecies residing at the edges of the species range. In this study, we compare tool use behaviours and potential drivers of these behaviours in the Wamba bonobo population located in central Democratic Republic of Congo with the Goulougo chimpanzee population of northern Republic of Congo.

Despite years of field research at multiple study sites, there are few reports of tool use by bonobos in natural settings (Kano, 1982b; Ingmanson, 1996; Hohmann & Fruth, 2003a). As we will show in this paper, the species repertoire is comprised of 13 tool use behaviours, compared to more than forty for

chimpanzees (Sanz & Morgan, 2007). In striking contrast to chimpanzees, there are no reports of bonobos using tools in a feeding context except using a leaf sponge to drink water. This is despite the fact that bonobos are capable of using tools to obtain food, as shown by reports from captive populations (Jordan, 1982; Gold, 2002; Gruber et al., 2010; Shumaker et al., 2011; Boose et al., 2013).

Ecological and social factors are typically examined in isolation, but it is likely that a combination of these factors shape the emergence and maintenance of tool use in natural settings. Recent studies addressing the drivers of tool use cite some iteration of the Necessity and Opportunity Hypotheses, which state that tool use is a behavioural response to the absolute abundance of ecological resources or opportunities in the environment (Spagnoletti et al., 2012; Koops et al., 2013; Sanz et al., 2013b). More specifically, the Necessity Hypothesis posits that tool use is a response to resource scarcity which drives its practitioners to exploit novel food items during times of low resource availability (Fox et al., 1999). The Opportunity Hypothesis proposes that repeated exposure to appropriate conditions, such as encounters with target items and availability of tool materials, prompts the emergence and/or maintenance of tool use behaviours (Fox et al., 1999). Shifting the emphasis away from absolute abundance, the Relative Profitability Hypothesis suggests that tool-assisted feeding strategies targeted at embedded food items would be expected when it is more profitable than conventional methods of gathering more accessible foods (Rutz et al., 2010; Rutz & St Clair, 2012). Representing the social forces in the evolution of tool use, the Invention Hypothesis states that “behaviours such as tool use are rarely invented, and that the spread and maintenance of such behaviours requires sufficient opportunities for observational learning via social proximity to conspecifics” (Fox et al., 2004: p. 163). Recent research in both wild and captive settings has led to increasing recognition of the role of social transmission in maintaining technological traditions (Lonsdorf, 2006; Whiten et al., 2007).

The aim of this study is to review differences in bonobo and chimpanzee tool use repertoires and assess to what extent these differences can be attributed to necessity, opportunity, relative profitability, or invention (Table 1). We address these hypotheses using behavioural observations and ecological data from bonobos at Wamba in Democratic Republic of Congo and chimpanzees of the Goulougo Triangle in Republic of Congo. (1) The absence

**Table 1.**

Hypotheses to explain the difference in tool use for foraging.

| Hypothesis                            | Prediction   | Data to be examined  | Results  |
|---------------------------------------|--|--|--|
| (1) Necessity hypothesis              | Preferred foods are more abundant at Wamba   | Total basal area of trees per unit area  | Not supported (basal area was similar between two sites)   |
|                                       | Bonobos at Wamba experience a lesser degree of seasonal resource scarcity                    | Pattern and degree of fluctuation of fruit availability<br>Feeding behaviour during the season of fruit scarcity | Not fully supported (lesser degree of fluctuation of fruit availability, but the difference was small; feeding behaviour during fruit scarcity was similar).                     |
| (2) Opportunity hypothesis            | Tool use opportunities are absent or far less abundant at Wamba                              | Availability and abundance of foods potentially eaten with tools   | Not fully supported (similar foods potentially eaten with tools existed in both sites, but species level identification or quantitative data for comparison were not available). |
| (3) Relative profitability hypothesis | Energetic gains of tool-assisted strategies exceed that of conventional foraging in Goulougo | Per-unit-time energetic gain of tool-assisted and conventional feeding behaviours                                | Not examined in this study.  |
| (4) Invention hypothesis              | Parties of chimpanzees in Goulougo are larger than those of bonobos at Wamba                 | Mean party size  | Not supported (party size in Goulougo was smaller than that at Wamba).   |

of tool use for feeding by bonobos would be explained by the Necessity Hypothesis if their preferred foods are more abundant and if they experience a lesser degree of seasonal resource scarcity than chimpanzees. (2) To explain the absence of feeding tool use by bonobos, one might also postulate

that tool use opportunities are absent or far less abundant in bonobo habitats than chimpanzee habitats, which would support the Opportunity Hypothesis. (3) The Relative Profitability Hypothesis predicts that the energetic gains of tool-assisted strategies exceed that of conventional feeding. (4) With regard to the Invention Hypothesis, one could predict that chimpanzee parties are larger and thus provide more opportunities for social transmission of technological information among independent individuals. In this manuscript, we also summarize and propose additional possible explanations and evolutionary scenarios for the differences in tool use between *Pan* species.

## 2. Methods

### 2.1. Wamba, Democratic Republic of the Congo

The Wamba study area is located in the northern section of the Luo Scientific Reserve (22°34'E, 0°01'N), Democratic Republic of the Congo. This area is included in the Congo-equatorial climatic zone. The main habitat type is primary forest, including some areas of old secondary forest. This habitat type occurs on terra firma and is characterized by species of the Caesalpiniaceae family, with some narrow bands of monodominant *Gilbertiodendron dewevrei* forest occurring along the boundaries of swamp forests. The second main habitat type is swamp forest that exists along the Luo River and its tributaries. Most of the swamp forest is inundated all year, but a part of it near the terra firma is seasonally inundated. This habitat type is characterized by a complex mosaic of species, mainly representing the Caesalpiniaceae and Euphorbiaceae families. The northern section of the Luo Scientific Reserve contains homesteads, and so this area also includes agricultural complexes and young secondary forest (Idani et al., 1994; Hashimoto et al., 1998).

To monitor fruit abundance, we used five line transects and reconnaissance paths, the total length of which was 22.550 km (Mulavwa et al., 2008). Each trail was surveyed twice a month. We recorded the number of clusters of fallen fruit that were found within 1 m on each side of the trail, the number of fruits in each cluster, species of fruit, and whether they were ripe or unripe. The validity of this approach was established by Furuichi et al. (2001) who showed that the abundance of chimpanzee fruit foods at Kalinzu in Uganda was sufficiently evaluated by the number of clusters of ripe fallen fruits. Furthermore, Mulavwa et al. (2008) compared the numbers of ripe-fruit clusters of all species and the food species of bonobos at Wamba, and

found that these numbers fluctuated proportionately. Therefore, in this study, we evaluated abundance of fruit foods based on the number of clusters of ripe fallen fruits of all species per km of transect.

A main study group of bonobos, group E, was habituated to the presence of researchers and has been observed since 1976. The group has subsequently split into two groups, E1 and E2. Another group, P, was also habituated and has been observed since the 1980's. Observations were made using artificial provisioning during some part of each year until 1996, but currently groups E1 and P are being observed from nest to nest under the natural conditions (Kano, 1992; Furuichi et al., 2012). In November 2012, group E1 consisted of 31 individuals, including 7 adult males and 9 adult females, and an eastern subgroup of P that is also continuously monitored by researchers consisted of 26 individuals, including 5 adult males and 7 adult females.

Tool use behaviours have been documented through direct observation throughout the study period (Kano, 1982b; Ingmanson, 1996). In this study, we report previously unpublished observations of tool use behaviours by bonobos at Wamba that were made before the end of 2012.

We employed the definition of the 1-h party size proposed by Hashimoto et al. (2001) for evaluating party sizes of chimpanzees. While following a party, we recorded the names of all bonobos in sight at the beginning of each hour and continued recording those bonobos that appeared in the party throughout the rest of the hour. Thus, the 1-h party represents the minimum number of bonobos that were present in the party during each 1-h observation. We also recorded the observation time in minutes in each 1-h segment. We obtained the daily 1-h party size by averaging all those observations recorded in a day, excluding those with less than 30 min of observation.

## *2.2. Goulougo Triangle, Republic of Congo*

The Goulougo Triangle study area is located along the southern boundary of the Nouabalé-Ndoki National Park (16°51'–16°56'E, 2°05'–3°03'E), Republic of Congo. The climate in northern Republic of Congo can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones. The lowland tropical forests of northern Congo are part of the regional centre of endemism Guinea–Congolian that ranges from Nigeria to the Congo Basin (White, 1986). The different habitat types in the Goulougo Triangle

have been assessed by ground surveys and satellite imagery classification (Devos et al., 2008). The main habitat types are mixed-species forest (semi-evergreen forest with high heterogeneity of species composition and occurs on terra firma), monodominant *G. dewevrei* forest (single-species formation of *G. dewevrei* which occurs along watercourses as well as on interfluvial plateaus), and gallery/swamp forest (consists of diverse flora associated with watercourses, that may be permanently or seasonally inundated).

Relative abundance of preferred chimpanzee foods was systematically assessed through establishment of two trail networks to monitor the phenological states of tree species and strangler figs known to be consumed by apes (Chapman et al., 1994). A total of 607 trees representing 47 species were monitored each month in the Goualougo Triangle. The ground under each monitored tree was systematically surveyed to determine the abundance of mature fruit fall. Relative abundance of fruit was estimated on a scale of 0 to 4, with higher scores indicating more fruit. In this study, we evaluated abundance of fruit foods based on the proportion of monitored trees with mature fruit fall.

Direct observations of the chimpanzees in the Goualougo Triangle have been ongoing since February, 1999. Individual chimpanzees were identified from their distinct physical characteristics and these data compiled in a population history database. The main study group is the Moto community which consisted of 71 individuals, including 17 adult males and 24 adult females (Morgan, 2007).

Tool use behaviours have been documented through direct observation during reconnaissance surveys of chimpanzees since the initiation of research at this site. In 2003, we also began remote video monitoring of tool use sites. For all observations of tool use, observers record the identification of the chimpanzee, type of object used, target of object, actions, context and/or goal of the tool use behaviour, and the outcome.

20-min group scans of party composition and behaviour were recorded during chimpanzee encounters. Chimpanzee parties were considered to be all individuals travelling, feeding, resting or socializing within 50 m of one another (definition adopted from (Wrangham et al., 1992; Wilson et al., 2001)). For this study, we included information from the first scan conducted each hour so as to provide a direct comparison with the 1-h sampling of bonobo party size at Wamba. Daily values of party size were based on average sizes of all recorded 20-min group scans per day, excluding those with only orphans present.

### 3. Results

#### 3.1. Habitat types and climate

Bonobos and chimpanzees inhabit a wide range of habitats across equatorial Africa (Table 2). The habitat types of bonobos range from savannah with patches of forest with 1666–1778 mm annual rainfall at Lukuru to rain forest with 2733 mm rainfall at Wamba. On the other hand, the habitat types of chimpanzees range from grassland and woodland with 954 mm rainfall at Assirik to rain forest with 3244 mm rainfall at Seringbara, including semi-evergreen forest with 1690 mm rainfall in the Goulougo Triangle. Thus, the habitat conditions of bonobos and chimpanzees largely overlap with an exception of the driest extreme in chimpanzees.

Habitat classification of satellite imagery showed that the Wamba forest is comprised mainly of primary and old secondary forest dominated by representatives of the Caesalpiniaceae family (65.5%), with swamp forest (18.9%) and young secondary forest (15.6%) representing a smaller proportion of the bonobo range (Hashimoto et al., 1998; Terada et al., unpublished data). Mixed species semi-evergreen forest (71.5%) was found to be the dominant habitat in the Goulougo Triangle, with monodominant *Gilbertiodendron dewevrei* (Caesalpiniaceae) evergreen (21.7%) and swamp forest (6.1%) also represented (Devos et al., 2008).

#### 3.2. Ape density, home range and habitat use

Ape densities were nearly identical between the two study sites. At Wamba, bonobo densities were reported to be 1.4–2.5 individuals/km<sup>2</sup> (excluding infants) based on home range estimates (Hashimoto et al., 1998). Chimpanzee density in the Goulougo Triangle was estimated to be 1.5 chimpanzees/km<sup>2</sup> (excluding infants) from line transect surveys and 2.2 chimpanzees based on home range estimates (Morgan et al., 2006). The home ranges of bonobo communities at Wamba were estimated to be 12.3–17.8 km<sup>2</sup> for the E1 study group and 22.5–31.5 km<sup>2</sup> for the E2 study group (Hashimoto et al., 1998). The Moto chimpanzee community range was estimated to be 17.3 to 19.2 km<sup>2</sup> (Morgan et al., 2006). The home ranges of both species were heterogeneous in habitat composition, but with some evidence of preference for dry forest habitats by both bonobos and chimpanzees. Both direct observations of habituated groups and nest surveys indicated that use of swamps by bonobos may exceed visitation to inundated habitats by chimpanzees (Hashimoto et al., 1998; Morgan et al., 2006; Mulavwa et al., 2010).



**Table 2.**  
Environmental conditions of study sites.

| Species             | Site               | Country | Habitat type   | Altitude (m) | Annual mean rainfall (mm)                                       | Days of rain | No. of dry months (<100 mm/month)                   | Temperature (°C) |           | Source  |
|---------------------|--------------------|---------|--|--------------|---|--------------|---|------------------|-----------|---|
|                     |                    |         |  |              |   |              |   | Mean max.        | Mean min. |   |
| <i>Pan paniscus</i> | Lac Tumba-         | DRC     | Mixed mature swampy, mixed mature seasonally inundated, mixed mature terra firma, old-secondary, and young secondary forest, circular patch of a forest-savanna mosaic | 300–700      | Around 1770 in the northern part/1500–1600 in the southern part |              | Minor dry seasons in February and July              |                  |           | Inogwabini et al. (2008); Serckx et al. (2014)      |
|                     | Lac Mai            |         |  |              |   |              |   |                  |           |   |
|                     | Ndombe hinter-land |         |  |              |   |              |   |                  |           |   |
|                     | Lui Kotale         | DRC     | Primary evergreen lowland tropical rain forest   |              | above 2000  |              | Short dry season in Feb, longer one between May–Aug | 28               | 21        | Beaune et al. (2012, 2013); Hohmann & Fruth (2003b) |
|                     | Lomako             | DRC     | Primary climax, evergreen, polyspecific rain-forest, with smaller areas of secondary growth, slope forest and swamp forest   | 390          | 1960  |              | No conspicuous dry season                           | 27.3             | 21.2      | White (1992); Myers Thompson (2002)                 |

**Table 2.**  
(Continued.)

| Species                      | Site    | Country | Habitat type  | Altitude (m) | Annual mean rainfall (mm)   | Days of rain | No. of dry months (<100 mm/month)                | Temperature (°C)      |                         | Source  |
|------------------------------|---------|---------|---|--------------|---|--------------|--|-----------------------|-------------------------|---|
|                              |         |         |   |              |   |              |  | Mean max.             | Mean min.               |   |
| <i>Pan troglodytes verus</i> | Wamba   | DRC     | Predominant primary and old secondary, with young secondary, agricultural fields, and swamp | around 390   | 2733 ± 283 (in 2004–2006, 2008, 2010–2012)                                |              | 1 to 2 months mostly around December and January | Monthly mean 31 ± 1.1 | Monthly mean 21.1 ± 0.4 | Furuichi et al., unpublished data for 2004–2012 |
|                              | Lukuru  | DRC     | Dry forest and grassland  | 564          | long-term data (1941–1963) at proximate sites: 1666 (Ilebo), 1778 (Lodja) |              |  | 35.5                  | 19.5                    | Myers Thompson (2002)                           |
|                              | Assirik | Senegal | Grassland and woodland with small amounts of riverine forest and bamboo thicket             | 100–311      | 954 (824–1224) (in 1976–1979)   | 84           | 7  | 35                    | 23                      | McGrew et al. (1981); Hunt & McGrew (2002)      |

**Table 2.**  
(Continued.)

| Species                            | Site         | Country       | Habitat type   | Altitude (m)  | Annual mean rainfall (mm) | Days of rain                            | No. of dry months (<100 mm/month) | Temperature (°C)                |  | Source                                  |
|------------------------------------|--------------|---------------|--|---------------|---------------------------|---|-----------------------------------|---------------------------------|--|---|
|                                    |              |               |  |               |                           |   |                                   | Mean max.                       | Mean min.                                    |   |
| <i>Pan troglodytes troglodytes</i> | Serings-bara | Guinea        | Primary tropical forest, montane forest, riverine forest, high-altitude grasslands                 | 600–1752      | 3244 (in 2008)            | 4                                       | 4                                 | 24.5                            | 18.7   | Koops (2011); Koops et al. (2012, 2013) |
|                                    | Bossou       | Guinea        | Mosaic of primary, secondary, riverine, and scrub forest, as well as farmland                      | 550 (village) | 2230 (in 1995)            | 4                                       | 4                                 | 26.1 (1.5 m high in the forest) | 21.0 (1.5 m high in the forest)              | Yamakoshi, 1998; Takemoto, 2004         |
|                                    | Tai          | Côte d'Ivoire | Evergreen lowland rain forest (with only the swamp forest along the rivulet less densely forested) |               | 1829                      | 3 in Figure 1.3 (Boesch & Boesch, 2000) | 30                                | 24                              | Boesch & Boesch (2000); Hunt & McGrew (2002) |   |
|                                    | Lopé         | Gabon         | Tropical rain forest   |               | 1531                      |   |                                   |                                 |  | Hunt & McGrew (2002)                    |

**Table 2.**  
(Continued.)

| Species                   | Site                | Country | Habitat type   | Altitude (m) | Annual mean rainfall (mm) | Days of rain | No. of dry months (<100 mm/month)      | Temperature (°C) |            | Source                                       |
|---------------------------|---------------------|---------|--|--------------|---------------------------|--------------|--|------------------|------------|--|
|                           |                     |         |  |              |                           |              |  | Mean max.        | Mean min.  |  |
| <i>Pan troglodytes</i>    | Noua-bale-Ndoki     | Congo   | Swamp forest, <i>Gilbertiodendron</i> forest, and mixed species forest   | 1430         | 1430                      |              | December–February                      |                  |            | Nishihara (1995)                             |
|                           | Goua-lougo Triangle | Congo   | Predominant mixed species semi-evergreen forest, with monodominant <i>Gilbertiodendron dewevrei</i> evergreen and swamp forest |              | 1690 ± 27 (in 2007–2011)  |              | 2–4 months around December and January | 23.7 ± 0.8       | 21.5 ± 0.6 | Morgan et al. (2006); Sanz & Morgan (2013b)  |
| <i>Pan schweinfurthii</i> | Kahuzi-Biega        | DRC     | Bamboo forest (37%), primary montane forest (28%), secondary montane forest (20%), swamp (7%)                                  | 2050–2350    | 1800                      |              |  |                  |            | Yamagiwa et al. (1996); Hunt & McGrew (2002) |

**Table 2.**  
(Continued.)

| Species | Site    | Country | Habitat type  | Altitude (m) | Annual mean rainfall (mm)   | Days of rain | No. of dry months (<100 mm/month)  | Temperature (°C) |           | Source                                 |
|---------|---------|---------|---|--------------|---|--------------|--|------------------|-----------|--|
|         |         |         |   |              |   |              |  | Mean max.        | Mean min. |  |
|         | Kalinzu | Uganda  | Medium altitude moist evergreen forest                                | 1000–        | 1584 (years: 1997–1998)   |              | 6 months (Jan–Mar, Jun–Aug)  | 25–28            | 14–17     | Howerd (1991); Hashimoto et al. (1999) |
|         |         |         |   | 1500         |   |              |  |                  |           |  |
|         | Kibale  | Uganda  | Moist semi-deciduous forest with grassland, woodland and swamp forest | 1110–        | 1475 (in 1970–1991), 1749 (in 1990–2001) (Kanyawara); 1393 ± 200 (in 1998–2009) (Ngogo) |              |  | 23               | 16        | Hunt & McGrew (2002); Watts (2012)     |
|         |         |         |   | 1590/        |   |              |  |                  |           |  |
|         |         |         |   | 1470–        |   |              |  |                  |           |  |
|         |         |         |   | 1750         |   |              |  |                  |           |  |
|         | Budongo | Uganda  | Moist, semi-deciduous tropical rain forest and grassland              | 1100         | 1600 (range 1240–2187, in 1993–2000)  |              | between mid-December and mid-February (50 mm or less per month); 4 months with <100 mm | 32               | 19        | Wallis (2002); Reynolds (2005)         |
|         |         |         |   | (aver-       |   |              |  |                  |           |  |
|         |         |         |   | age)         |   |              |  |                  |           |  |

**Table 2.**  
(Continued.)

| Species | Site    | Country  | Habitat type  | Altitude (m) | Annual mean rainfall (mm) | Days of rain | No. of dry months (<100 mm/month)  | Temperature (°C) |           | Source                                     |
|---------|---------|----------|---|--------------|---------------------------|--------------|------------------------------------|------------------|-----------|--|
|         |         |          |   |              |                           |              |                                    | Mean max.        | Mean min. |  |
|         | Semliki | Uganda   | Dry <i>Combretum ghasalense</i> savanna and <i>Borassus aethiopicum</i> palm savannah with gallery forest |              | 1206                      | 151          | 5                                  | 34               | 20        | Hunt & McGrew (2002); Samson & Hunt (2012) |
|         | Gombe   | Tanzania | Alternating thick riverine forests, deciduous woodland, and hilltop grassland                             |              | 1775                      | 152          | 6 (dry season from May to October) | 28               | 19        | Hunt & McGrew (2002); Wallis (2002)        |
|         | Mahale  | Tanzania | Semi-deciduous savannah woodland with montane forest and continuous gallery forest                        | 780–1300     | 1836                      | 143          | 5                                  | 29               | 18        | Nishida (1990); Takasaki et al. (1990)     |

**Table 2.**  
(Continued.)

| Species  | Site | Country  | Habitat type  | Altitude (m) | Annual mean rainfall (mm)                          | Days of rain | No. of dry months (<100 mm/month)                              | Temperature (°C)                     |  | Source   |
|----------|------|----------|---|--------------|--|--------------|--|--------------------------------------|--|--|
|          |      |          |   |              |  |              |  | Mean max.                            | Mean min.                                |  |
| Kasakati |      | Tanzania | Woodland (59%), savannah (16%), grassland (16%), forest (10%) | 750          | 962 (in 1941–1970 (Kigoma))                        |              | 6 months of <60 mm (1941–1970)                                 | 28                                   | 19                                       | McGrew et al. (1981); Moore (1992)                           |
|          |      |          |   |              |  |              |  | (1941–1970 at Kigoma)                | (1941–1970 at Kigoma)                    |  |
| Ugalla   |      | Tanzania | Woodland (91%), swamp (5%), bamboo (3%)                       | 900–1800     | 1012.3 ± 139.1 (in 1973–1988) (Uvinza); 955 (Issa) |              | 5.2 ± 0.8 months with <60 mm (1973–1988); May–Oct with <100 mm | Average daily max: 34 (Aug)–28 (Nov) | Average daily max: 17.2 (Jan)–14.4 (Aug) | McGrew et al. (1981); Moore (1992); Hernandez-Aguilar (2009) |

### 3.3. Tool use repertoire

The bonobo tool use repertoire was comprised of 13 different types of tools (Table 3), with 10 types of tool use exhibited by the Wamba population.

**Table 3.**

Compilation of tool using behaviours observed in wild bonobos.

| Context | Behaviour       | Code | Description   | Sex of performer | Observed sites |        |
|---------|-----------------|------|---|------------------|----------------|--------|
|         |                 |      |   |                  | Wamba          | Lomako |
| Social  | Play start      | 2*   | Taking a branch, small leafy twig or fruit in hand or mouth and chasing of others in a play context. Possession of object sometimes changes (sharing the same object)   | M, F             | +              | +      |
|         | Drag branch     | 3*   | Dragging a branch toward one or more target individual(s) in threat. Targets sometimes ignore this agonistic approach. Dragging a branch before departure or during ranging without targeting conspecifics. Usually performed by males to propose direction of ranging. | M, F             | +              | +      |
|         | Drop twigs      | –    | Clipping twigs or small branches and dropping them from tree to get attention from opposite sex (may be to solicit copulation)  | M, F**           | +              | –      |
|         | Aimed-throw     | 49   | Throwing sticks and branches at human observers and at other bonobos. Bonobos at Wamba just drop twigs or branches to human observers.  | M, F             | +              | +      |
|         | Leaf-clip mouth | 53   | Clipping leaves from herbs or trees by mouth to get attention from play partner.  | M, F             | –              | +      |



**Table 3.**  
(Continued.)

| Context               | Behaviour                 | Code | Description  | Sex of performer | Observed sites |        |
|-----------------------|---------------------------|------|--|------------------|----------------|--------|
|                       |                           |      |  |                  | Wamba          | Lomako |
|                       | Leaf-clip fingers         | 54   | Clipping leaves from herbs or trees by finger to solicit mates.  | F                | –              | +      |
| Comfort, protection   | Leaf-umbrella or rain-hat | –    | Detaching small branches or twigs and put them on their head under heavy rain  | M, F             | +              | –      |
|                       | Leaf cover                | –    | Detaching small branch or twig and using it as a cover over their nest. Common during the rainy season, possibly for thermoregulation. At Wamba one adult male bent a small branch to cover his body on his day nest | M, F             | +              | +      |
|                       | Fly-whisk                 | 47   | Swatting or whisking away sweat bees by waving and shaking small, leafy twigs  | F                | +              | +      |
| Self-groom, stimulate | Leaf-napkin               | 50   | Using leaves to wipe faeces or urine from one's own body   | M, F             | +              | –      |
|                       | Toothpick                 | –    | After feeding, using a small twig to remove debris from between teeth  | M                | +              | –      |
| Feeding               | Stick scratch             | –    | Scratching one's own back with small twig  | M, F             | +              | –      |
|                       | Leaf-sponge               | 4*   | Dipping water from a tree hole using moss. Seemed to be equivalent of leaf sponge behavior by chimpanzees  | F                | –              | +      |

Contexts refer to those in Sanz & Morgan (2007). Names and code numbers of behaviours refer to those in Whiten et al. (1999), except for what are not observed in chimpanzees (marked –). Source of information for Wamba: Kano (1982b, 1997); Ingmanson (1996); this study; for Lomako: Hohmann & Fruth (2003a).

\* Universal chimpanzee tool use behaviours (Whiten et al., 1999).

\*\* Performance of this behaviour by females was first reported by this study.

**Table 4.**

Types of tool behaviours observed in chimpanzees and bonobos.

|            | Number of all types | Number of types at each site  | Context |                     |                       |         |       |
|------------|---------------------|-------------------------------|---------|---------------------|-----------------------|---------|-------|
|            |                     |                               | Social  | Comfort, protection | Self-groom, stimulate | Feeding | Other |
| Chimpanzee | 42                  | 6 (Assirik)–<br>22 (Goulougo) | 5       | 4                   | 5                     | 25      | 3     |
| Bonobo     | 13                  | 8 (Lomako)–<br>10 (Wamba)     | 6       | 3                   | 3                     | 1       | 0     |

Data for chimpanzees from Sanz & Morgan (2007).

Chimpanzees in the Goulougo Triangle exhibited 22 different types of tool use, which is approximately half of the species repertoire (Sanz & Morgan, 2007). The number of tool behaviours found at chimpanzee study sites varied from 22 in Goulougo to 6 in Assirik. Hence, the numbers of tool behaviours at bonobos study sites (10 in Wamba and 8 in Lomako) are within the range of variation in chimpanzees (Table 4) (Sanz & Morgan, 2007). Chimpanzee tool use was most common in feeding contexts, but was also exhibited in self grooming/stimulation, comfort/protection, and social situations. Bonobo tool use mainly had social (self-grooming/stimulation and comfort/protection) functions, except for one behaviour for feeding (leaf sponge to drink water). Among 13 tool behaviours, 8 were common in chimpanzees and 5 were uniquely found in bonobos. Out of 4 chimpanzee universal tool behaviours, 3 were observed in bonobos (play start, drag branch, leaf-sponge) but 1 was not observed (investigatory probe).

A marked difference in tool behaviours between chimpanzees and bonobos is the very limited tool use for feeding in bonobos (Table 4). In chimpanzees, 25 of 42 tool behaviours were performed for feeding (Sanz & Morgan, 2007). By contrast, tool use for feeding was observed only once in Lomako, in the use of a leaf-sponge (Hohmann & Fruth, 2003a). Therefore, what we really need to examine is why wild bonobos do not use tools for feeding.

### 3.4. Abundance of preferred resources

Similar to other bonobo and chimpanzee populations, the diet of apes at Wamba and Goulougo was primarily comprised of ripe fruits (Kano & Mulavwa, 1984; Morgan & Sanz, 2006). As an indication of the overall

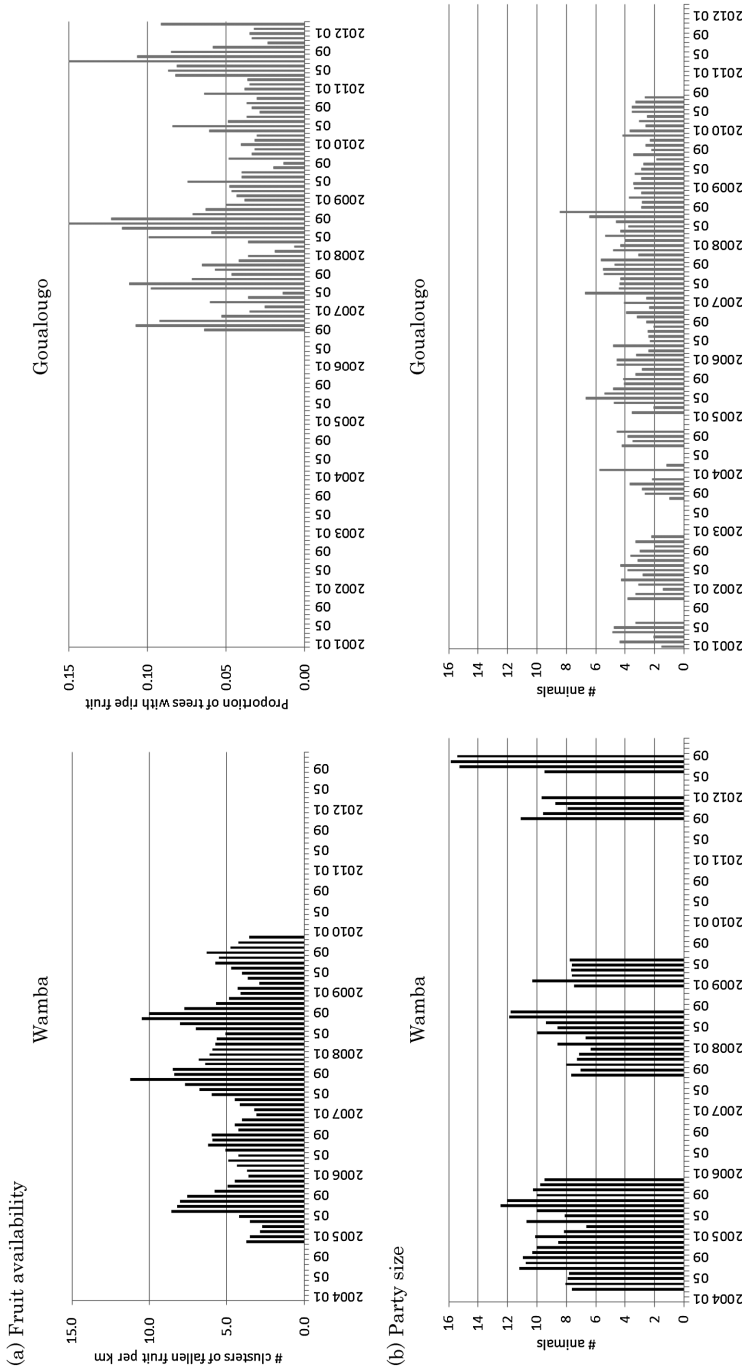
abundance of food resources, we compared the total basal area of all trees with DBH greater than 5 cm in Wamba and of all trees with DBH greater than 10 cm in Goualougo. The basal area for Wamba is 33.27 m<sup>2</sup> per hectare for primary forest (including old secondary forest), 28.50 for swamp forest, 21.90 for young secondary forest (calculated from DBH<sup>2</sup> in Idani et al., 1994) and that for Goualougo is 34.04 m<sup>2</sup> per hectare (Morgan & Sanz, 2006). Due to the difference in sampling (inclusion of a larger sample of trees than Goualougo), the per-hectare total basal area of trees at Wamba must be somewhat overestimated as compared to Goualougo. Therefore, we can conservatively conclude that the total basal area in Wamba is not greater than at Goualougo.

Though we do not have comparable data for absolute abundance of ripe fruit, we compared the pattern of seasonal fluctuation in abundance using parameters that represent proportion of trees with ripe fruit (Figure 1a). The monthly proportion of trees with ripe fruit on the ground showed similarly stochastic fluctuations between the sites, though the degree of fluctuation was greater in Goualougo (Wamba:  $5.5 \pm 2.0$  clusters per km of transect, CV = 0.35,  $N = 61$ ; Goualougo:  $5.6 \pm 3.2\%$  of monitored trees, CV = 0.56,  $N = 67$ ). When fruits were scarce, bonobos at Wamba increased their intake of seeds, leaves, and terrestrial herbs (Kano & Mulavwa, 1984), and chimpanzees in the Goualougo Triangle similarly compensated by increasing their intake of leaves (Morgan & Sanz, 2006; Sanz & Morgan, 2013b).

Overall, although the degree of fluctuation in availability of ripe fruit was greater in Goualougo, similar per-hectare tree basal areas and similar tendencies of food shift during fruit scarcity, together with similar density of bonobos and chimpanzees mentioned in the previous section, suggests that the differences in the food conditions between Wamba and Goualougo were much smaller than differences among sites of each species (Table 2).

### 3.5. Ecological opportunities for feeding with tools

In the Goualougo Triangle, tools are used to harvest several species of termites (*Macrotermes muelleri* and *M. lilljeborgi*), army ants (*Dorylus mayri*, *D. rubellus*, *D. sjoestedti* and *D. wilverthi*), and the honey of stingless bees (*Trigona* spp.). Although we have not yet assessed the availability and distribution of these different insect species at Wamba, we confirmed that these insects (or their products) are present. Seemingly, there are ample ecological opportunities (i.e., termites, army ants, bees and suitable raw materials)



**Figure 1.** Comparison of ecological variables at Wamba and Goualougo. (a) Seasonal fluctuation in availability of ripe fruit resources at Wamba and Goualougo. Values for Wamba show the number of clusters of ripe fallen fruit per km of transect. Values for Goualougo show proportion of food trees with ripe fruit on the ground. (b) Monthly mean of daily party sizes for the E1 group of bonobos at Wamba and chimpanzees at Goualougo. Party size included adults, adolescents, and juveniles, but excluded infants.

at Wamba for termite fishing, ant dipping, ant fishing, and honey gathering tool use, which is similar to research findings at Lui Kotale (McGrew et al., 2007). We also confirmed the presence of oil palms (*Elaeis guineensis*) at Wamba which are the target of pestle pounding and nut cracking by chimpanzees at Bossou and other sites (Humble & Matsuzawa, 2004).

### 3.6. Opportunities for social transmission of technical information

As shown in Figure 1b, bonobos at Wamba consistently gathered in larger parties than chimpanzees in Goulougo (monthly mean party size at Wamba:  $9.4 \pm 2.2$  animals,  $CV = 0.23$ ,  $N = 50$ ; Goulougo:  $3.5 \pm 1.3$  animals,  $CV = 0.36$ ,  $N = 97$ ). There was a significant difference in party size if we compared those in the periods for which data was available for both sites (matched-pair  $t$ -test,  $t = -15.1$ ,  $df = 38$ ,  $p < 0.0001$ ). This difference in party size was further corroborated by mean nest group size of  $9.3 \pm 4.9$  ( $N = 215$ , range 1, 24) bonobo nests in Wamba (Mulavwa et al., 2010) versus  $2.75 \pm 1.88$  ( $N = 375$ , range: 1, 12) chimpanzee nests in Goulougo (Morgan et al., 2006).

### 3.7. Correlations among examined factors

We examined potential relationships among factors that may influence tool use behaviours: fruit abundance and party size in each site. For Wamba, there was no significant correlation between these factors ( $r = 0.31$ , n.s.). On the other hand for Goulougo, significant correlation was found between these factors ( $r = 0.40$ ,  $n = 48$ ,  $p < 0.01$ ).

## 4. Discussion

The aim of this study was to review differences in chimpanzee and bonobo tool use and examine whether these differences could be attributed to current hypotheses outlining various ecological and social factors suggested to be responsible for the emergence and maintenance of tool traditions (Table 1). Our comparison of tool behaviours between bonobos and chimpanzees revealed that the main difference between the two species exists in their repertoires of tool use for feeding, which is large and diverse in chimpanzees and nearly absent in bonobos. On the other hand, our comparisons of ecological and social conditions between Wamba and Goulougo, and comparisons of habitat conditions across various *Pan* study sites, suggested that it is difficult to explain the differences in tool use repertoires between the two species based

on current ecological or social conditions. Our review of current evidence for *Pan* tool use led us to conclude that understanding the differences in the expression of tool use between chimpanzees and bonobos will require alternative ecological, behavioural, or social explanations.

In the reported difference in tool use between wild bonobos and chimpanzees, we may have overemphasized the contrast or false dichotomy between the two *Pan* species (Stanford, 1998; Fruth et al., 1999). The size of the Wamba tool repertoire was smaller than that of chimpanzees in Goulougo, but still within the range of the number of tools used by each chimpanzee (Sanz & Morgan, 2007). Although we did not quantify the frequency of tool use in this comparison, our impression is that tool use was less frequently exhibited by bonobos than chimpanzees. This species difference is largely due to the fact that wild bonobos do not use tools in feeding, except for an observation of tool use for drinking water by bonobos in Lomako (Hohmann & Fruth, 2003a). In Goulougo and in other chimpanzee populations, tool-assisted feeding occurs on a regular basis and can occupy a significant portion of the daily activity budget (Pandolfi et al., 2003; Bogart & Pruetz, 2011). Another difference is the absence of investigatory probing in bonobos which is a universal behaviour among chimpanzee populations (Whiten et al., 2001). Many of the behavioural elements involved in investigatory probing can be generalized to tool-assisted feeding situations that involve probes or dipping implements, such as termite fishing, ant dipping, or fluid dipping (Sanz & Morgan, 2010). It has been well-documented that bonobos have the physical and cognitive abilities to exhibit such tool behaviours (Gruber et al., 2010; Boose et al., 2013), and so there may exist other factors which elicit these tool use behaviours in wild chimpanzees, but not in bonobos.

For the Necessity Hypothesis to explain the difference in bonobo and chimpanzee tool use, we would expect to find that bonobos have a more stable food resource base than chimpanzees. This would effectively alleviate the need for tool-assisted fallback strategies. In support of this, chimpanzee tool use was negatively correlated with abundance of ripe fruit at Bossou in Guinea (Yamakoshi, 1998). In environments with few typically preferred foods, tool use may also be a strategy to harvest staple food items. This may be the case for some types of chimpanzee tool use at savannah sites, such as the termite gathering of chimpanzees at Fongoli in Senegal (Bogart &

Pruetz, 2011) and possibly the tuber harvesting by chimpanzees at Ugalla in Tanzania (Hernandez-Aguilar et al., 2007).

However, a recent review of studies that have explored the ecological dimension of the presence or absence of technology clearly shows that necessity may play a less prominent role in prompting and promoting tool use than previously suggested (Sanz & Morgan, 2013b). The Necessity Hypothesis was explicitly tested and a lack of support was cited for nut cracking tool use by capuchins at Boa Vista in Brazil (Spagnoletti et al., 2012), tool use to extract insects from tree holes and extract seeds from *Neesia* fruit by orangutans across Borneo and Sumatra (Fox et al., 2004), and various forms of chimpanzee tool use at Seringbara in Guinea (Koops et al., 2013). The Goulougo chimpanzee population also does not seem to compensate for the lack of fruit resources by increasing their frequency of tool use for social insects or honey (Sanz & Morgan, 2013b). Rather, opportunities to gather termites, ants, and honey were available throughout the year to this chimpanzee population and enhanced by the use of tool sets (Sanz et al., 2004, 2010; Sanz & Morgan, 2009). Profiles of tool use at the savannah sites of Assirik in Senegal and Ugalla in Tanzania did not fit the traditional predictions of the Necessity Hypothesis in that tool use did not increase during periods of food scarcity (Hernandez-Aguilar et al., 2007; Bogart & Pruetz, 2011), but rather may be a necessary response to the lower overall abundance of preferred resources in arid habitats.

Our comparison between Wamba and Goulougo revealed that availability of ripe fruit, the main food of bonobos and chimpanzees, showed similar patterns of seasonal fluctuation, and therefore did not support the Necessity Hypothesis to explain the *Pan* difference in tool repertoires for feeding. The extent of fluctuation was somewhat greater in Goulougo, suggesting that Goulougo chimpanzees might experience more severe periods of fruit scarcity. However, Sanz & Morgan (2013b) reported that frequency of tool use for feeding by chimpanzees in Goulougo was not related to the proportion of fruiting trees, suggesting that this degree of difference in seasonal fluctuation may not sufficiently explain the marked difference in tool use for feeding between bonobos at Wamba and chimpanzees at Goulougo. During times of fruit scarcity, both apes increased their consumption of terrestrial herbaceous vegetation and leaves which fit the profile of traditional fallback foods (Marshall & Wrangham, 2007). Recent research also showed that there is no substantial difference in the kind and use of fallback food between

chimpanzees and bonobos (Harrison & Marshall, 2011). Furthermore, unpublished data by KK and DM showed that the density of terrestrial herbs was not higher in Wamba than in Goualougo (Wamba: 230 plots of  $2 \times 2$  m,  $1.51 \pm 2.10$  stems of Marantaceae and Zingiberaceae/m<sup>2</sup>; Goualougo: 7 plots of  $5 \times 50$  m,  $2.08 \pm 0.74$  stems of herbs/m<sup>2</sup>). Hence, it is unlikely that the availability of fallback foods during fruit scarcity explains the lack of tool use for feeding in bonobos.

According to the Opportunity Hypothesis, tool use is related to the frequency of encounters with particular tool targets (termites, ants, honey, etc.) or tool materials that may vary seasonally or between sites. For example, a higher abundance of arboreal insects provided increased opportunities for orangutans to invent tool use at Suaq Balimbing compared to other sites (Fox et al., 2004). Termite gathering by chimpanzees at Gombe is also thought to be opportunistic, as it occurs during the rainy season when termites are more accessible (McGrew et al., 1979; McGrew & Collins, 1985). In contrast, termite fishing has been documented throughout the year at several sites within central Africa (Sabater Pi, 1974, 1979; McGrew et al., 1979; Suzuki et al., 1995; Deblauwe, 2009). Termite mounds (*Macrotermes*) are rare and peripheral to the chimpanzee range at Seringbara in Guinea and no evidence of tool use in termite predation has been detected within this population (Koops et al., 2013). However, chimpanzees at Seringbara use tools to harvest army ants, which are both abundant and widespread across the area (Koops et al., 2013).

Our study revealed that habitat type, vegetation, and seasonal variation in climate at Wamba and Goualougo are fairly similar, and we did not identify any obvious differences between the sites that would preclude the possibility for bonobo tool use for feeding. At the bonobo study site Lui Kotal, assessment of opportunities for insectivory revealed that the same tool use opportunities were present and in some cases exceeded abundances reported from chimpanzee sites (McGrew et al., 2007). A detailed study assessing the availability of army ants, termites, nut producing trees and potential tool materials at Wamba is currently underway. Furthermore, the range of habitat types of chimpanzees and bonobos overlap almost completely from savannah to rain forest. Due to such large within-species variation and between-species overlap, it is difficult for the Opportunity Hypothesis to explain presence of tool use for feeding in all studied chimpanzee populations and almost complete absence of it in wild bonobos.



The Relative Profitability Hypothesis suggests that tools will be used to harvest embedded food items when the energetic benefits outweigh the gains from conventional feeding of more easily accessible food items (Rutz et al., 2010; Rutz & St Clair, 2012). There are several indications that the energetic benefits of tool use exceed those of conventional feeding in birds (Tebbich et al., 2002; Rutz et al., 2010). Nut cracking by chimpanzees has also been shown to be an energetically profitable behaviour, which can yield several thousand calories per day (Gunther & Boesch, 1993). Contradictory to this Relative Profitability Hypothesis, past research has shown that some forms of chimpanzee tool use may not necessarily be the most efficient means of calorie or protein intake. For example, a detailed review of ant-fishing behaviour among chimpanzees at Mahale revealed negligible nutritional gain from ant-fishing which was suggested to be a ‘leisure’ activity (Nishie, 2011). As mentioned above, bonobo tool use occurred mostly in the social and self-directed contexts, and therefore we had no information to examine the profitability of tool use for feeding in bonobos. A more comprehensive evaluation of bonobo diet and nutritional intake may reveal whether or not conventional feeding is more profitable for this species than employing tool-assisted strategies.

With regard to the Invention Hypothesis, it is predicted that more frequent or complex tool use will occur in settings with enhanced opportunities for social transmission. This hypothesis would explain the absence of tool use in bonobos if bonobos gather in smaller parties or have weaker social relations within their groups compared to chimpanzees. Our comparison indicated, however, that bonobo parties at Wamba were larger than chimpanzee parties at Goulougo. A recent comparison of many study sites of chimpanzees and bonobos indicated that differences in party size between the species are not statistically significant but that female bonobos attend party gatherings much more frequently relative to the very low attendance ratio of female chimpanzees (Furuichi, 2009). This seems like a prime social setting for the spread of technological traditions in bonobos. Especially, since studies have reported a female bias in tool use among wild chimpanzees (McGrew, 1979; Lonsdorf, 2005) and captive bonobos (Boose et al., 2013), which has yet to be documented among wild bonobos. Importantly, it remains to be established whether increased gregariousness in bonobos also reflects an increase in close-range social learning opportunities. Moreover, we need to assess how levels of gregariousness and party composition, and thus social

learning opportunities, vary across feeding and non-feeding contexts in both chimpanzees and bonobos. Priority of access to food resources exhibited by bonobo females (Furuichi, 1997; Surbeck & Hohmann, 2013) may reduce the need for food gathering with tools. Furthermore, we may want to question whether the party size is indeed an important factor for transmission of tool behaviours. Studies from several sites, including Gombe and Goualougo (Lonsdorf, 2006; Sanz & Morgan, 2013a), suggested that party sizes while termite fishing were relatively small, and the majority of parties were mothers with dependent offspring. If the transmission of tool behaviours mainly occurred between mother and offspring but not among adults, the party size may have no influence on tool behaviours even if the transmission of technological information is important for the existence of tool use.

Thus, as far as we know from the current information, differences in ecological or social conditions may fail to explain differences in bonobo and chimpanzee technological repertoires. It might be because these behaviours evolved in past ecological and social conditions that differ from contemporary settings. A recent study reported that present-day geographical features failed to explain the genetic structure of bonobos, and that current genetic diversity was formed by paleoenvironmental circumstances during the Pleistocene (Kawamoto et al., 2013). During the Pleistocene Epoch which began 2.5 million years ago, forested areas in Africa were reduced to smaller refugia during glacial periods (Mayr & Ohara, 1986; Plana, 2004). Such environmental changes became more conspicuous after 1 million years ago, which coincides with the divergence of the bonobo and chimpanzee lineages (Won & Hey, 2005). The range of ancestral chimpanzees experienced more extensive drying and fragmentation of forests during the late Pleistocene than the habitat of ancestral bonobos on the left bank of the Congo River where large forest refugia were maintained even during dry periods. Therefore, tool-assisted feeding might have had greater adaptive value for the ancestors of modern chimpanzees who were coping with greater variability in food resource availability, more arid habitats, and potentially increased competition with other species than past bonobo populations. It is also possible that feeding technology evolved independently in the different chimpanzee subspecies as they repeatedly experienced dry periods. In their examination of tool use patterns among Ugandan chimpanzee populations, Gruber et al. (2012) suggested that ancestral chimpanzee populations in the region may have coped with harsher environments during the last Ice Age which may

have prompted various behavioural innovations, such as extractive tool use. A major problem exists in this explanation however. If the ability for tool use evolved only in chimpanzees under certain conditions in the past, and therefore chimpanzees currently living in all types of habitats inherently use tools for feeding while bonobos in any type of habitat do not, then why is there no substantial difference in the ability for tool use under experimental conditions? This question needs to be further investigated through comparative studies both in the wild and captivity.

Although further studies are needed, it is possible that the differences in tool using propensities between chimpanzees and bonobos in the wild reflect divergent behavioural predispositions rather than differences in cognitive abilities. Comparative studies of the physical and cognitive abilities of great apes have failed to explain the paucity of tool use by bonobos. Within captive settings, bonobo tool use repertoires are as large and diverse as chimpanzees (Gruber et al., 2010). This is unlike gorillas, who use tools for feeding but acquire the behaviour more slowly and perform it less frequently than chimpanzees, suggesting a species difference in predisposition (Boysen et al., 1999; Lonsdorf et al., 2009). Even in experimental settings where individuals had limited experience with tools, both chimpanzees and bonobos demonstrated understanding of tool functional properties (Herrmann et al., 2008).

The species differences in cognition and behavioural propensities between chimpanzees and bonobos were aptly expressed in a range of cognitive problem solving tasks. Bonobos surpassed chimpanzees in solving tasks related to the social world (i.e., theory of mind, understanding of social causality), whereas chimpanzees showed more skill in tasks related to the physical world (i.e., use of tools, understanding of physical causality) (Herrmann et al., 2010). In a comparison of several captive groups, the only major difference between chimpanzee and bonobo tool use was that bonobos of all age and sex classes used tools in a play context (Gruber et al., 2010). The propensity of adult bonobos to engage in play is thought to reflect their neotenuous nature, as well as environmental conditions that afford leisure time and a behavioural preference for certain types of social interaction.

As mentioned above, some chimpanzee tool use does not seem to be the most effective means of increasing energy intake, but may be performed when individuals have leisure time (Nishie, 2011). On the other hand, bonobos spend much of their leisure time in play and play is common among

adults (Enomoto, 1990; Palagi, 2006). Such differences in behavioural preference may explain why bonobos are likely to perform like chimpanzees in experimental conditions, but do not regularly perform tool use in natural settings. This potential difference in behavioural predispositions toward tool use could be further investigated by comparing levels of object manipulation and exploratory tendency in chimpanzees and bonobos (Koops et al., data not shown).

It has been proposed that we are currently living in the “Anthropocene Epoch” which is shaped by human influences on the environment. Although apes have persisted through shifting climatic condition, there is no historical analogue for the rate and degree of environmental change caused by anthropogenic disturbances. The long-term survival of wild bonobos and chimpanzees is increasingly endangered by poaching, habitat destruction and conversion, and infectious diseases. The Disturbance Hypothesis suggests that ape cultures are fragile and that anthropogenic disturbances may affect the social mechanisms which maintain these traditions (van Schaik, 2001). Recognizing the conservation value of animal cultures, scientists have suggested specific strategies for conserving and managing animals that learn socially and share cultures (Whitehead et al., 2004; Laiolo & Jovani, 2007; Whitehead, 2010). Such measures must be implemented immediately if we hope to continue advancing our understanding of behavioural diversity of our closest living relatives.

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