Ecological and social correlates of chimpanzee tool use

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The emergence of technology has been suggested to coincide with scarcity of staple resources that led to innovations in the form of tool-assisted strategies to diversify or augment typical diets. We examined seasonal patterns of several types of tool use exhibited by a chimpanzee (Pan troglodytes) population residing in central Africa, to determine whether their technical skills provided access to fallback resources when preferred food items were scarce. Chimpanzees in the Goualougo Triangle exhibit a diverse repertoire of tool behaviours, many of which are exhibited throughout the year. Further, they have developed specific tool sets to overcome the issues of accessibility to particular food items. Our conclusion is that these chimpanzees use a sophisticated tool technology to cope with seasonal changes in relative food abundance and gain access to high-quality foods. Subgroup sizes were smaller in tool using contexts than other foraging contexts, suggesting that the size of the social group may not be as important in promoting complex tool traditions as the frequency and type of social interactions. Further, reports from other populations and species showed that tool use may occur more often in response to ecological opportunities and relative profitability of foraging techniques than scarcity of resources.

1. Introduction

Scientists have long attempted to identify the factors that coincided with the emergence of complex tool use within the hominin lineage. The earliest evidence of stone tool use consists of cut marks on animal bones dated to 3.4 million years (Myr) ago [1]. However, discoveries of past tool technology are both biased and limited by artefact preservation [2]. All living apes use tools, and common chimpanzees (Pan troglodytes) and orangutans (Pongo spp.) regularly exercise these capacities in their natural environments [3,4]. It is therefore likely that the actual origin of tool use within our lineage dates back much further, and at least to the Miocene epoch (from 23 to 5 Myr ago) when there were dozens of ape species coping with shifting climates [5]. Living primates provide an opportunity to examine the dynamic ecological and social settings in which primates live, and aid in generating and testing hypotheses of how complex tool technology emerged and was maintained among its earliest practitioners. While tool use has been dismissed as a ‘prime mover’ in early hominid evolution [6], there is no doubt that diverse and complex tool technologies have been an incredibly important aspect of human evolution.

Examination of the factors that elicit tool use within natural-living animal populations can provide insights into the evolutionary history of the emergence and flourishing of technology within the human lineage. Potts [7] has suggested that habitat instabilities may have favoured advanced cognitive abilities among the great apes who persisted through the end of the Miocene epoch. These primates presumably developed foraging strategies to locate alternative food items when preferred resources were not available. Marshall & Wrangham [8] proposed that selection pressures may differ between preferred food items versus ‘fallback foods’ that are consumed when preferred items are scarce. Preferred foods are likely to shape harvesting adaptations and general cognitive abilities related to locating foods, such as locomotor adaptations. By contrast, it has been proposed
that fallback foods drive diverse aspects of processing adaptations, including dental adaptations, digestive adaptations and tool use [8]. Further, fallback foods may have evolved more substantial defences against primate consumption than resources associated with periods of high food availability [9] and subsequent selection pressure may have prompted the manufacture and use of tools to access them. In evolutionary terms, more effective foraging strategies would have resulted in energy gains that increased the fitness of its practitioners. In this study, we examined seasonal patterns of tool-assisted foraging behaviour to examine the ecological and social correlates of chimpanzee tool use. We are particularly interested in the factors which may have elicited the diverse and relatively complex tool use behaviour of our study population in the Goualougo Triangle, Republic of Congo.

It is of course possible that present-day tool using contexts differ from the selective pressures and ecological conditions that shaped tool behaviours in the evolutionary past. The formation of forests can span centuries. Owing to unique and varying trajectories in forest-stand development and diversity, historical patterns of food resource fluctuation could have prompted the emergence of tool use in a species which now lives in a more ecologically stable environment. Thus, the Goualougo chimpanzees may be persisting in performing behaviours reflective of selective factors and conditions that initially triggered their appearance, but are no longer prevalent. Palaeoecological analysis has shown that the floristic composition of the Goualougo and neighbouring forests has varied considerably over the past 2580 years [10,11]. In their examination of the patterns of tool use among East African chimpanzee populations, Gruber et al. [12] suggested that ancestral chimpanzee populations in the region may have been coping with harsher environments during the last Ice Age which prompted various behavioural innovations, such as extractive tool use.

Several animal species have the capabilities to manipulate external objects in a controlled fashion during extractive foraging [3], but there are few who regularly and flexibly use objects to achieve particular goals in natural settings [13]. Chimpanzees are among the most consistent and prolific non-human tool users [3,14], based on the frequency and diversity of their tool behaviours. All studied chimpanzee populations exhibit some form of tool use [14,15], but there is wide variability in the size and complexity of tool repertoires among study sites [16–18]. The repertoire of wild orangutan tool using behaviours is also relatively large and diverse, consisting of 42 tool variants that are used in several different contexts including physical comfort, subsistence and communication [19]. However, many of these tool behaviours are exhibited relatively infrequently. Woodpecker finches (Cactospiza pallida), New Caledonian crows (Corvus moneduloides) and bottlenose dolphins (Tursiops sp.) have also come to the forefront as prominent tool users. Woodpecker finches in the Galápagos Islands use twigs or cactus spines to pry arthropods from tree holes [20]. Tebbich et al. [21] recently reported woodpecker finches using tools manufactured from barbed twigs of introduced blackberry bushes to extract prey from under the bark of a native tree species, demonstrating their abilities to modify tools in a flexible manner and exploit novel environmental opportunities. New Caledonian crows use stick tools to extract beetle larvae from their burrows in candlenut trees (Aleurites moluccana), and Pandanus spp. tools and hooked stick tools in other foraging contexts [22,23]. Bottlenose dolphins in Shark Bay of Australia use sponge tools to locate and flush out burrowing prey on the sea floor [24]. It is presumed that the adaptive function of such tool-assisted foraging strategies is to increase access to high-quality food resources.

A unifying theory of the emergence of tool use has yet to be proposed which adequately explains the variation in tool diversity and frequency observed among natural-living animal populations. Fox et al. [25] proposed three non-mutually exclusive hypotheses to explain differences in the expression of tool use among great ape populations. The ‘necessity hypothesis’ suggests tool use is a response to resource scarcity, which enables its practitioners to exploit novel food items during times when resource abundance is low. Based on this hypothesis, one could predict that frequency and/or diversity of tool use increases during times of resource scarcity. By contrast, the ‘opportunity hypothesis’ proposes that repeated exposure to appropriate conditions (such as encounters with target items and tool materials) prompts the emergence and/or maintenance of tool using behaviours [26,27]. When reviewing possible ecological drivers for the evolution of extractive tool use in New Caledonian crows, Rutz & St Clair [22] recently emphasized the importance of examining the relative profitability of foraging for embedded versus non-embedded foods. The ‘relative profitability hypothesis’ simply posits that extractive tool use should be expressed whenever it is relatively more profitable than alternative, non-tool-assisted foraging strategies [28]. In effect, the relative profitability hypothesis encompasses the previously mentioned ecological hypotheses (see also §4). Fox et al.’s [25] third hypothesis focuses on the social factors driving tool use. The ‘invention hypothesis’ (also referred to as the ‘limited invention hypothesis’ in Fox et al. [25]) proposes that ‘behaviours such as tool use are rarely invented, and that the spread and maintenance of such behaviour requires sufficient opportunities for observational learning via social proximity to conspecifics’ [29, p. 163]. As described in the following sections, previous field studies of tool using animals have provided mixed results in the evaluation of these hypotheses (table 1).

Support for the necessity hypothesis has been found among finches and primates. Woodpecker finches attained half of their prey with the use of tools in the dry season within an arid zone where food was limited and hard to access [20]. By contrast, tools were rarely used by finches in a zone where food was abundant and easily accessible. Chimpanzees increased use of tools during periods of fruit scarcity at Bossou, Guinea [31]. Additional suggestions of tool use during times of necessity have been asserted for bearded capuchins in northeastern Brazil [45] and long-tailed macaques in Thailand [43], but the necessity hypothesis was not explicitly tested in these particular studies. There are also situations in which it is difficult to differentiate responses to necessity and opportunity. Adult female chimpanzees in the Tai forest opportunistically exploit Coula edulis nuts with tools during their period of seasonal abundance that could also be a response to necessity as the chimpanzees experienced a negative energy balance on half of the days surveyed [34]. While it is commonly suggested that limited food distribution and abundance may prompt the invention of novel foraging strategies, abundance of resources can also furnish the time and energy to pursue such activities. Watts & Mitani [46] reported that chimpanzee hunting of red colobus monkeys was most common during periods of fruit abundance and that the chimpanzees hunt most when they can easily meet
<table>
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<td>across sites, Sumatra</td>
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<td>macaque</td>
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<td>dig tubers/insects, crack items</td>
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<td>new Caledonian crow</td>
<td>Grande Terre, New Caledonia</td>
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<td>bottlenose dolphin</td>
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<td>sponge to locate and flush out prey</td>
<td>opportunity, profitability</td>
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Hypotheses for the evolution of tool use were not explicitly tested in the original study. We attempted to assign hypotheses based on information in the original published reports, with the supporting evidence listed below. However, there is relatively little information within these manuscripts to assess the invention hypothesis, and the relative profitability hypothesis was only recently outlined (Rutz et al. [30]; Rutz & St Clair [22]), so remains to be empirically examined in most of these taxa/populations.

Sources (page numbers refer to original publications):
- Yamakoshi [31].
- Koops et al. [32].
- Gunther & Boesch [33] and N’Guessan et al. [34] (necessity: negative energy balance among some community members across seasons; opportunity: nut cracking tool use coincides with abundance of nuts; profitability: energetic gain from nut cracking).
- Bogart & Pruetz [35, p. 11] (necessity: based on overall savannah environment rather than negative correlation with staple foods, ‘invertebrates are an important source of protein and other essential nutrients in a highly seasonal environment’, but termites are a staple component of the Fongoli chimpanzee diet, and their consumption is not correlated with periods of low fruit availability).
- McBeath & McGrew [36] and McGrew et al. [37] (opportunity: termite fishing related to rainfall).
- McGrew et al. [37, p. 198] (opportunity: seasonality in fishing for termites is linked to the annual reproductive cycle of termites, which in turn is linked to the onset of the rainy season).
- McGrew [38] (opportunity: ant dipping tool use occurs only during certain months of the year).
- O’Malley et al. [39, p. 650] (opportunity: ‘changes in insect prey availability over time and/or the characteristics of one popular ant-fishing site may have influenced the establishment of ant fishing’; invention: ‘first documented case of successful transmission of a novel cultural behaviour between wild chimpanzee communities’).
- Nishie [40, pp. 344, 338] (opportunity: chimpanzees fish for ants with tools constantly throughout the year; not necessity: ‘chimpanzees do not increase ant-fishing in the late wet and early dry seasons when major fruit availability is relatively low at Mahale’).
- Uehara [41, p. 44] (opportunity: chimpanzees use several techniques (including tool use) to feed on termites, which are in accordance with phenological changes in the prey insect’s activity).
energy needs via other sources. Rather than replace the energy yield from preferred foods, small quantities of nutrient rich resources may be sufficient to maintain certain foraging behaviours [47].

Support for the opportunity hypothesis intersects with the profitability of exploiting food items that are not accessible to others. In contrast to the necessity hypothesis, the opportunity hypothesis focuses on encounter rates with tool using opportunities and/or tool materials. Fox et al. [29] found that ecological factors most likely explained differences in tool use between orangutan populations and that abundance of arboreal insects provided increased opportunity for the invention of tool using behaviours at Suwq Balimbing compared with other sites. Termite gathering by chimpanzees at Gombe is also thought to be opportunistic, as it occurs during the rainy season when termites are more accessible and fruits tend to be more abundant [37,48]. By contrast, termite fishing has been documented throughout the year at several sites within central Africa [37,49] and at the savannah site of Fongoli in West Africa [39]. In central Africa, chimpanzees have developed specialized tool sets to harvest termites year-round [52–54], and ecological opportunities to harvest termites seem to be particularly abundant at Fongoli where these insects are a staple food in the chimpanzee diet [35]. By contrast, termite nests are rare and peripheral to the chimpanzee range at Seringbara in Guinea, and no evidence of tool use in this context has been detected within this population [32]. However, tool use to gather army ants has been documented in Seringbara, which may be a response to ecological opportunities as army ants are both abundant and widespread across the area [32]. The frequency of opportunities may also be key, as the mere presence of particular ant prey does not provide a sufficient explanation for the observed patterns of chimpanzee tool use [55,56]. It has been suggested that tool use in New Caledonian crows emerged as an evolved adaptation in response to an abundance of embedded food resources for which there were no competitors [22]; importantly, foraging with tools is thought to be energetically highly rewarding, which leads us to examine the relative profitability of tool-assisted versus conventional foraging techniques.

The relative profitability hypothesis suggests that tool-assisted foraging strategies targeted at embedded food items are more profitable than conventional methods of gathering more accessible foods [22]. Only a few beetle larvae are necessary to satisfy the daily energy requirements of New Caledonian crows and so it seems that the benefits of tool use are likely to exceed conventional foraging techniques [28]. Dolphins commonly use echolocation in foraging for prey, but a population of dolphins in Australia have adopted the use of protective sponges to cover their rostra while probing the sea floor for prey hidden in the rubble [24]. Scientists have concluded that these dolphins are likely targeting burrowing prey that lack swimbladders and so are not detectable by conventional foraging methods. The use of sponge tools has effectively provided access to a food resource that is inaccessible to dolphins that do not use tools. Nut cracking by chimpanzees has also been shown to be an energetically profitable behaviour, which can yield several thousand calories per day [33]. Finally, foraging success in terms of prey items gathered by woodpecker finches was similar between tool use and conventional feeding techniques, but energy intake per time was higher when using tools [20].

The final explanation for the emergence of tool use is the invention hypothesis, which states that tool behaviour is invented rarely and/or may have difficulty spreading and being maintained [25]. One can predict that, because social learning requires some type of direct or indirect contact between individuals, it may be more common in high density or highly social animal populations. Support for the invention hypothesis is found in some of the tool behaviours of wild orangutans in Sumatra that live at relatively high densities in ‘a limited geographical area bounded by dispersal barriers, but without any obvious ecological correlates’ [25, p. 113]. Among chimpanzees, the number of individuals present in a party has been used as a proxy for social learning opportunities [57,58]. However, the number of individuals present in a party may not be as important as the number of individuals engaged in tool use, close proximity of tool using models, actual time spent tool using, connectivity within the group and potential types of social facilitation. Research examining the theoretical importance of social networks [59] and diffusion of tool using conventions through social groups [60] may provide a more implicit means to test the invention hypothesis. Recent field studies have also examined the social context of tool use in natural settings [30,40,61], where some technological traditions have presumably been maintained over generations and vast landscapes.

In this study, we examine whether the frequency, diversity and complexity of tool use within a population of chimpanzees...
residing in the Goualougo Triangle of the northern Republic of Congo is correlated with necessity, opportunity, relative profitability or invention. According to the necessity hypothesis, foods gathered with tool use would compensate for reduced abundance of ripe fruits. According to the opportunity hypothesis, tool use would track the relative abundance of particular tool targets (termites, ants, honey, etc.) or tool materials. The relative profitability hypothesis suggests that tools will be used to harvest embedded food items when energy intake rates outweigh those attained by conventional foraging for more easily accessible food items. With regard to the invention hypothesis, we predict that more frequent or complex tool use will occur in settings with enhanced opportunities for social transmission. The Goualougo chimpanzee population has a relatively diverse repertoire of tool using behaviour, which includes the regular use of several tool sets and particular tool modifications that have been shown to increase foraging efficiency [62]. Therefore, this investigation bears directly on the question of the current adaptive significance of tool-assisted foraging in wild animals and provides insights into the evolution of complex technology within our own lineage.

2. Methods

(a) Study site
The Goualougo Triangle study area is located along the southern boundary of the Nouabale-Ndoki National Park (E 16°51′–16°56′; N 2°05′–3°03′), Republic of Congo. The climate in the northern Republic of Congo can be described as transitional between the Congo-equatorial and subequatorial climatic zones.

(b) Data collection protocols
Direct observations of the chimpanzees in the Goualougo Triangle have been ongoing since February 1999. Individual chimpanzees were identified from their distinct physical characteristics held in a population history database. The main study group is the Moto community which consisted of 71 individuals at the time of this study, including 17 adult males and 24 adult females.

This chimpanzee population exhibits a diverse repertoire of tool using behaviours which occur in a variety of contexts [15]. Tool using 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 using behaviour, observers record the identification of the chimpanzee, type of object used, target of object, actions, context and/or goal of the tool using behaviour and the outcome. Video footage of tool using behaviour is recorded whenever possible. This study focuses on annual profiles of tool use in foraging for termites (Macrotermes muelleri, M. lilljeborgi), army ants (Dorylus maggi, D. rubellus, D. sjostedti, D. wilverthi) and honey of stingless bees (Trigona spp.).

We assessed the frequency of tool use in the termite gathering context from remote video recordings conducted between March 2005 and June 2008. Remote video monitoring units consist of video cameras in weatherproof housing that are triggered to record for pre-set intervals by passive infrared sensors (for a more detailed description of these methods, see [33]). These cameras were placed at termite nests with previous traces or observations of chimpanzee tool use. Six mature females and five mature males were confirmed to exhibit tool use behaviour at termite nests monitored with video cameras at least once per year throughout the study period. Video recordings were scored using INTERACT version 9 [63]. A tool using episode was defined as beginning when the chimpanzee manufactured a tool (or at the first moment after which they were observed with the tool) and ended when the tool was discarded or the task was abandoned.

Frequency of ant dipping was assessed through chimpanzee tool assemblages recovered at ant nests over a 41 month period between May 2004 and September 2007. Further details on tools used in gathering ants by this chimpanzee population can be found in [64].

Tool use in honey gathering was recorded opportunistically during daily reconnaissance surveys in the study area. The dataset for this study was collected between September 2006 and March 2009. Because honey gathering is a relatively rare behaviour, our analysis represents all individuals observed each month during the study period.

Instantaneous 20-min group scans of party composition and behaviour were recorded during all chimpanzee encounters between January 2006 and August 2010. Chimpanzee parties were considered to be all individuals travelling, feeding, resting or socializing within 50 m of one another (definition adopted from [65,66]). In addition to noting the number of individuals present in the party, the basic activity patterns of all individuals were recorded at each scan interval. A total of 11 024 party scans were recorded during the study period, of which 5075 involved feeding observations. The proportion of scans with observations of fruit and leaf feeding was compiled for each month of the study period. However, caution should be exercised in interpreting relationships which could be partly driven by the ‘unit-sum constraint’ inherent in proportional data.

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 this ape population [67]. A total of 607 trees representing 47 species were monitored each month in the Goualougo Triangle. The crown of each monitored tree was visually examined to determine the abundance of fruit (unripe, ripe), leaves (old, new) and flowers. Relative abundance of fruit was estimated on a scale of 0–4, with higher scores indicating more fruit. Similarly, abundance of flowers and leaves (new and mature) were rated on a scale of 0–4.

Rainfall and temperature were recorded daily in the Nouabale-Ndoki National Park. Stationary rain gauges and thermometers with minimum and maximum temperature gauges were stationed in the Goualougo Triangle and Mbeli Bai base camps. To assess the influence of climate on tool use, we calculated the total monthly rainfall, as well as monthly average minimum and maximum temperatures, throughout the study period in our analyses.

Termite nest densities were estimated as part of systematic botanical surveys that were conducted throughout the Goualougo study area from 2009 to 2012. Survey plots measured 50 × 50 m, and all termite nests within the plots were enumerated and described. Our sampling effort included 42 plots. Botanical surveys were also conducted at termite nests to determine abundance of suitable tool materials in the environment. All herbaceous and woody stems within 20 m of an active tool use site were identified and the distance from the tool site measured. Surveys were conducted at 10 termite nests.

(c) Statistics
Multiple regression was used to examine the relationship between rainfall and fruit abundance over a period of 67 months, with the predictor being monthly rainfall and the response being the proportion of trees with ripe fruit. Both variables were square root transformed to achieve approximately symmetrical distributions and fulfill the assumptions of normally distributed and homogeneous residuals (assessed by visual inspection of residuals plotted against fitted values and
DFbeta values revealed model instability to be no obvious issue. Autocorrelation was accounted for as above, but, because it was controlled for by including it (log-transformed) as an offset term. The total number of scans was counted separately for each data point, the residuals of all other data points, whereby we weighted their contribution to this average by the time lag between the specific data point and the residual. The resulting variable (‘autocorrelation term’) was then included into the model as an additional predictor variable. The weight function had the shape of a Gaussian distribution with a mean of zero (i.e. maximum weight at a time lag of zero) and a standard deviation chosen such that the likelihood of the model with the autocorrelation term included was maximized.

To address concerns of the unit-sum constraint in our analysis of feeding ecology, we examined fruit and leaf feeding as percentages of the overall activity budget. A negative binomial model was used to examine our data on chimpanzee feeding ecology which spanned 56 months, with the predictor being the proportion of fruit feeding scans (square root transformed) and the response representing leaf feeding scans. The total number of scans was controlled for by including it (log-transformed) as an offset term. Autocorrelation was accounted for as above, but, because it was not significant ($p = 0.96$), it was removed from the final model. DFbeta values revealed model instability to be no obvious issue. To facilitate comparisons with other studies that examine the importance of food parts as a subset of only feeding observations, we also report the number of fruit and leaf feeding scans as a subset of feeding observations. This was accomplished using a generalized linear model (GLM) with negative binomial error structure and autocorrelation accounted for as described above ($p = 0.51$).

Total time spent gathering termites with tools was determined for each subject and then standardized per subject to a sum of unity. Linear models assuming normally distributed and homogeneous residuals were run for temperature, rainfall, flowering trees, fruiting trees and leaf abundance. The autocorrelation term was evaluated for each model individually.

To examine the relationship between ant gathering and chimpanzee food abundance, we used separate GLMs with negative binomial error structure for each of the three predictors of resource abundance (flowering trees which was square root transformed, fruiting trees and abundance of leaves). Autocorrelation was incorporated as in the other models. Total sample size was 26 months. A single GLM (including both predictors) with negative binomial error structure was used to examine the relationship between tool use in ant gathering and climatic variables. Rainfall was log-transformed. Autocorrelation was incorporated as in the other models. Sample size was 41 months.

qq-plot of residuals). Influential cases were no issue (assessed by DFbeta values and DFfits [68]). The predictor was $z$-transformed to a mean of zero and a standard deviation of unity. Temporal autocorrelation was accounted for by explicitly taking it into the model. Specifically, we first ran the model as described above and derived the residuals from it. We then averaged, separately for each data point, the residuals of all other data points, whereby we weighted their contribution to this average by the time lag between the specific data point and the residual. The resulting variable (‘autocorrelation term’) was then included into the model as an additional predictor variable. The weight function had the shape of a Gaussian distribution with a mean of zero (i.e. maximum weight at a time lag of zero) and a standard deviation chosen such that the likelihood of the model with the autocorrelation term included was maximized.

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The frequency of honey gathering was assessed over a 40 month period using a GLM with negative binomial error structure. Autocorrelation was accounted for as in the other models.

All models were run in R [69], and negative binomial GLMs were run using the function glm.nb of the R package MASS [70]. When we chose a negative binomial error structure, this was carried out, because the response was a count, but the assumption of no overdispersion (as made by a Poisson regression) was violated. The autocorrelation term was implemented using a function written by R. Mundry.

3. Results

(a) Rainfall and climate monitoring

Annual rainfall averaged (+ s.d.) 1689.6 ± 27 mm between 2007 and 2011 in the Goualougo Triangle. The main rainy season is typically from August through November, and the main dry season from December to February (figures 1 and 2). A short rainy season and a short dry season occur in the intervening months. The average minimum and maximum temperatures (+ s.d.) were 21.5 ± 0.6°C and 23.7 ± 0.8°C during the study period.

Figure 1. Rainfall and temperature in the Goualougo Triangle, Republic of Congo.

Figure 2. A positive relationship between proportion of fruiting trees and rainfall was documented in northern Congo.
Figure 3. Proportion of chimpanzee party scan observations spent foraging on fruits and leaves.

(b) Relative abundance of chimpanzee foods
Based on phenological monitoring of chimpanzee food items, the period of highest fruit abundance was from April to September. There was a clear positive relation between rainfall and fruit abundance (estimate $\pm$ s.e. $= 0.015 \pm 0.006$, $t_{44} = 2.56$, $p = 0.013$). The resource-scarce period can be characterized as October through March.

(c) Chimpanzee feeding ecology
When preferred fruits were not available, chimpanzees included a higher proportion of leaves in their diet (figures 3 and 4). Of the scan observations that contained feeding observations, chimpanzees spent an average of 68.9% of their foraging time consuming fruits and 21.3% consuming leaves. When fruit and leaf feeding were examined as a subset of feeding scans, it was revealed that the number of fruit feeding scans was negatively related to the number of leaf feeding scans (estimate $\pm$ s.e. $= -0.01 + 0.01$, $z = -4.19$, $p < 0.001$). The same relationship was found when fruit and leaf feeding were examined as percentages of all scan observations (estimate $\pm$ s.e. $= -1.894 + 0.719$, $t_{34} = -2.64$, $p = 0.008$).

(d) Annual profiles of tool using behaviours
Similar to Suzuki et al. [53], we found that chimpanzee tool use to gather termites occurred throughout the year and was not limited to a particular season (figure 5). Tool use in termite fishing was not related to measures of seasonality or resource abundance, including temperature (estimate $\pm$ s.e. $= -0.009 \pm 0.074$, $t_{20} = -0.13$, $p = 0.9$), rainfall (estimate $\pm$ s.e. $= 0.004 \pm 0.009$, $t_{20} = 0.48$, $p = 0.634$), frutiting trees (estimate $\pm$ s.e. $= 1.326 \pm 1.067$, $t_{20} = 1.24$, $p = 0.228$), flowering trees (estimate $\pm$ s.e. $= -0.643 \pm 0.43$, $t_{20} = -1.5$, $p = 0.151$) or abundance of leaves (estimate $\pm$ s.e. $= 9.323 \pm 5.548$, $t_{20} = 1.68$, $p = 0.108$). Rather than tracking seasonal abundance of termites, this chimpanzee population has developed two specialized tool sets to overcome the obstacles of access presented by epigal (characterized by earthen mounds or towers) and subterranean termite nests. A tool set composed of a perforating twig, and a fishing probe was used to open the surface of epigal nests and then used this tunnel to insert a fishing probe to extract the termites [15,53]. The epigal nests of *M. muelleri* were found throughout the study area at an estimated density of 0.48 mounds per hectare (10.5 ha of survey effort), which provides ecological opportunities similar to Gombe (0.7 mounds ha$^{-1}$, from 1.42 ha of survey effort) and Bilenge at Mahale (0.46 mounds ha$^{-1}$, from 2.18 ha of survey effort) in Tanzania [71], but far less than Fongoli in Senegal (23.6 mounds ha$^{-1}$, from 5.12 ha of survey effort) [35]. Botanical surveys around termite nests revealed that preferred fishing tool materials were readily available at termite nests, with the average distance (±s.d.) to the closest preferred tool material being 6.35 ± 5.33 m ($n = 10$ termite nests). Some of the termite nests in the Goualougo Triangle study area have persisted for more than 10 years, and thus provide a predictable location where insects can be harvested and information about the tool using task gathered either indirectly from discarded tools or directly from observations of conspecifics visiting the same site. Figure 9a shows the close proximity of tool users in this context. As discussed in the following section, party size during termite fishing is smaller than in other foraging

Figure 4. Chimpanzees consumed a higher proportion of leaves when preferred fruits were not available, as shown in the relationship between proportion of party scans in which the apes were observed feeding on leaves or fruits.
contexts but the social network depicts dense connectivity within the community [61]. In addition, the average length of termite fishing bouts in the Goualougo Triangle was relatively short (average duration $\pm$ s.d. = 6.05 $\pm$ 2.55 min, $n = 11$ individuals, totalling 463 bouts) when compared with other sites (average termite fishing bouts of 22.6 min were reported from the wet season, and 33.6 min in the dry season at Fongoli, Senegal) [35].

Chimpanzees used a tool set composed of a perforating twig and a dipping wand to gather ants throughout the year. There are times of the year when ant predation is more frequent than during other periods (figures 6 and 7), and which seemed to coincide with the beginning of the main rainy season [66]. This was confirmed by our finding that ant gathering was positively related to rainfall (estimate $\pm$ s.e. = 0.511 $\pm$ 0.209, $t_{23} = 2.44$, $p = 0.015$). We did not find a negative correlation between army ant gathering and relative abundance of chimpanzee foods, including flowers (estimate $\pm$ s.e. = 4.608 $\pm$ 3.578, $t_{23} = 1.29$, $p = 0.198$), fruits (estimate $\pm$ s.e. = 5.581 $\pm$ 7.525, $t_{23} = 0.74$, $p = 0.458$) or leaves (estimate $\pm$ s.e. = $-7.732 \pm 34.166$, $t_{23} = -0.23$, $p = 0.821$). Our analysis also did not detect a relationship between ant gathering and temperature (estimate $\pm$ s.e. = $-0.176 \pm 0.271$, $t_{23} = -0.65$, $p = 0.515$).

Tool use in honey gathering occurred throughout the year, but the low frequency of occurrence precluded analysis at the individual level. Statistical analysis did not show any significant relationships between this behaviour and our measures of seasonality or resource abundance, including temperature (estimate $\pm$ s.e. = $0.603 \pm 0.408$, $t_{23} = 1.48$, $p = 0.139$), rainfall (estimate $\pm$ s.e. = $-0.001 \pm 0.003$, $t_{23} = -0.33$, $p = 0.741$), flowering trees (estimate $\pm$ s.e. = $-0.802 \pm 2.624$, $t_{23} = -0.31$, $p = 0.76$), fruiting trees (estimate $\pm$ s.e. = $2.859 \pm 3.346$, $t_{23} = 0.85$, $p = 0.393$) or abundance of leaves (estimate $\pm$ s.e. = $-20.856 \pm 29.909$, $t_{23} = -0.7$, $p = 0.486$). Although not evident within single years, overall patterns of honey gathering roughly coincided with the flowering of trees when observations were pooled over the entire study period (figure 8).

A slight discordance between peak flowering events and tool
use is expected due to the delay in honey production by bees. Estimates of beehive abundance are not available from the study site, but suitable tool materials are readily available as the tools are most often fashioned from branches in the same tree canopy where the beehive is located. Honey gathering has been most often observed when individuals are alone or with their dependent offspring [61], but the sound of pounding clubs against the hive entrance can be detected from distances greater than 50 m that could stimulate interest among individuals in nearby parties. The arboreal setting also increases the distance that the tool user is visible compared with most terrestrial tool using settings (figure 9b), but may not provide adequate substrate for conspecifics to gather in close proximity to the tool user.

(e) Social opportunities and tool use
When resource scarcity is extreme, the fission–fusion social structure of chimpanzee societies enables them to flexibly respond by reducing the size of their parties. However, average chimpanzee party sizes observed in the Goualougo Triangle remained stable throughout the year (average party size ± s.d. = 4.47 ± 1.47, n = 56 months). Foraging parties were largest when chimpanzees were feeding on fruits, flowers and leaves [61]. Foraging subgroups at termite nests were relatively small (2.23 ± 1.57 individuals), but several types of indirect and direct social facilitation have been documented that could aid in maintaining the complex and diverse tool traditions of this chimpanzee population. Indirect social input from conspecifics included discarded tools and changes to the substrate at tool using sites. In the Goualougo Triangle, an average of 3.0 termite fishing probes (n = 685, range = 1–30) can be found at active termite nests [61] and 3.7 tools (n = 284, range = 1–18) at ant nests [64]. Honey gathering typically occurs in the forest canopy. Tools may be ‘conserved’ for use during the same tool using episode by placing them on branches near the target bee hive [16], but most discarded tools are dropped to the ground and so displaced from the tool using site. Resource abundance and distribution can influence tolerance of individuals at a feeding site. Termite nests are located throughout the Goualougo Triangle study area, at densities which provide multiple tool using opportunities within the home range of any individual. This may explain why the average number of individuals in chimpanzee parties at termite nests is typically smaller than parties foraging on other resources [61]. Such social gatherings provide information about the location of target prey and link tool-assisted foraging strategies to those targets. Chimpanzees were tolerant of tool users, and allowed others within close proximity during 27% of honey gathering attempts and 72% of termite fishing episodes [72]. Further, 7% of termite gathering tools were shared among individuals in a chimpanzee party visiting a tool using site [72].

4. Discussion
In this study, we examined possible ecological and social correlates of the diverse and complex tool using behaviour exhibited by a chimpanzee population residing in central Africa. First, we determined whether technical skills provided access to fallback food resources when preferred food items were scarce. Fruits are the preferred food item of these chimpanzees and their relative abundance fluctuated seasonally in the Goualougo Triangle study area. During times of relatively low fruit abundance, the chimpanzees increased their consumption of leaves, which fit the traditional definition of fallback foods, being highly abundant and of relatively poor nutritional quality [8]. However, variation in the abundance and nutritional quality of different leaf resources consumed by apes should be more specifically examined. The Goualougo chimpanzee population did not seem to compensate for the lack of fruit resources by increasing their frequency of tool use for social insects or honey. Further, our 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 using behaviours than previously suggested (table 1). We did show that opportunities to gather termites, ants and honey were available throughout the year and enhanced by the use of tool sets. Ant dipping was related to rainfall, and honey gathering showed some coincidence with patterns of tree flowering which precedes the peak periods of honey production. Rather than use tools to harvest fallback resources in response to seasonal fluctuations in preferred food resources, our conclusion is that these chimpanzees used their technical skills to maintain year-round access to embedded food items. In addition to ecological drivers, social factors are also likely to play a role in the invention and maintenance of complex tool using behaviours. Party size was consistent throughout the year and relatively small in tool using contexts within the Goualougo Triangle, which prompts further examination of social tolerance and specific types of social interaction on the evolution of technological traditions [13,73,74].

To compensate for scarcity of preferred resources, fallback foods must provide a major source of energy and be consumed at a degree that effectively replaces the nutrients provided by preferred food items. This seems feasible in the case of pestle pounding of oil palms and cracking of nuts among chimpanzees of Bossou in Guinea [31] and the nut cracking of Tai chimpanzees in Ivory Coast [33]. Although the food items harvested with tools are a rich source of nutrients, they comprise a
relatively small component of the diet of the nut cracking capuchins at Fazenda Boa Vista in Brazil [44] and insect harvesting orangutans at Suaq Balimbing in Sumatra [29]. Chimpanzees at both Gombe in Tanzania and Fongoli in Senegal allocate significant foraging time to harvesting Macrotermes during particular months [35]. Termites can be a significant source of several important nutrients, including manganese, protein and amino acids [46, 75], and are considered an important food in the Fongoli chimpanzee diet [35]. However, social insects do not fit the typical profile of fallback food resources [8]. While army ants may provide additional protein and micronutrients when they are consumed by chimpanzees, Koops et al. [32] speculated that their nutritional contribution to the diet may not be adequate to compensate for ripe fruits during times of scarcity. It was reported that the nutritional value of arboreal ants harvested with tools at Mahale appears to be negligible [40]. The amount of honey gathered from stingless bees (Trigona spp.) is much less than the honey contained from Apis spp. hives, and is unlikely to compensate for reduced abundance of fruits. The primary nutritional benefit of honey gathering is carbohydrates (primarily fructose, glucose and about 25 different oligosaccharides) [76]. Honey also contains small amounts of proteins, enzymes, amino acids, minerals, vitamins and polyphenols [76]. Further research is required to evaluate if foods gathered with the aid of tools provide sufficient nutrition to serve as fallback foods or are indeed energetically more profitable than other food types.

Chimpanzees, macaques and capuchins are some of the most versatile primate species with regard to their ability to survive in different habitat types. Some habitats in which these primates live may not offer traditional fallback foods, and so primates are prompted to procure higher quality resources when their staple food items are scarce. This could be the case with the seafood harvesting macaques on islands in the Andaman Sea [77] or the termite harvesting chimpanzees of Fongoli in Senegal [35, 78]. Further, tool use may also be necessitated in localities where feeding competition within or between species is high [26]. Interspecific feeding competition could result in decreased abundance of particular foods through direct or scramble competition. Patterns of food consumption by other species could also mask or amplify seasonal patterns of food resource abundance. Interspecific competition could be elevated in central Africa where chimpanzees coexist with gorillas and other primates [79]. While segregated foraging and utilization of specialized feeding strategies are the typical coping mechanism of sympatric species that show a high degree of dietary overlap [80, 81], another option would be the diversification or intensification of tool use strategies [16, 82]. Reduced risk of predation is another ecological factor which could be associated with the evolution of tool use through reduced mortality which favours evolution of life histories that are more conducive to cognitive adaptations. Reduced predation may also relax anti-predator vigilance and associated behaviours which could then liberate more time for object interaction and exploratory behaviours [22].

Changing ecological circumstances may also influence the emergence of tool use. Recent shifts in habitats caused by conversion or degradation may cause apes to increase the frequency of some particular types of tool use to compensate for missing resources. Pestle pounding tool use occurs in the canopy of oil palm trees (Elaeis guineensis) and is so limited by the distribution of this species, which is closely associated with human cultivation [26]. While pestle pounding has been documented in the Bossou chimpanzee community [26], the presence of oil palms was not sufficient to promote tool use in the neighbouring chimpanzee communities of Seringbara in Guinea and Yealé in Ivory Coast [32]. Another example of anthropogenic activities providing tool using opportunities is with the possible introduction of candlenut trees which harbour the beetle larvae that are extracted with tools by crows in New Caledonia [22].

There are several possible reasons why the necessity hypothesis fails to explain tool use in a number of species and situations. One issue with testing the ecological hypotheses could be that relative abundance of preferred food items is not a valid proxy for necessity. It is possible that necessity is more nuanced and driven by requirements for particular micronutrients which do not need to be consumed in large quantities. Another explanation for the failure of the necessity hypothesis would be that in certain ecological settings the food resources may decrease during certain periods but do not reach a level of scarcity that prompts one to take additional action. However, a wide variety of animals depend on seasonally variable food resources, and in most cases, this has not resulted in selection for tool using behaviours [22] (for further details, see below). Animals may also be using multiple coping strategies. For example, chimpanzees of the Tai Forest in Ivory Coast...
show varying responses to seasonal variation in fruit resources including an increase in foraging activities [34], reduction in daily travel [83], and exploitation of high-quality food resources such as *Coula edulis* when available [34]. Finally, it is also possible that ecological and social conditions in the past may have differed from the current tool using context (see §1).

The Goualougo Triangle chimpanzee population provides an interesting case study to evaluate the validity of the opportunity hypothesis. The abundance of tool using opportunities to gather army ants and honey show seasonal variation (through the nesting patterns of ants and the honey production of bees) [16,64], with chimpanzee tool use showing some indication of tracking these target resources. The Goualougo chimpanzees also regularly prey upon three different species of termites that live throughout the year in earthen mounds, whose protective structures present a significant obstacle to the foraging ape. In both the ant dipping and termite fishing contexts, chimpanzees use tool sets to overcome accessibility

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**Figure 9.** (a) Adult male and juvenile chimpanzee forage in close proximity to one another at an epigeal termite nest using a perforated twig and a fishing probe to extract termites. (b) By contrast, the arboreal setting of honey gathering often precludes individuals from being within close proximity to the target beehive. However, the sound of pounding clubs against the target beehive entrance can be audibly detected and often visually observed, as here, from greater distances than typical terrestrial tool using sites. Photo credit: Ian Nichols. (Online version in colour.)
issues; each of the tool sets is composed of a first tool used to access the prey and a second tool to gather the insects. Multiple tools are also used by chimpanzees in central Africa to open beehives and dip for honey [16,18]. In these foraging contexts, chimpanzees have overcome the constraints of their environment through technological innovations that served to increase their tool using opportunities and in some cases, tool modifications that enhance the profitability of tool-assisted foraging [62]. Although certain aspects of opportunity may trigger tool use, mere ecological opportunity may not be sufficient to support a tool using tradition [12,55]. Rather, emergence of a particular tool behaviour may require a certain threshold of abundance: (i) to provide repeated exposure to the target resource; (ii) to make the foraging for this food resource energetically profitable; (iii) to allow the tool user to gain sufficient experience with the tool using task; and/or (iv) to provide exposure to socially transmitted information. The inconsistency in support for the necessity and opportunity hypotheses prompt us to question if they best represent the proximate drivers of tool use. Rutz & St Clair [22] unequivocally assert that a general lack of suitable food in the environment is not a sufficient explanation for the evolution of tool use because many animal populations are expected to be food limited but do not develop tool technologies. Therefore, the absolute amount of food in the environment might be less important than the relative profitabilities of different foraging modes. They suggest that the relative profitabilities of attaining embedded and non-embedded foods may be a driving force in the evolution of tool-assisted foraging strategies. One would then predict that tool use would be performed whenever it is more profitable than non-tool-assisted foraging techniques (i.e. it is an optimal foraging strategy), explaining both possible responses to resource scarcity and ecological opportunities within a single conceptual framework. Seasonal patterns in tool use behaviour could then simply be attributed to shifts in the relative profitabilities of different foraging techniques. Social factors driving tool use also merit further examination and more rigorous testing of the invention hypothesis. Our results prompt us to question whether the number of conspecifics in the party or even at the tool using site is a good proxy for the potential of social transmission. We observed that it was often a subset of individuals in a chimpanzee party that actually engaged in tool using behaviour. Others may be within the immediate party, but not stimulated by the tool using event and so are not representative of the opportunities for social transmission. Rather, the number of individuals showing interest in the tool site and/or tool behaviour may be a much more informative measure. Within the Goualougo Triangle, we found that the number of individuals at the tool using site was surprisingly small and visit duration was shorter than at other sites, yet sufficient to yield interconnectedness among all mature members of the community in a termite gathering social network [61]. We suggest that group members can gain important information about the characteristics of the tool site, required tools, techniques and outcomes from other tool users who act as tolerant or possibly even instructive models. This may serve to facilitate the acquisition of tool using skills and promote conformity in specific behavioural traditions within social groups [84] and populations [37,85]. Further, patterns of innovation (the successful diffusion or spread of an invention) are likely to drastically differ between tool using contexts. Foraging at a terrestrial termite nest has a very different ecological and social setting compared with arboreal honey gathering [86]. As recently reviewed in Meulman et al. [86], the actual physical setting of tool use (terrestrial versus arboreal) may be crucial for acquiring and maintaining complex tool variants, particularly expressions of cumulative technology.

As illustrated by many of the contributions to this special issue and other compilations [3,4], our understanding of the tool using abilities of animals has remarkably increased in the past decade. There have also been great strides in documenting the diversity of these tool using skills and the natural environments in which they occur. Further, research in this field has progressed from descriptive accounts to more hypothesis-driven research to determine the factors shaping particular behaviours. Longitudinal studies have also provided unique vantages into the development, maintenance and innovation of these skills. Such research moves us toward a more comprehensive understanding of how animals interact with and shape their environment through the use of technology. However, the opportunities to study these behaviours among wild apes are increasingly endangered by habitat destruction and conversion, illegal hunting and infectious diseases. Many would agree that there is a moral obligation to ensure the preservation of our closest living relatives, but we also have an obligation to safeguard their unique traditions which have their own rich evolutionary histories [87–89].

Acknowledgements. We are deeply appreciative of the opportunity to work in the Nouabalé-Ndoki National Park and especially at the Goualougo Triangle. This work would not be possible without the continued support of the Ministère de l’Economie Forestière et du Développement Durable (République du Congo), Ministère de la Recherche Scientifique (République du Congo) and the Wildlife Conservation Society’s Congo Programme. Special thanks are due to J. M. Fay, P. Teifer, P. Elkan, S. Elkan, B. Curran, M. Gately, E. Stokes, T. Breuer, P. Nguembe and D. Dos Santos. We are deeply indebted to R. Mundry for his continuing support and willingness to conduct the statistical analyses for this manuscript. This research greatly benefited from discussions and insights from E. Lonsdorf and C. Boesch. We thank C. Rutz and two anonymous referees for their excellent comments and suggestions which greatly improved this manuscript. We also recognize the tireless dedication of J. R. Onononga, C. Eyan-Ayina, S. Ndolo, A. Nzeheke, W. Mayoukou, M. Meguessa, I. Singono and the Goualougo tracking team. Grateful acknowledgement of funding is due to the US Fish and Wildlife Service, National Geographic Society and Columbus Zooological Park.

References


31. Uehara S. 1982 Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudocanthotermes spiniger*). *Folia Primatol*. 37, 44–76.


37. Tennie C, Gilby I, Mundry R. 2009 The meat-scrap hypothesis: small quantities of meat may promote cooperative hunting in wild chimpanzees (*Pan


