Human perception on symmetry, raw material and size of Palaeolithic handaxes


Published in:
Lithics

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

Publisher rights
© 2017 The Author(s). Published by the Lithic Studies Society. All rights reserved. This work is made available online in accordance with the publisher’s policies. Please refer to any applicable terms of use of the publisher.

General rights
Copyright for the publications made accessible via the Queen’s University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The Research Portal is Queen’s institutional repository that provides access to Queen’s research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person’s rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.
HUMAN PERCEPTION OF SYMMETRY, RAW MATERIAL AND SIZE OF PALAEOLITHIC HANDAXES
Daniela Tumler¹,², Laura Basell³ and Fiona Coward⁴

ABSTRACT

It has often been assumed that handaxes were crafted and used primarily by adult males (Hawkes et al. 1997; Kohn & Mithen 1999; Niekus et al. 2012). However, there is no clear scientific or ethnographic evidence to support this. This study aimed to assess modern perceptions of essential morphological traits, including symmetry, raw material and size of handaxes, with a view to ascertaining whether differences exist between males and females in different age groups in their perception of bifaces. A statistical analysis was performed on data gathered through questioning more than 300 individuals, including males and females, adults and subadults (divided into juveniles and children). The study showed that most people prefer symmetrical to asymmetrical handaxes. In particular, females demonstrated a statistically significant preference for symmetrical handaxes. Juveniles and children were significantly more attracted towards symmetrical bifaces than adults, and adult females prefer smaller tools. These results suggest new avenues for research into Palaeolithic tool manufacture and use.


Keywords: Palaeolithic, handaxe, biface, children, juvenile, women, symmetry, raw material, experimental archaeology

INTRODUCTION

Extensive research has been conducted on some early tools produced by hominins, namely handaxes. Despite considerable variability in form, handaxes (or bifaces) have a broad base narrowing to a rounded point, with both surfaces flaked to create sharp edges around the entire periphery (Klein 2009). Handaxes appeared between 1.8 and ~1.6 million years ago (mya) (Lepre et al. 2011) and persisted until about 200,000 years ago. They are mainly associated with Homo ergaster, H. erectus, H. heidelbergensis, H. neanderthalensis and H. sapiens in Africa, Europe, China, western Asia and the Indian subcontinent (Lycett 2008; Wang et al. 2012). Various lithic raw materials were used to make handaxes, including obsidian, basalt, chert, flint, ignimbrite, quartzite and quartz, although organic materials such as bone were also employed (Wei et al. 2015). It has been postulated that handaxes were used for a variety of tasks including butchery, meat and vegetable processing, excavation of underground storage organs (e.g. tubers), as weapons, stripping bark from trees, cracking nuts, excavating for burrowing animals and/or as flake dispensers/cores (Jones 1980; Machin et al. 2007). It has been argued that the degree of symmetry, the type of raw material used and the size of the handaxe play an important role for tool effectiveness (Jones 1980; Machin et al. 2007). However, could the degree of symmetry, size and overall appearance also have been influenced by the sex or age of the knapper?

Who produced handaxes?

Stapert (2007) has argued that handaxes were predominantly or even exclusively used by men, based on the assumption that adult males were primarily responsible for hunting and the acquisition of meat. While today many researchers would probably consider women as

¹Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow, Poole, BH12 5BB.
²Institute for Mummy Studies, Eurac Research, Drususallee/Viale Druso 1, 39100 Bozen/Bolzano, Italy. E-mail: daniela.tumler@eurac.edu
³Archaeology and Palaeoecology, School of Natural and Built Environment, Queen’s University Belfast, Belfast, BT7 1NN. E-mail: l.basell@qub.ac.uk
⁴Department of Archaeology, Anthropology and Forensic Science, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow, Poole, BH12 5BB. E-mail: f.coward@bournemouth.ac.uk
active participants in producing and using handaxes, it remains noticeable that women are rarely, if ever, explicitly mentioned in this context, with the possible exception of experimental archaeology (e.g. Stout et al. 2005). Sperling’s (1991) critique still stands: when discussed or illustrated, for example in artists’ reconstructions widely available on the web and frequently reproduced by the media, the activities associated with Palaeolithic women tend to be child rearing and food gathering (e.g. Figure 1) (see also Zihlman 1997; Greaney et al. 2015).

Occasional exceptions include one of the first reconstructions of Boxgrove by Ivan Lapper (Figure 2) and the interesting suggestion by Snow (2013) that many Upper Palaeolithic hand prints in caves (and therefore the associated art) were made by women. However, such examples of women as actors remain few.

**What evidence is there to suggest who made handaxes?**

It is certainly challenging to assign some activities or their by-products to a specific sex without being able to observe such behaviour and especially in the absence of living analogues for comparison. Nevertheless, several sources can inform us about who produced these artefacts during the Palaeolithic. These include primate behaviour, hunter-gatherer activity, evolutionary biology and the artefacts themselves.

In recent years, a great deal of research has been conducted into primate tool use (Haslam et al. 2009). As our closest living relatives, the behaviour of chimpanzees is considered of particular relevance in informing interpretations of hominin behaviour. Boesch & Boesch’s (1981) classic study documenting the nut-cracking behaviour of Tai chimpanzees observed that females exclusively carried out these activities. Males appeared to lack concentration and had difficulty in motor control, making it more difficult to open the nuts (ibid.). In addition, subadult females seemed more motivated to learn these skills and thus learned faster and more efficiently than males. A more recent study on tool-assisted hunting in *Pan troglodytes verus* groups from Fongoli, Senegal (Pruetz et al. 2015), showed that, contrary to expectations that males would hunt more than females, both sexes and all age groups hunted equally. Likewise, females are the primary lithic tool producers in some human societies, for example among Konso women in south
Ethiopia (Arthur 2010), where girls of 6–8 years are encouraged by their female relatives to observe and learn this skill. Certainly, in most contemporary lithic-using societies, men play an important role in tool manufacture and use; however, this role allocation can vary significantly among different cultures. Generally, material culture is highly influenced by a complex interplay between social and biological factors (Pfaffenberger 1992).

However, attempts to reconstruct sexual division of labour in Palaeolithic societies are extremely difficult. Ethnographic research provides the only possible analogues for social organisation and division of labour among past populations, and suggests that whether males hunt or gather depends primarily on the availability of resources (Bird 1999). Nevertheless, in modern hunter-gatherer communities, men tend to favour prey that is very widely distributed and irregularly acquired, i.e. hunting, whereas women prefer to rely on more predictable resources, i.e. gathering (Hawkes et al. 1997). Thus, males can advertise their phenotypic quality and increase their mating chances by acquiring foods inaccessible to, but of high nutritional value for, females and their future offspring (Bird 1999; Marlowe 2007).

**Subadults in the Palaeolithic**

The presence and activities of subadults in Palaeolithic societies are often ignored (Pettitt 2011), despite them comprising about half of the known skeletal remains, as is the case for Neanderthals (Stapert 2007). Although children mainly depend upon the food acquisition skills of adults, they do contribute to the economy of the group and, depending on the local environment, may gather, hunt, capture small animals and care for younger children, tasks that become more specialised with increased age (Hawkes et al. 1995; Shea 2006). Other group members see children as economically and technologically similar to adults, despite still being ‘in training’ (Shea 2006).
Further studies have shown that by 7–11 years old children have the strength and the cognitive skills necessary to produce flaked tools (Shea 2006). There is also substantial ethnographic evidence of children being involved in flint-knapping activities learned simply by observation, imitation and/or applying the trial and error principle (Politis 2005; Stapert 2007; Arthur 2010; Hildebrand 2012). Thus, subadults could easily produce handaxes, although their tools may not be as accomplished as those of an experienced knapper. Some archaeological examples of poor quality tools that were possibly associated with subadults have been found at Boxgrove, United Kingdom, and Mauer, Germany (Politis 2005; Shea 2006; Stapert 2007). Altogether, there is nothing to suggest that females and subadults could not have engaged in past lithic tool production (Gero 1991; Costin 2015).

No research has suggested that handaxes produced by females differ in efficiency from those produced by males in any significant way. However, it has been argued that the degree of symmetry, the type of raw material used and the size of the handaxe all seem to play an important role in tool effectiveness (Jones 1980; Machin et al. 2007; Arthur 2010; Costin 2015). Various experimental studies have shown that handaxe symmetry is positively associated with butchery effectiveness and also that different types of raw material affect tool sharpness, which inevitably impacts tool use (Jones 1980; Brantingham & Olsen 2000; Stout et al. 2005; Machin et al. 2007). This study aims to determine the responses of modern individuals to symmetry, raw material and size of a handaxe as a first step in ascertaining whether the perception of such factors differs according to sex and age.

MATERIALS AND METHODS

Handaxes

Four handaxes were commissioned for this experiment from the experimental archaeologist Wulf Hein. These were deliberately designed to be of different raw materials, symmetry and size. The three black/grey flint handaxes and one brown quartzite handaxe are displayed in Figure 3 and a description of their variables is provided in Table 1. Prior to answering a questionnaire, all participants were given an information sheet on bifaces (see Supplementary Online Material) to ensure participants shared a common baseline level of information about the implements they were examining.

The handaxes were displayed to the participants as shown in Figure 3. The rounded base pointed towards the participant, who was allowed to pick up and examine the lithics. For each question, only the two handaxes relevant to the specific question were offered. As a control, one of these was always A.

Figure 3. Handaxes used in the experiment.
Table 1. Description of handaxe variables. The index of asymmetry was calculated based on the Fliptest proposed by Dunn & Hardaker (2005).

<table>
<thead>
<tr>
<th>Handaxe</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variable</td>
<td>symmetry</td>
<td>asymmetry</td>
<td>raw material</td>
<td>size</td>
</tr>
<tr>
<td>Raw material</td>
<td>flint</td>
<td>flint</td>
<td>quartz</td>
<td>flint</td>
</tr>
<tr>
<td>Length (mm)</td>
<td>185</td>
<td>200</td>
<td>195</td>
<td>130</td>
</tr>
<tr>
<td>Width (mm)</td>
<td>100</td>
<td>95</td>
<td>95</td>
<td>70</td>
</tr>
<tr>
<td>Thickness (mm)</td>
<td>40</td>
<td>35</td>
<td>40</td>
<td>30</td>
</tr>
<tr>
<td>Weight (g)</td>
<td>670</td>
<td>530</td>
<td>660</td>
<td>215</td>
</tr>
<tr>
<td>Index of asymmetry</td>
<td>1.78</td>
<td>6.72</td>
<td>2.31</td>
<td>2.27</td>
</tr>
</tbody>
</table>

Data collection

Data were collected using multiple-choice questionnaires. Participants identified themselves as either male or female, gave their age and were asked the following three questions, which were designed to test the participants’ preference for symmetrical or asymmetrical handaxes, as well as raw material and size.

Question 1: What shape do you prefer: the symmetrical or the asymmetrical handaxe?

Question 2: What raw material do you like better: flint or quartzite?

Question 3: Which do you find more functional: the larger or the smaller handaxe?

This final question was explained to the participants, who were encouraged to try the handaxes themselves.

Participants and data gathering

The age groups used for the analysis were chosen based on the physical development stages of modern humans and the role of that developmental stage in different cultures (Zeller 1987; Hermann et al. 1990). In foraging societies, children start helping adults with domestic tasks between the ages of 5 and 7, and the amount of involvement and workload increases with puberty at around 10 years (MacDonald 2007). Therefore, participants were divided into age categories as outlined in Table 2.

Participates were drawn from four institutions in the Province of Bolzano, Italy. These were: primary and secondary schools (students from 5–6 years to 13–14 years), from the school catchment areas of Schulsprengel Schlanders and Schulsprengel Latsch; ArcheoPark Schnals, a museum and archaeological park focussed primarily on later prehistory; and Eurac Research, an applied research centre. All participants were informed about how the collected data would be processed and used. An ethics review was completed and the legal guardians of minors were contacted and informed well ahead of data collection. Data were collected from 363 individuals (180 males, 183 females) and entered into an Excel database. A chi-square test was carried out using SPSS to determine the statistical significance of results.

Table 2. Age categorisation used for the current experiment.

<table>
<thead>
<tr>
<th>Age category</th>
<th>Age ranges (in years)</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>26–60</td>
<td>Hermann et al. 1990</td>
</tr>
</tbody>
</table>
RESULTS

Sex and symmetry

Both sexes prefer the more symmetrical handaxe (A) to the asymmetrical handaxe (B) (Figure 4). Females show a slightly higher preference for handaxe A (65%) than males (53%). The chi-square test showed a highly significant relationship between sex and symmetry (chi-square = 5.678, df = 1, p = 0.017). Therefore, the null hypothesis of no significant difference in preference between the sexes was rejected.

Sex and raw material

Male and female responses showed an overall preference for the flint over the quartz handaxe. Although there were slight differences between male (58%) and female (56%) responses, these were not statistically significant (chi-square = 0.269, df = 1, p = 0.605).

Sex and size

Figure 6 clearly shows that there is a higher preference for symmetry (handaxe A) in children (67%) and juveniles (63%) than for asymmetry (handaxe B). In contrast, 52% of adults preferred handaxe B and 48% handaxe A. A positive relationship between age and symmetry was confirmed by chi-square test (chi-square = 9.427, df = 2, p = 0.009).

Age and raw material/size

The data that focussed on preferences for handaxe raw material indicate a higher preference for the flint handaxe regardless of age. A preference for the flint handaxe may be due to the fact that most people associate handaxes with flint. The chi-square test (chi-square = 1.953, df = 2, p = 0.377) showed no statistically significant relationship between age and raw material. Likewise, Question 3 on handaxe size indicated a preference for the smaller handaxe D, but differences among age groups were not statistically significant (chi-square = 3.750, df = 2, p = 0.153).

DISCUSSION

Female participants in this survey exhibited a stronger preference than males for symmetrical and small handaxes. In addition, younger participants were significantly more likely to prefer symmetrical to asymmetrical handaxes. In contrast, no significant patterns were found with regard to preference for raw material by sex, or for any preference for size or raw material among age groups.

Figure 4. Male and female preferences for handaxes A and B.
Figure 5. Handaxe size preference of males and females.

Figure 6. Children, juvenile and adult responses for handaxe symmetry.
Symmetry

Many species, such as chickens and bumblebees show a preference for symmetry (Møller & Pomiankowski 1993; Mascalzoni et al. 2012; Culbert & Forrest 2016). Indigenous human groups with no previous training or schooling share core geometrical knowledge and were able to distinguish symmetry from asymmetry (Dehaene et al. 2006). This is argued to have been selected for by the need to distinguish non-living from living organisms (Enquist & Arak 1994; Giurfa et al. 1996; Wilson & Wilkinson 2002; Beck et al. 2005; Hodgson 2009). Increased sensitivity to symmetry may also aid in assessing the genetic fitness of other individuals, particularly potential mating partners (Møller & Pomiankowski 1993; Møller & Eriksson 1995; Hirstein & Ramachandran 1999; Wilson & Wilkinson 2002; Rodrigues et al. 2004; Sanchez-Pages & Turiegano 2010). Could this sensitivity to symmetry have extended to handaxes?

Many handaxes are argued to display more elaborate knapping after around 0.6 mya and to be highly, even ‘overly’ symmetrical (Saragusti & Sharon 1998; Lycett 2008; Hodgson 2009), suggesting positive selection for symmetry, which is also demonstrated in the current experiment. Shape modification of a tool primarily affects functionality; the degree of symmetry of a handaxe increases its effectiveness for butchery (Machin et al. 2007), and thus the ability to produce a more symmetrical handaxe would enhance the energy intake of a given individual. It may have also attracted other individuals’ attention (cf. Waitt & Little 2006), and potentially improved the social status of the pioneer individual (Nowell & Davidson 2010). However, it has been argued that Mode 2 technologies (Acheulean handaxes) require a higher level of ‘intentionality’ or ‘mind-reading’ to learn. Mode 1 technologies (Oldowan tools) can arguably be considered to be ‘transparent’ in the sense that they are easily recreated simply through observation of their manufacture, or even from study of the objects themselves. However, the manufacture of a handaxe is a more complex process that involves ‘opaque’ stages of processing; the ‘rough out’ stage includes actions that are not immediately self-explanatory. Therefore, recreating the manufacturing process requires not only close observation but also highly developed skills of true ‘imitation’, not simple mechanical replication. A certain level of intentionality may thus be required in order to be able to follow someone else’s thoughts and intentions (see references in Coward 2016). An increase in handaxe symmetry in the archaeological record has thus been argued to be associated with the evolution of more complex forms of intentionality and theory of mind (McPherron 2000; Hodgson 2015; McNabb & Cole 2015). Thus, individuals who were able to identify symmetry, and as a result produce a more symmetrical handaxe, should have experienced greater biological reproductive fitness and success (Kohn & Mithen 1999; Lycett 2008).

As discussed above, symmetry may be particularly important to females, who bear much higher costs of reproduction and hence choose their mates more carefully to secure offspring survival (Kappler et al. 2004; Jurmain et al. 2005). Therefore, if symmetry reflects mate or tool quality then females should be more sensitive to it. The results of this experiment demonstrate that females actually display a significantly higher preference for symmetry in handaxes than males (65% vs 53%; chi-square = 5.678, df = 1, p = 0.017; Figure 4). One possible explanation is that the ability to detect symmetry increases females’ reproductive success, either by allowing production of more symmetrical and therefore effective tools and/or by mating with males who do so. However, it is worth noting that, although the differences are statistically significant, they are not extremely large, and a majority of males in this experiment also favour symmetrical handaxes. As a result, symmetry preference may be a more general indicator of skill or theory of mind.

Symmetry preferences also seem to be linked to age. Humans develop mechanisms to detect symmetry at an early age (Dehaene et al. 2006); four-month-old infants can distinguish different forms of symmetry (Beck et al. 2005). Hence, children, juveniles and adults alike should exhibit similar preferences for symmetry. However, while children (67%) and juveniles (63%) display high preferences for symmetry, adults as a group (48%) appear to
show no preference (Figure 6). Why might younger individuals be more likely to be able to identify symmetry (Corbey et al. 2016)? Frequent engagement in activities applying visuomotor skills facilitates imitation of such actions (Hodgson 2012). Thus, as children learn much faster than adults, with sufficient practice they may have learned to produce a symmetrical handaxe very quickly. Also striking is that juveniles’ preference for the symmetrical handaxe (63%; Figure 6) is intermediate between those of children and adults, who show no clear preference (48% symmetrical; 52% asymmetrical). One possibility is that, despite the demonstrated significance of symmetry for tool effectiveness during butchery (Machin et al. 2007), adults may be more sensitive to other variables relating to tool efficiency, e.g. raw material or socio-cultural factors.

**Raw material**

Raw material quality is a crucial determinant of the shape of a tool and also its sharpness. Raw material is a variable that cannot be controlled as easily as the shape of a tool, as it depends on availability in the local environment (Orton 2008). Fine-grained lithics, such as cryptocrystalline silica/chert and silcrete, are more predictable in terms of fracturing and therefore allow finer retouch, sharp edges and thus the production of more delicate tools (Brantingham & Olsen 2000; Stout et al. 2005). In contrast, due to their unpredictable fracturing patterns, coarser-grained lithics like quartzite are more difficult to retouch and work more generally, and are also more likely to fragment, especially if the toolmaker is inexperienced (Cotterell & Kamminga 1990; Domanski et al. 1994; Tallavaara et al. 2010). Nevertheless, lower quality raw materials, such as quartzite, were used for handaxe manufacture where high quality raw materials were unavailable, presumably for tasks that do not require very sharp edges or a highly symmetrical tool-shape (Orton 2008).

Overall, the results of the present study display higher preference for flint as a raw material over quartzite. However, no substantial differences among the responses of different sex and age groups to handaxes made on different raw materials are apparent. This may imply that all individuals possess the ability to recognize raw materials suitable for tool production, although availability may be highly variable in different locations.

**Size**

Like symmetry, tool size is primarily determined by the toolmaker. Goren-Inbar et al. (2011) have argued that the size of the giant handaxes from Gesher Benot Ya’aqov may restrict their usefulness as butchery tools. They suggest, however, that these handaxes were used as raw material stocks, as they are associated with evidence of base camp activities and the presence of bifaces, rather than being used as tools themselves. Jones (1980) tested handaxe butchering efficiency for different sized handaxes and concluded that large bifacially flaked tools (150–200 mm) are more efficient than small flakes. Larger tools were more efficient and required less force when butchering a large animal, whereas smaller tools were more efficient for more detailed cutting tasks (Jones 1980).

The present study shows that significantly more females (79%) than males (63%; chi-square = 10.189, df = 1, p = 0.001; Figure 5) prefer the smaller tool, possibly implying that females are likely to produce smaller handaxes. Yet, as males also prefer smaller tools, their production and use may vary depending on the task that needs to be accomplished. An individual’s activity may be linked with the selection of tool size, as small numbers of both sexes (females 21%, males 37%; chi-square = 10.189, df = 1, p = 0.001; Figure 5) prefer the larger handaxe. Heavy-duty butchery, for which larger handaxes seem to be more efficient, is only one part of hominin food procurement and processing. For other tasks, such as the production of wooden tools or the processing of fruits, a smaller tool may have been more efficient and would have allowed for a greater degree of precision. If females and males were involved in different tasks, they may have required different tools to accomplish these, so this difference could be reflective of differences in the participants’ perceived use of handaxe function. Alternatively, the differences might be related to participants’ perception of ease of use in relation to their own hand size based on handling the tool. Sexual dimorphism in
different elements of hands is known to exist in humans (e.g. Karakostis et al. 2013) and much attention has been paid to variability between species in regard to hominin hand anatomy in relation to tool use (e.g. Marzke 2013). It is not possible to generalise within Homo sapiens that women have smaller hands (and so would find a smaller biface easier to use), as this will vary according to the population under study. However, where sample sizes are large enough and hands are preserved, within-species variation in hand size and anatomy might be worthy of future consideration in this context.

With regard to age, adults (72%), juveniles (65%) and children (76%) display an evident preference for the smaller handaxe. Children are unlikely to be involved in heavy-duty butchery, but may undertake other tasks that require the use of lithic tools, such as gathering. However the data on biface size and age are not statistically significant (chi-square = 3.750, df = 2, p = 0.153). Therefore, it seems likely that preferences regarding handaxe size may be influenced by the tasks individuals undertake, rather than by their age per se.

**CONCLUSION**

The current study demonstrates that preferences for the symmetry, raw material and size of handaxes vary significantly by sex and age. The results demonstrate that females, as well as juveniles and children, are capable of detecting variables associated with tool effectiveness. The current data may not be generalisable, and may not apply to extinct hominin species or even other hominid species. Nevertheless, they clearly show the extent to which sex and age could influence preference for a particular type of tool, and therefore suggest the reconsideration of the generally accepted assumption that the manufacture and use of handaxes should exclusively be attributed to adult men. Sex and age of lithic manufacturers should thus be considered in future studies on the broader context of lithics, as these two factors may significantly influence the outcome of lithic production and use.

In conclusion, the current research indicates that adult females, juveniles and children display a statistically significant preference for symmetrical handaxes, and that adult females favour smaller tools over larger ones. These results can be interpreted in various ways and may shed new light on the question of modern human perceptions of and preferences for different handaxe variables. However, the present research only scratches the surface in answering the question of who produced handaxes. Further research tackling the current question from various different angles is, therefore, required.

**ACKNOWLEDGEMENTS**

This study was conducted as part of D. Tumler’s undergraduate dissertation at Bournemouth University, supervised by L. Basell and F. Coward. Thanks are due to Schulsprengel Schlanders, Schulsprengel Latsch, Archeopark Schnals and Eurac Research Bozen, Italy, for allowing us to use their premises for data collection, and to Wulf Hein in particular, who custom-made the handaxes for the present research.

**REFERENCES**


Pruetz, J.D., Bertolani, P., Boyer Ontl, K., Lindshield, S., Shelley, M. & Wessling, E.G. 2015. New evidence on the tool-assisted hunting exhibited by...
chimpanzees (Pan troglodytes verus) in a savannah habitat at Fongoli, Senegal. Royal Society Open Science 2: 1–11.


