

## MAHALE AND GOMBE COMPARED: PATTERNS OF RESEARCH ON WILD CHIMPANZEES IN TANZANIA OVER FOUR DECADES

W.C. McGREW

*Departments of Anthropology and Zoology, Miami University and  
Leverhulme Centre for Human Evolutionary Studies, University of Cambridge*

**ABSTRACT** Students of science have contrasted Japanese and Western primatology. This paper aims to test such claims by comparing two long-term African field projects, Mahale and Gombe, in terms of research productivity as measured by scientific publications. Gombe, directed by Jane Goodall since 1960, and Mahale, directed by Toshisada Nishida since 1965, have much in common, in addition to their main focus on the eastern chimpanzee, *Pan troglodytes schweinfurthii*. They have produced similar total numbers of journal articles, books and chapters since the projects were founded. When these are categorized by subject matter, the main topics make up a similar proportion of publications, e.g. social relations, behavioural ecology, sex and reproduction, etc. Although most research output is on similar subjects, there are important differences between the sites, e.g. Mahale emphasizing medicinal plant use, Gombe predominating in modelling human evolution. Both sites favour publishing in *Primates* among the specialist primatological journals, but important differences exist in publishing elsewhere. Overall, there are more similarities than differences in scientific publishing between Mahale and Gombe, despite the asymmetry in flow of personnel between the two sites.

**Key Words:** *Pan troglodytes*; Chimpanzee; Gombe; Mahale.

## INTRODUCTION

Primatology began independently in Japan and in the West (here taken to be Europe and North America), and much has been said about their differences in viewpoint (e.g. Asquith, 1986, 2000; Takasaki, 2000; de Waal, 2001). In western publications, Japanese primatology has been characterized variously as: lacking rigour (Asquith, 1986: 69), anthropomorphic (de Waal, 2001: 118), anti-socio-biological (Takasaki, 2000: 160-163), marginalized (Asquith, 2000: 172), anecdotal, descriptive and impressionistic (Asquith, 2000: 170), by comparison with its western counterparts. More specifically, the primatological journal *Primates* has been characterized as a "last resort", the articles in which were not to be trusted (Asquith, 2000: 209). These are serious claims, yet there seems to be no evidence of systematic and empirical comparison between Japanese and Western primatological scientific output, in order to test them.

One way to pursue this is to "yoke" for comparison two similar primatological projects in which as many variables as possible are held constant: onset and duration (1960s to present), place (eastern shore of Lake Tanganyika, in Tanzania), subject of study (*Pan troglodytes schweinfurthii*), ecotype (mosaic tropical forest), etc. (See Table 2 below for details.) This leaves as the main indepen-

dent variable the contrasting cultural backgrounds of the investigators, Japanese or Western. Mahale and Gombe fulfil this criterion, as personified in the two founding researchers, Toshisada Nishida and Jane Goodall. Each site is unique and neither is wholly representative (e.g. chimpology is but a fraction of primatology), but the two are reasonably well-matched.

A direct measure of scientific productivity is publication, especially in widely-circulated, peer-reviewed periodicals and monographs. More precisely, one can look at frequency, subject matter and outlets, as the when, what and where of publishing, in which the more publications, on the widest range of topics, in the highest-profile channels, the better.

The aim of this analysis is to compare the scientific output of two well-known and long-established African research projects in primatology that focus on one of the most attractive species: Mahale (Nishida, 1990) and Gombe (Goodall, 1986). These studies of wild chimpanzees may tell us something about the similarities and differences between Japanese and Western primatology.

## METHODS

To compare scholarly productivity between Gombe and Mahale, I sought complete listings of academic publications resulting from research done at each site. Wilson (2003) provides a bibliography of publications (N=468, as of 27 Aug. 2003) of the Gombe Stream Research Centre. The website of the Mahale Wildlife Conservation Society ([http://mahale.web.infoseek.co.jp/papers/e\\_papers\\_top.html](http://mahale.web.infoseek.co.jp/papers/e_papers_top.html)) lists publications (N=246, through 2003) from Mahale. Both list references in English.

For this exercise, I counted only published journal articles, book chapters and books or monographs. I excluded abstracts, theses, dissertations, reports, newsletters, popular articles, and duplicate listings.

I counted only publications about chimpanzees, which meant omitting many publications about baboons from Gombe. Publications that featured both Gombe and Mahale were counted in each site's totals; such redundancies were few. This reduced the usable sample for Gombe to 252 references, and 227 for Mahale.

Table 1 lists and defines 12 categories that account for 85% (N=408) of the 479 references; the thirteenth category, Miscellaneous, comprises the remainder. The classificatory scheme is inclusive but intuitive and *a posteriori*. Some categories may seem arbitrary and idiosyncratic, e.g. "medicinal plant use" could have been included in "behavioural ecology". Each paper was assigned by forced-choice to one category only, based on perceived primary emphasis. This was often hard: a (hypothetical) article on dominance and reproductive success could be classed in Social Relations or in Sex and Reproduction. As a test of intra-coder reliability, the Mahale data-set was independently recoded after a three month interlude. Using the standard formula of agreements (agreements & disagreements), the reliability coefficient was 0.87, which was

**Table 1.** Definitions of categories of publications, in descending order of frequency.

| Categories              | Definitions                                                                                                       |
|-------------------------|-------------------------------------------------------------------------------------------------------------------|
| Social Relations        | social interaction, relations, structure, organisation, demography                                                |
| Behavioural Ecology     | chimpanzee diet, foraging, ranging, laterality, predation by, anti-predator by, etc. (except medicinal plant use) |
| Sex & Reproduction      | courtship, copulation, mate choice, pregnancy, birth, etc.                                                        |
| Medicinal Plant Use     | non-nutritive ingestion or topical application of vegetation                                                      |
| Behavioural Development | ontogeny of infancy, childhood, and adolescence                                                                   |
| Culture                 | socially learned traditions and customs characteristic of a social group                                          |
| Technology              | tool making and use, including nest/bed                                                                           |
| Ecology                 | habitat, resources, predators, competitors, inter-species, species range, etc.                                    |
| Morbidity & Mortality   | disease, injury, death, parasites                                                                                 |
| Acoustic Communication  | vocalisation, drumming                                                                                            |
| Human Evolution         | chimpanzees as models for human origins                                                                           |
| Position                | posture, locomotion                                                                                               |
| Miscellaneous           | infanticide, & cannibalism, anatomy, physiology, genetics, conservation, other                                    |

**Table 2.** Comparison of two field sites of study of wild chimpanzees: Gombe and Mahale.

| Variable                      | Gombe                                     | Mahale                                    |
|-------------------------------|-------------------------------------------|-------------------------------------------|
| Location                      | 4° 40'S, 29° 38'E                         | 6° 07'S, 29° 44'E                         |
| Status                        | National park                             | National park                             |
| Area                          | 32 km <sup>2</sup>                        | 1613 km <sup>2</sup>                      |
| Altitude                      | 775 (lakeshore)-1500 m                    | 775 (lakeshore)-2515 m                    |
| Rainfall (annual)             | 1600 mm                                   | 1836 mm                                   |
| Vegetation                    | Open grassland to closed evergreen forest | Open grassland to closed evergreen forest |
| Other Primates                | >6 spp.                                   | 8 spp.                                    |
| Predators                     | Leopard?                                  | Leopard, lion                             |
| Provisioning                  | Yes, then no                              | Yes, then no                              |
| Habituation                   | Kasakela, Mitumba communities             | M-unit group                              |
| Study Period                  | 1960-present                              | 1965-present                              |
| Ecotourism                    | Yes                                       | Yes                                       |
| Illegal Hunting               | Yes                                       | Yes                                       |
| Resident Humans               | Yes                                       | Yes                                       |
| Anthropogenic Health Problems | Yes                                       | Yes                                       |
| Founding Researcher           | Jane Goodall                              | Toshisada Nishida                         |

Source: McGrew et al. (1996)

deemed acceptable. (Complete coding data are available from the author).

Table 2 lists prominent characteristics of each site (taken from McGrew et al., 1996). Many apparent similarities may show significant differences in detail, e.g., both have ecotourism but it is handled differently. Some apparent differences are probably irrelevant, e.g., the higher altitudes available at Mahale are probably of no direct consequence to research. Some comparisons remain to be resolved, e.g., is Mahale really a wetter site than Gombe, in an ecologically meaningful way? All in all, the two sites seem well-matched enough to justify comparison, that is, any differences found in research productivity are unlikely to be ecologically determined.

## RESULTS

The rate of appearance of scientific publications on wild chimpanzees from the two sites is remarkably similar: 227 in 38 years ( $\bar{x}$  = 6.0 per year) at Mahale versus 252 in 43 years ( $\bar{x}$  = 5.9 per year) at Gombe. Table 3 shows that the patterning of publication over time, on a decade-by-decade basis, differed: Mahale's numbers have grown steadily from its beginnings in 1965, although there are signs that productivity is levelling off in the 2000s. Gombe grew more rapidly in the 1960s and 1970s, then fell in 1980s only to rise again in the 1990s. Based on the first four years of the 2000's, productivity at Gombe is again in decline. However, on the basis of overall similar productivity in publications from the beginning to the present, further comparisons are made below.

Table 4 ranks the publications of Mahale and Gombe by topic and overall frequency. For example, the two sites together have yielded 87 papers on social relations through 2003, etc. All topics with 13 or fewer publications are combined here as Miscellaneous (15% of the total of 479 papers). Ethological topics predominate: it is not until the eighth-ranking topic, Ecology that a non-behavioural topic appears on the list. Empirical publications are overwhelmingly prevalent: only the eleventh-ranking topic, Human Evolution, is the exception, although many of the miscellaneous publications are also non-empirical.

**Table 3.** Scientific publications on chimpanzees by decades at Gombe and Mahale.

| Decade | Gombe       |     | Mahale     |     | Total        |     |
|--------|-------------|-----|------------|-----|--------------|-----|
|        | N           | %   | N          | %   | N            | %   |
| 1960s  | 14          | 6   | 1          | 0   | 15           | 3   |
| 1970s  | 73          | 29  | 9          | 4   | 82           | 17  |
| 1980s  | 46          | 18  | 64         | 28  | 110          | 23  |
| 1990s  | 93          | 37  | 113        | 50  | 206          | 43  |
| 2000s* | 25 (62.5**) | 10  | 40 (100**) | 18  | 65 (162.5**) | 14  |
| Total  | 252         | 100 | 227        | 100 | 479          | 100 |

\*As of 2003

\*\*Predicted total if productivity of first four years of decade were sustained over next six years

**Table 4.** Twelve most common topics of scientific publications\* on chimpanzees from Gombe and Mahale, plus all other topics combined as Miscellaneous.

| Rank  | Topic                   | Gombe | Mahale | Total |
|-------|-------------------------|-------|--------|-------|
| 1.    | Social Relations        | 45    | 42     | 87    |
| 2.    | Behavioural Ecology     | 33    | 31     | 64    |
| 3.    | Sex & Reproduction      | 21    | 14     | 35    |
| 4.    | Medicinal Plant Use     | 6     | 28     | 34    |
| 5.    | Behavioural Development | 19    | 13     | 32    |
| 6.    | Culture                 | 17    | 14     | 31    |
| 7.    | Technology              | 14    | 16     | 30    |
| 8.    | Ecology                 | 6     | 20     | 26    |
| 9.    | Morbidity & Mortality   | 15    | 6      | 21    |
| 10.   | Acoustic Communication  | 9     | 9      | 18    |
| 11.   | Human Evolution         | 15    | 1      | 16    |
| 12.   | Posture & Locomotion    | 7     | 7      | 14    |
|       | Miscellaneous           | 45    | 26     | 71    |
| Total |                         | 252   | 227    | 479   |

\*Published journal articles, book chapters, monographs only. Excludes abstracts, theses, dissertations, popular pieces, reports, unpublished manuscripts, etc.

**Table 5.** Similarities in topic of publications on chimpanzees from Mahale and Gombe, in descending order of frequency.

| Topic                   | Gombe (N=252) |      | Mahale (N=227) |      |
|-------------------------|---------------|------|----------------|------|
|                         | frequency     | %    | frequency      | %    |
| Social Relations        | 45            | 17.9 | 42             | 18.5 |
| Behavioural Ecology     | 33            | 13.1 | 31             | 13.7 |
| Sex & Reproduction      | 21            | 8.3  | 14             | 6.2  |
| Behavioural Development | 19            | 7.5  | 13             | 5.7  |
| Culture                 | 17            | 6.7  | 14             | 6.2  |
| Technology              | 14            | 5.6  | 16             | 7.0  |
| Acoustic Communication  | 9             | 3.6  | 9              | 4.0  |
| Posture & Locomotion    | 7             | 2.8  | 7              | 3.1  |
| Aging                   | 1             | 0.4  | 2              | 0.9  |
| Nest/Bed                | 1             | 0.4  | 1              | 0.4  |
| Total                   | 167           | 66.3 | 149            | 65.6 |

In terms of topics of research reported in publications, Mahale and Gombe show more *similarities* than differences. Table 5 shows that the relative frequency of eight of the 13 topics in Table 4 does not differ across sites. These similarities make up about two-thirds of the publications in each case, at 66% on average. If the eight topics from Social Relations to Position show comparable positive preferences for topics, then Aging and Nest/Bed show negative preferences. Both Gombe and Mahale have done little research in these areas.

However, Table 6 shows *differences* in choice of research topics between Mahale and Gombe. Two of the ranked topics in Table 4 were reported more often at Mahale: Medicinal Plants and Ecology, plus a more specialised topic, Cannibalism and Infanticide. For Gombe, two of the ranked topics, Morbidity and Mortality, and Human Evolution, yielded more publications than at Mahale.

**Table 6.** Differences in topics of publications on chimpanzees from Gombe and Mahale.

| Topic                     | Gombe (N=252) |     | Mahale (N=227) |      |
|---------------------------|---------------|-----|----------------|------|
|                           | frequency     | %   | frequency      | %    |
| Medicinal Plant           | 6             | 2.4 | 28             | 12.3 |
| Ecology                   | 6             | 2.4 | 20             | 8.9  |
| Cannibalism & Infanticide | 2             | 0.8 | 10             | 4.4  |
| Morbidity & Mortality     | 15            | 6.0 | 6              | 2.6  |
| Human Evolution           | 15            | 6.0 | 1              | 0.4  |
| Anatomy & Physiology      | 8             | 3.2 | 3              | 1.3  |
| Genetics                  | 8             | 3.2 | 0              | 0.0  |
| Conservation Biology      | 4             | 1.6 | 1              | 0.4  |

Also, three more specialised, non-behavioural topics, Anatomy and Physiology, Genetics, and Conservation Biology showed the same Gombe predominance, although the numbers of publications are low in these cases.

Given the parallels between Mahale and Gombe, geographic and ecological, as well as methodological and logistical, e.g. both use the town of Kigoma as a source of communications, supplies, travel, etc., one might expect scientific cross-fertilisation between the sites. There has been little, and it has been one-sided. Several Westerners have published papers based on work done at both places: C. Boesch, M. Huffman, K. Hunt, L. Marchant, W. McGrew, J. Mitani, C. Tutin; other westerners have been guest investigators at Mahale: R. & J. Byrne, N. Corp, L. Turner. The special case of Michael Huffman defies easy classification; he is American by origin but has spent most of his career based in Japan. Fully 36% (82 of 227) of the publications from Mahale include as co-authors, westerners who did research at Mahale. Even if Huffman's 34 publications are excluded, the remaining 48 still amount to more than a fifth of Mahale's total scientific publications.

At Gombe, no Japanese primatologist has worked long-term; there appears to be only one guest publication, based on a six-day visit (Shimada, 2002).

Table 7 shows the disposition of articles published in refereed scientific journals about the wild chimpanzees of Mahale and Gombe. The journals are classed as one of six categories: The "Big Four" journals of primatology (in order of age: *Primates* (P), *Folia Primatologica* (FP), *International Journal of Primatology* (IJP), *American Journal of Primatology*) (AJP), plus all other journals published in Japan or in the West. Not surprisingly, Mahale's researchers, who are mostly Japanese, prefer to publish more often in *Primates* (47 vs. 32) than in the other three primatological journals. Perhaps surprisingly, however, Gombe's researchers, although overwhelmingly Western, do too (18 vs. 16). Even more surprisingly, Mahale's researchers published twice as many articles (N=32) in the Western primatological journals than did Gombe's researchers (N=16).

**Table 7.** Articles on wild chimpanzees published in English in refereed scientific journals, by frequency and proportion.

| Site   |           | "Big Four" in Primatology |                 |                  |                  | Other Journals       |                       | Total |
|--------|-----------|---------------------------|-----------------|------------------|------------------|----------------------|-----------------------|-------|
|        |           | Primates <sup>a</sup>     | FP <sup>b</sup> | IJP <sup>c</sup> | AJP <sup>d</sup> | Western <sup>e</sup> | Japanese <sup>f</sup> |       |
| Mahale | frequency | 47                        | 12              | 12               | 8                | 43                   | 19                    | 141   |
|        | %         | 33                        | 8.5             | 8.5              | 6                | 31                   | 13                    | 100%  |
| Gombe  | frequency | 18                        | 7               | 5                | 4                | 102                  | 1                     | 137   |
|        | %         | 13                        | 5               | 4                | 3                | 74                   | 1                     | 100%  |
| Total  | frequency | 65                        | 19              | 17               | 12               | 145                  | 20                    | 278   |
|        | %         | 23                        | 7               | 6                | 4                | 52                   | 7                     | 99%   |

a) *Primates*, published in Japan since 1957

b) *Folia Primatologica*, published in Switzerland since 1963

c) *International Journal of Primatology*, published in USA since 1980

d) *American Journal of Primatology*, published in USA since 1981

e) Western = published in Europe or North America

f) Japanese = published in Japan

## DISCUSSION

The almost identical magnitude of output of about six publications per year from each of the two sites is remarkable, given the variation in the projects' histories. Mahale's productivity has grown steadily; what started as a one-person operation (Nishida, 1968) became a near-constant small-group team effort, with Nishida regularly, if intermittently, active throughout its history. Gombe mushroomed from its one-person beginning (Goodall, 1962) to a large-scale undertaking within a decade, including dozens of undergraduate assistants (Goodall, 1971, 1990). This boom probably accounts for the jump in output in the 1970s, but it came to a sudden halt in May, 1975, when guerrillas from Zaire (now Democratic Republic of Congo) kidnapped researchers and field work was shut down. (Although all expatriates were evacuated, Tanzanian field assistants maintained the continuity of basic data collection throughout the lean years.) Given the lag effect in publishing, the kidnapping probably accounts for the drop in publications in the 1980s from Gombe. Despite Goodall's withdrawal from active research after the 1970s, a resurgence in research occurred in the late 1980s and early 1990s, which seems now to have peaked. Despite ups and downs, it is impressive that the two projects have produced almost 500 scientific publications. The predominance of topics based on behavioural data shown in Table 4 is not surprising, given that both projects have fully habituated groups of chimpanzees to observe at close-range. This probably explains the low ranking of Ecology, at least at Gombe, where it ranks last among the top 12 topics. Researchers who can watch food sharing rarely spend time doing plant phenology.

As shown in Table 5, Social Relations and Behavioural Ecology together are the foundations of research at both sites, accounting for almost a third of publications. This is hardly surprising, given a study-species that is omnivorous and

shows a fission-fusion social structure. Similarly, the two natural pairings of Sex and Reproduction + Behavioural Development, and Culture + Technology, are notably salient in a study-species that is large-brained and innovative.

More surprising is the equivalent lack of interest in certain topics: Although great apes live for decades and show marked life history changes (e.g. male politics by retired alpha males) or lack of them (e.g. absence of female menopause), only one paper (Huffman, 1990) from Mahale or Gombe project has tackled gerontology. Similarly, although the most common and arguably most important technology in chimpanzee daily life is their regular construction of shelters, neither project has investigated this phenomenon. In Gombe's history, the only publication on nesting was the first one of all (Goodall, 1962)!

The differences between topics chosen for study and publication at Mahale and Gombe are intriguing. As shown in Table 5, research on Medicinal Plant Use is mostly done at Mahale, although it was originally described jointly for both sites (Wrangham & Nishida, 1983). There is no reason to believe that Medicinal Plant Use is better developed or more common at Mahale than at Gombe; no one at Gombe seems to have followed up the original findings. Mahale's predominance in ecological publications may be accounted for by its much bigger area (e.g. more groups of apes living in a greater variety of habitats) and biodiversity (e.g. lions as predators), but in neither area has the vegetation been well analysed nor monitored over its obvious long-term changes. Finally, although Cannibalism and Infanticide were first described at Gombe (Bygott, 1972), it has been far more studied at Mahale, (e.g. Nishida & Kawanaka, 1985). This suggests that the phenomenon is more common or complex at Mahale, but this awaits systematic comparison.

Gombe's more frequent Miscellaneous publications are in large part due to a series of general papers about the site written by Goodall (e.g. Goodall, 1973). Morbidity and Mortality being more often written about at Gombe may result from a continuing history of intermittent anthropogenic outbreaks of disease, and consequent deaths. Although she was trained in zoology (ethology) at Cambridge by Robert Hinde, and not in anthropology, Goodall (e.g. Goodall, 1975) from the beginning wrote of the implications of research on apes for understanding human origins. This was encouraged by two other mentors, Louis Leakey and David Hamburg. Gombe's papers on anatomy and physiology comprise osteological analyses of the skeletal material made available by the recovery after death of its subjects (e.g. Jurmain, 1997). Gombe's predominance in genetical research based on non-invasive sampling of biological material from the apes led to a series of influential articles by Phillip Morin et al. (e.g. 1994). There is a suggestion that Gombe's greater vulnerability from its smaller population size and tiny surface area has sparked more interest in conservation biology, but the numbers are too small to draw conclusions.

Overall, however, Mahale and Gombe have more in common than not in terms of the preferred topics of (published) research, as shown by the total percentages in Tables 5 and 6. Perhaps the most startling disparity between Mahale and Gombe is the asymmetry in scientific exchange between the two research

projects. From the mid-1970s onward, Mahale has welcomed western scientists in collaborative research, whether they be post-graduate or post-doctoral students, or older professionals. Gombe has never reciprocated with regard to Japanese counterparts, but without data on supply and demand for places at field sites, any explanation is provisional. Perhaps Michael Huffman's presence at Mahale has been a catalyst that is absent at Gombe. Perhaps Jane Goodall's not having a permanent academic base has hampered the development of exchanges of students and faculty. Ideally, there would be more flow of personnel, and so of ideas and methods, between the two sites.

Venue of publication, at least for journal articles, differs between Mahale and Gombe, as shown in Table 7. Gombe's researchers clearly prefer to publish their results in western, non-primatological journals (74%) with the two main journals of biological anthropology, *American Journal of Physical Anthropology* and *Journal of Human Evolution*, being the most common. Gombe's researchers almost never publish in Japanese non-primatological journals, perhaps because of lack of exposure to them in the West.

Mahale's researchers split their publications between east (46%) and west (54%). If one considers just the "Big Four" primatological journals, there is no evidence of parochialism relative to Gombe, as Mahale scientists publish more often in the American (*AJP*), European (*FP*) and international (*IJP*) journals, as well as in the Japanese one. Both the first Japanese primatological research report to appear in a western journal (Nishida, 1973) and the first article to be published by a Japanese scientist in a non-Japanese primatological journal (Nishida, 1976) came from Mahale (Asquith, 2000). Furthermore, the first comprehensive ethogram published for *Pan troglodytes* came from Mahale (Nishida et al., 1999). Finally, there is no difference between Mahale and Gombe researchers in predominance accorded to *Primates*, among the primatological journals. In both cases, the total for *Primates* exceeds that of the other three journals combined.

More important than the cultural backgrounds of investigators may be their individual interests, at least as indicated by their publications. Both Nishida and Goodall were clearly interested in socio-sexual life, behavioural ecology and elementary technology from the beginning; neither showed interest in community or ecosystem ecology. For other topics, individual scientists took the lead and did focused, comparative studies at Mahale and Gombe: Michael Huffman on medicinal plant use, Kevin Hunt on posture and locomotion, John Mitani on vocal communication, Linda Marchant and William McGrew on manual laterality. In conclusion, it is not apparent from the scientific publications of Mahale and Gombe that there is any significant difference between Japanese and Western primatology in rigour, anthropomorphism, theoretical basis, marginality, objectivity, or precision. Nor is there any apparent difference in the quality or status of *Primates* compared with other primatological journals. Other variables (e.g. citation analyses, impact values) and other data-sets (e.g. Arashiyama versus Cayo Santiago for macaques) would broaden the picture and need to be done.

**ACKNOWLEDGEMENTS** I am grateful to: Juichi Yamagiwa for the invitation to take part in the symposium, African Great Apes: Evolution, Diversity and Conservation, Kyoto, 3-5 March, 2004, where a preliminary version of this paper was given; Linda Marchant for critical comments on the manuscript; Diana Deaton for manuscript preparation; Jacklyn Ramsey and Samantha Russak for research assistance; Toshisada Nishida for his invitation in July 1974 to do research at Mahale and for his unfailing generosity ever since; all colleagues and companions for their help during my stints at Gombe (1972, 1973, 1974, 1982, 1992) and at Mahale (1975, 1982, 1996). This paper is dedicated to the memory of Junichiro Itani, who hosted my first visit to Mahale in January, 1975.

## REFERENCES

- Asquith, P.J. 1986. Anthropomorphism and the Japanese and Western traditions in primatology. In (J.G. Else & P.C. Lee, eds.) *Primate Ontogeny. Cognition and Social Behaviour*, pp. 61-71. Cambridge University Press, Cambridge.
- 2000. Negotiating science: internationalisation and Japanese primatology. In (S.C. Strum & L.M. Fedigan, eds.) *Primate Encounters. Models of Science. Gender. and Society*, pp. 165-183. University of Chicago Press, Chicago.
- Bygott, J.D. 1972. Cannibalism among wild chimpanzees. *Nature*, 238: 410-411.
- Goodall, J. 1962. Nest building behavior in the free ranging chimpanzee. *Annals of the New York Academy of Sciences*, 102: 445-467.
- 1971. *In the Shadow of Man*. William Collins, London.
- 1973. The behavior of chimpanzees in their natural habitat. *American Journal of Psychiatry*, 130: 1-12.
- 1975. The chimpanzee: a model for the behaviour of early man? In (V. Goodall, ed.) *Quest for Man*, pp. 130-169. Pall Mall Press, London.
- 1986. *The Chimpanzees of Gombe. Patterns of Behavior*. Harvard University Press, Cambridge, MA.
- 1990. *Through a Window. My Thirty Years with the Chimpanzees of Gombe*. Houghton Mifflin, Boston.
- Huffman, M.A. 1990. Some socio-behavioural manifestations of old age. In (T. Nishida, ed.) *The Chimpanzees of the Mahale Mountains*, pp. 237-255. University of Tokyo Press, Tokyo.
- Jurmain, R. 1997. Skeletal evidence of trauma in African apes, with special reference to the Gombe chimpanzees. *Primates*, 38: 1-14.
- McGrew, W.C., L.F. Marchant & T. Nishida (eds.) 1996. *Great Ape Societies*. Cambridge University Press, Cambridge.
- Morin, P.A., J.J. Moore, R. Chakraborty, L. Jin, J. Goodall & D.S. Woodruff 1994. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science*, 265: 1193-1201.
- Nishida, T. 1968. The social grouping of wild chimpanzees in the Mahali mountains. *Primates*, 9: 167-224.
- 1973. The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. *Journal of Human Evolution*, 2: 357-370.
- 1976. The bark-eating habits in primates, with special reference to their status in the diet of wild chimpanzees. *Folia Primatologica*, 25: 277-287.

- Nishida, T. (ed.) (1990) *The Chimpanzees of the Mahale Mountains. Sexual and Life History Strategies*. University of Tokyo Press, Tokyo.
- Nishida, T., T. Kano, J. Goodall, W.C. McGrew & M. Nakamura 1999. Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, 107: 141-188.
- Nishida, T. & K. Kawanaka 1985. Within-group cannibalism by adult male chimpanzees. *Primates*, 26: 274-284.
- Shimada, M. 2002. Social scratch among the chimpanzees of Gombe. *Pan Africa News*, 9: 21-23.
- Takasaki, H. 2000. Traditions of the Kyoto school of field primatology in Japan. In (S.C. Strum & L.M. Fedigan, eds.) *Primate Encounters. Models of Science. Gender and Society*, pp. 151-164. University of Chicago Press, Chicago.
- de Waal, F. 2001. *The Ape and the Sushi Master. Cultural Reflections of a Primatologist*. Basic Books, New York.
- Wilson, M.L. 2003. *A Gombe Bibliography*. Gombe Stream Research Centre, Kigoma, Tanzania.
- Wrangham, R.W. & T. Nishida 1983. *Aspilia* spp. Leaves: a puzzle in the feeding behavior of wild chimpanzees. *Primates*, 24: 276-282.

————— Accepted April 18, 2007

Author's Name and Address: William C. McGREW, *Leverhulme Centre for Human Evolutionary Studies, University of Cambridge, Henry Wellcome Building Fitzwilliam Street Cambridge CB2 1QH, UNITED KINGDOM.*  
E-mail: [wcm21@cam.ac.uk](mailto:wcm21@cam.ac.uk)

