The Behaviour and Adaptation of Reintroduced Chimpanzees (*Pan troglodytes troglodytes*) in the Republic of Congo

Kay H. Farmer

Thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

University of Stirling
Department of Psychology

June 2002

Declaration

I declare that this thesis was written by myself and is the result of my own work. Data were collected by myself and a number of field assistants. This work has not been submitted in consideration for any other degree or award.

Kay H. Farmer

Abstract

Increasing and unsustainable demands on Africa's natural resources are having a profound effect on wild primate populations. Whilst wild populations are decreasing, numbers of orphaned primates, sanctuaries and attempts to reintroduce primates back to the natural environment, are increasing. Data were collected on the present status of African ape sanctuaries from questionnaires distributed to sanctuary managers. Across Africa there are 18 sanctuaries housing over 500 African great apes. Facilities and ideologies vary but the majority of sanctuaries profess a commitment to conservation through education, local capacity building, facilitating the enforcement of wildlife laws and other activities. From 1996 to 2001 the non-governmental organisation Habitat Ecologique et Liberté des Primates has released 37 wild-born chimpanzees (*Pan troglodytes troglodytes*) from an island sanctuary to mainland forest in the Conkouati-Douli National Park, Republic of Congo. Twenty-seven chimpanzees have been successfully reintroduced, three are known to have died and the status of seven remains unknown. This thesis investigated the behavioural adaptation of 15 of these released chimpanzees and reviews the reintroduction process employed. Analyses of post-release behavioural data revealed that activity budgets and diet were comparable to those of wild chimpanzees, and that seasonal variation influenced feeding behaviour and plant species selection. The chimpanzees utilised both terrestrial and arboreal zones and all nested in trees. A number of recommendations are made for future reintroduction projects. These include selecting a release site that has no, or a low density of, wild conspecifics; developing a relationship of trust between chimpanzee and caretakers without excessive dependency; using the release site for pre-release training; use of radio telemetry; post-release support and monitoring. This study has revealed the many complex factors that are involved in the reintroduction process. Future attempts to reintroduce chimpanzees should be guided by the experiences and recommendations of the present study to maximise success.

Acknowledgements

I gratefully acknowledge the help, support and encouragement of many people without whom this thesis would not have been possible.

An Economic and Social Research Council studentship enabled me to undertake this study. However, I would like to also thank the following organisations that contributed towards additional project costs: Care for the Wild International, Department of Psychology at the University of Stirling, East Midland Zoological Association (Twycross Zoo), International Fund for Animal Welfare (UK), International Primate Protection League (UK), People's Trust for Endangered Species, Primate Society of Great Britain, St. Andrew Animal Fund and Tusk Trust. All of these are gratefully acknowledged.

I thank the Government of the Republic of Congo, in particular Monsieur Henri Djombo, the Minister of Forest Economy, for permission to live and work in the country. I would like to thank Aliette Jamart, the Director of Habitat Ecologique et Liberté des Primates, for allowing me to conduct the research at her project and for providing access to previously collected data. I would also like to thank Aliette Jamart and Jean-Jacques Fontaine for their hospitality in Pointe-Noire and logistical assistance in the Congo. I am especially grateful to Jean-Jacques Fontaine for spending long periods of time at a photocopier on my behalf. Also thanks to Dr. Myriam Vacher-Vallas, Dr. Jorge Paredes and Jean-Jacques Fontaine for answering my many questions.

There are many persons that I worked along side in the forests at Conkouati and who contributed data to this study. However, I would particularly like to thank Mesmin Bongo, Jean-Marie Carenton, Sabine Couvent, Emmanuel Dilmbaka, Guy Goma, Yvon Movoungou Massala, Alexi Mayet, Nestin Moutogo, Sylvain Pambou, Stephanie Romeu, Aline Rouher, Jean-Patrick Suraud, Anselme Taty, Eric Tchimdongo and Carmen Vidal.

I am especially indebted to Emmanuel Dilmbaka whose relationship and knowledge of the chimpanzees facilitated this study.

At Stirling, I would especially like to thank my supervisor Dr. Hannah Buchanan-Smith for her continual support and advice throughout the PhD. I would also like to thank my second supervisor Dr. Jim Anderson. I am deeply indebted to Dr. Kate Howie for advice with statistical analyses of the data. Dr. Caroline Tutin instigated the study and I would like to thank her for her advice and help in the initial stages. I would also like to thank Dr Jim King (from the University of Arizona) for allowing me to use and adapt his chimpanzee personality questionnaire although it has not been included in the thesis. On a more personnel note I would like to thank Dougie, Richard, Lois, Tanya, Andrew, Jean and Sarah for all their help along the way.

I thank the following African sanctuary personnel for completing the questionnaire: Bala Amarasekaran, Graziella Cotman, Debby Cox, Martin Fanguinoveny, Peter Gray, Ian Henderson, Aliette Jamart, Peter Jenkins, Beki Kamya, David Lucas, John MacLachlan, Judy McConnery, Crispin Mahamba, Stella Marsden, Chris Mitchell, Annie Olivecrona, Liz Pearson, Linda Percy, Estelle Raballand, David Siddle, Sheri Speede and Ateh Wilson.

Throughout this PhD I have presented papers and posters at conferences and participated in workshops. I would like to thank the following organisations for providing the financial support that facilitated my attendance: Department of Psychology at the University of Stirling, European Commission, Habitat Ecologique et Liberté des Primates, Hayashira Foundation, International Primate Protection League (UK), People's Trust for Endangered Species, Scottish International Education Trust, The Primate Conservation and Welfare Society and the Universities Federation for Animal Welfare.

Publications and conference presentations

The following publications and conference presentations have been adapted from work detailed in this thesis:

Farmer, K.H. Pan African Sanctuary Alliance: status and range of activities for great ape conservation. Under review for American Journal of Primatology.

Farmer, K. H., Jamart, A., & Buchanan-Smith, H. M. (2002). The behaviour and adaptation of chimpanzees (*Pan troglodytes troglodytes*) reintroduced to mainland forest from an island sanctuary, Republic of Congo. Abstract published in the proceedings of the XIXth Congress of the International Primatological Society, Beijing, China.

Farmer, K.H. (2002) African ape sanctuaries: present status and range of activities Abstract published in the proceedings of the XIXth Congress of the International Primatological Society, Beijing, China.

Farmer, K.H., & Jamart, A. (2002). Habitat Ecologique et Liberté des Primates – a case study of chimpanzee reintroduction. In P. Soorae (Eds.) Re-introduction News, 21, 16-18. Abu Dhabi, UAE: IUCN/SSC Re-introduction Specialist Group.

Farmer, K.H, Jamart, A., & Buchanan-Smith, H.B. (2001a). The behaviour and adaptation of wild-born reintroduced chimpanzees (*Pan troglodytes troglodytes*), Republic of Congo. Abstract published in the proceedings of the 4th International Support of African and Asian Great Apes (SAGA) symposium, Okayama, Japan.

Farmer, K.H. (2001). African ape sanctuaries: committing to conservation. Abstract published in the proceedings of the Zoos and Aquariums: Committing to Conservation conference, Brevard Zoo, Florida, USA.

Farmer, K.H., Jamart, A., & Buchanan-Smith, H.M. (2001b). The adaptation of reintroduced chimpanzees to continuous forest in the Conkouati Reserve, Republic of Congo. Primate Eye, 73, 6.

Farmer, K.H., Jamart, A., & Buchanan-Smith, H.M. (2001c). The nest building abilities of reintroduced chimpanzees: a comparison to their wild counterparts, and implications for survival. Abstract published in the proceedings of the XVIIIth Congress of the International Primatological Society, Adelaide, Australia.

Farmer, K.H. (2000a). The Behaviour and adaptation of reintroduced chimpanzees, *Pan troglodytes*, Republic of Congo. Primate Eye, 71, 13-14.

Farmer, K.H. (2000b). The Final Step To Freedom – Conkouati chimpanzees returned to the wild, I.P.P.L. News, 27 (2), 17-20.

Farmer, K.H. & Buchanan-Smith, H.M and Jamart, A. (2000a). The adaptation of reintroduced chimpanzees (*Pan troglodytes troglodytes*) to continuous forest in the Conkouati Reserve, Republic of Congo. Poster presented at the European Federation of Primatology meeting. London, England.

Farmer, K.H. & Buchanan-Smith, H.M and Jamart, A (2000b). Nest building: comparison between wild and reintroduced chimpanzees (*Pan troglodytes troglodytes*). Poster presented at the Scottish Conference on Animal Behaviour. Stirling, Scotland.

Contents

APPENDICES

PLATES

Unless otherwise stated the plates in this thesis are the property of the author and can only reproduced with permission.

Foreword

Reintroduction is being used increasingly as a tool to manage and preserve wildlife. Documenting the methods employed (including successes and failures) is vital if the process of reintroduction is to advance on anything other than a trial and error basis. Post-release monitoring that incorporates the systematic collection of data is important to guide future reintroduction programmes. This thesis, by documenting the process and results of a chimpanzee reintroduction project aims to contribute to a better understanding of the issues and processes involved. Furthermore, by presenting an overview of the current status of in-situ African ape sanctuaries, it is hoped that their role, goals, and activities, frequently misrepresented and misunderstood in the past, will be clarified. Having worked in African sanctuaries and reintroduction projects, this thesis is the realisation of a long-term ambition to highlight the contribution that sanctuaries make and to emphasise the importance of shared knowledge and communication. Furthermore, my aim was to examine if and how ex-captive chimpanzees can be reintroduced back to the wild to offer hope for the hundreds of chimpanzees presently living in African sanctuaries.

This thesis is organised into ten chapters. Chapter 1 provides an overview of the natural history and taxonomy of the chimpanzee, the threats facing chimpanzees in the wild and primate reintroduction. Components and considerations involved in the reintroduction of primates are described with examples from various projects where relevant. Chapter 2 presents the results of questionnaire data collected from managers of African ape sanctuaries. This chapter immediately follows the introduction because the topic is related to the issue of primate reintroduction, and its methodology is unconnected with the remaining thesis data chapters. Chapter 3 describes the study site and Chapter 4 describes and reviews the process of reintroducing chimpanzees. Chapter 5 details the general methodology. Chapters 6, 7, 8 and 9 present the main data. Each data chapter starts with an introduction followed by methodology, results and an interim discussion section covering the specific issues that are addressed in each data chapter. Chapter 6 examines activity budgets and Chapter 7 heights of activity, both in relation to various variables. Chapter 8 explores feeding behaviour and diet. The methodology for Chapters 6, 7 and 8 are all very similar and the data were all collected on the same check-sheet and then sub-divided for analyses. Chapter 9 examines the characteristics and structure of nests built by the reintroduced chimpanzees. Throughout all of the data chapters the behaviours of reintroduced and wild chimpanzees are compared.

Finally Chapter 10 consists of a broader concluding discussion that summarises the work presented in the thesis and relates it to issues described in the introduction. The thesis has been organised in this way to reflect the systematic process of reintroduction and should provide the reader with a more logical and manageable read.

Chapter 1

Introduction

1.1 Natural history of the chimpanzee

The chimpanzee, *Pan troglodytes*, has been intensively studied in the wild over the past 40 years. This has resulted in an extensive array of published literature on their ecology and behaviour from long-term field sites (e.g., Goodall, 1986; Heltne and Marquardt, 1989; Nishida, 1990; Wrangham, McGrew, De Waal and Heltne, 1994; McGrew, Marchant and Nishida, 1996; Boesch and Boesch-Achermann, 2000). Chimpanzees live in social groups called communities, that can consist of 20-100 individuals, within which temporary sub-groups are formed (except for the biological unit of female and dependant young) and membership of which is fluid. Sexual maturity occurs at approximately 10-12 years. Life span is estimated at 45-50 years and the average inter-birth interval is 5.5 years. Young chimpanzees are lactationally weaned from the age of 3-4 years but remain with their mothers for several more years. The majority of females transfer to neighbouring communities before reproducing, but males remain in their natal group. A dominance hierarchy exists among males. Interactions between communities are rare, but when they do occur, except when adolescent females transfer into a new community, are characterised by extreme aggression. Migrating females may be harassed by resident females but protected by the males. Adult males and unweaned youngsters are the most vulnerable to aggressive attacks in inter-community encounters.

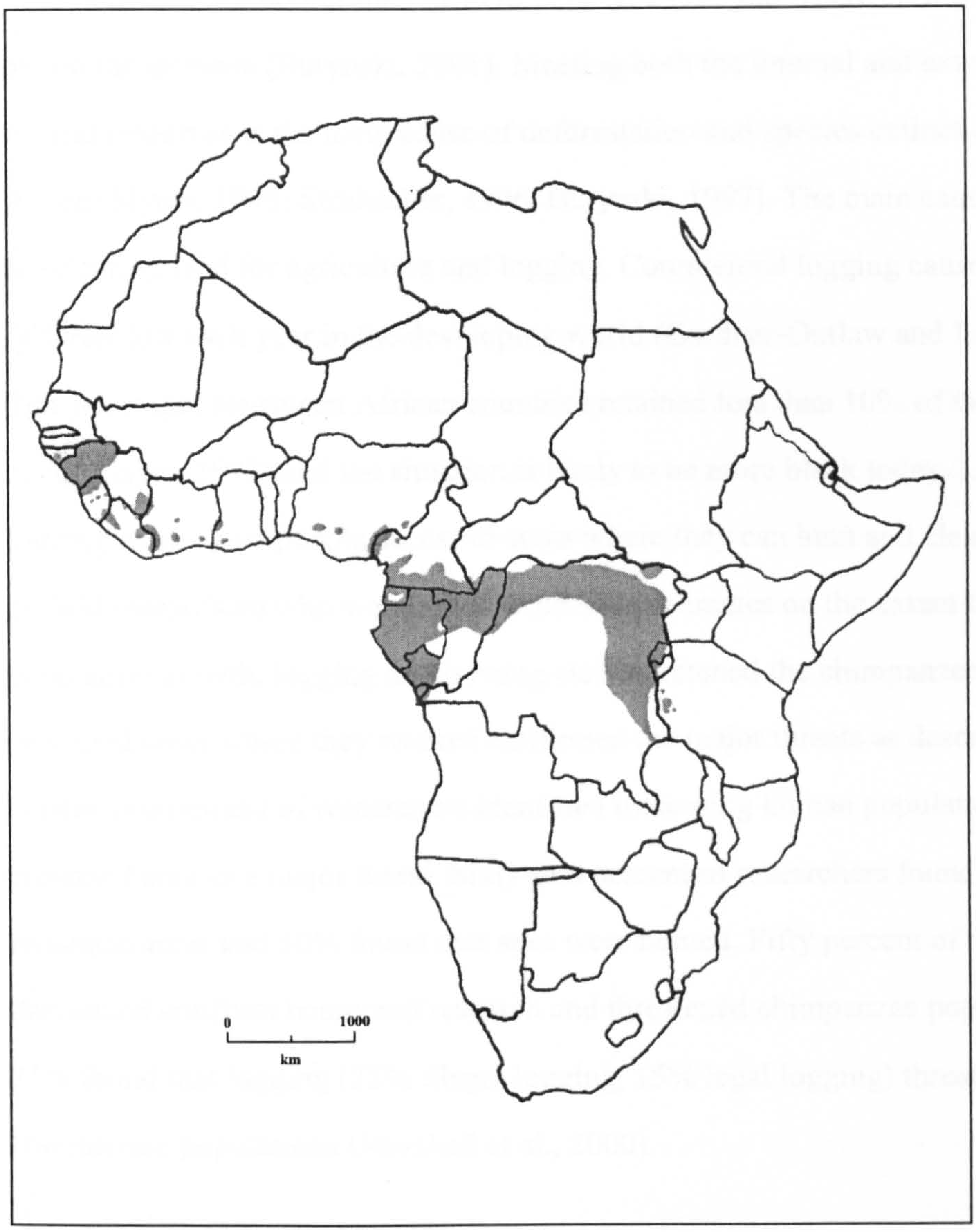
Chimpanzees occupy a wide range of habitats ranging from dense primary rain forest to dry savannah woodlands. The size of home range in forest habitats is large; between 7-50km^2 and overlaps between communities. Foraging dominates the day (Chapter 6) and diet is broad and varied (Chapter 8). At night each weaned chimpanzee builds a nest in a tree to sleep in (Chapter 9). Nests have become a valuable aid to surveys and censuses as they provide indirect evidence of ape numbers.

1.2 Taxonomy and status

Chimpanzees are classified into four main subspecies; the eastern *Pan troglodytes schweinfurthii*, the western *Pan troglodytes verus*, the central *Pan troglodytes troglodytes* and the recently classified eastern Nigerian - west Cameroon chimpanzee *Pan troglodytes vellerosus*. This thesis is concerned with the reintroduction of the central subspecies of chimpanzee. All four subspecies of chimpanzee are listed as Endangered in the IUCN Red List of Threatened Species (Hilton-Taylor, 2000). This means that they face a very high risk of extinction in the wild in the near future.

Chimpanzees are thought to be present in 22 countries (Butynski, 2001). The largest remaining populations occur in Central Africa, mainly in Cameroon, Democratic Republic of Congo and Gabon. Figure 1.1 provides a map of chimpanzee distribution. It is difficult to assess population size due to a lack of recent and precise numerical data, however, estimates suggest that fewer than 12,000 of the western subspecies remain, possibly 80,000 of the central and 13,000 of the eastern subspecies. This would make a total population (and this does not include the east Nigerian - west Cameroon subspecies which is restricted in range and probably low in number) of around 105,000 (Butynski, 2001). Specifically within the Republic of Congo there are thought to be approximately 10,000 chimpanzees remaining although this is based on survey data collected in the 1980's (Butynski, 2001). Consequently although chimpanzees have the broadest geographical distribution amongst all the great apes, populations are diminishing throughout their range. When ape researchers were recently asked to assess whether populations within protected areas in which they were working were decreasing, stable or rising, 91% of field workers concluded that populations were declining, 9% were stable and none were rising (Marshall, Holland Jones and Wrangham 2000).

Figure 1.1 Map showing the distribution of chimpanzee populations across Africa (dark areas represent distribution)



Source: Adapted from IUCN/SSC Primate Specialist Group (Oates, 1996)

1.3 Threats to wild chimpanzee populations

The current threats to chimpanzee populations, and indeed African wildlife in general, are complex and inextricably inter-linked. Probably the biggest threat is human population growth; after growing very slowly for most of human history, it has more than doubled in the last half century (Teleki, 2001). However, human population growth rates are falling in all continents except Africa (Fornos, 1998). In the Congo Basin annual human population growth ranges from 2.5-3.2% (Naughton-Treves and Weber, 2001). Africa is a continent where food production continues to decline, one-third of the population are malnourished, 22% of people are poorer than in 1975 (Conly, 1998) and where civil war and insecurity are on the increase (Butynski, 2001). Meeting both the internal and external demands for natural resources is the main cause of deforestation and species extinction in tropical Africa (Myers, 1993; Struhsaker, 1996; Butynski, 1997). The main causes for deforestation are clearing land for agriculture and logging. Commercial logging causes about one third of forest lost each year in the developing world (Gardner-Outlaw and Engelman, 1999). Ten years ago, seventeen African countries retained less than 10% of their original forest cover (Sayer, 1992) and the situation is likely to be more bleak today. Logging roads and logging trucks give people access to areas where they can hunt and clear forests. A survey of field researchers who were asked to provide estimates on the extent that human population growth, logging and hunting etc., threatened the chimpanzee populations in the protected areas where they worked confirmed the major threats as described above. Ninety-two percent of researchers identified increasing human population around the protected area as a major threat. Sixty-two percent of researchers found snares in the protected areas and 50% found that apes were hunted. Fifty percent of researchers found that armed conflicts hampered research and threatened chimpanzee populations, and finally 38% found that logging (23% illegal logging, 15% legal logging) threatened wild chimpanzee populations (Marshall et al., 2000).

Chimpanzees throughout their range are protected under both national and international law yet the commercial trade of hunting apes has increased dramatically throughout west and central Africa. The hunting of wild animals for food (bushmeat) is no longer a subsistence activity; the image of a hunter stalking a single animal to feed his family is a dim and distant myth. Hunters supply bushmeat (the meat of wild animals) to logging company workers and to people in distant towns and cities. One study in the Congo found that 5-7% of chimpanzee and gorilla populations were killed each year (Ape Alliance, 1998). This is a commercial trade, satisfying the needs and greeds of a growing urban population not only in Africa but overseas. Whilst consumption of bushmeat in remote areas may be common place, in large African cities it is considered a delicacy and prices reflect this (K. Abernathy, personal communication, 2002). Recently in the UK, customs and excise officers found that on one flight alone from Ghana, 110 passengers out of 120 were carrying bushmeat in their personal baggage (Rosen, 2002). Such is the scale of the problem.

1.4 Reintroduction

Protected area management is a preferred conservation practice to reintroduction (Stuart, 1991; Cowlishaw and Dunbar, 2000). However, loss of habitat and wildlife species, and improvements in captive breeding has given rise to an increasing interest in reintroduction (see Kleiman, 1989; Stanley-Price, 1989; Gipps, 1991; Beck, Rapaport, Stanley-Price and Wilson, 1994; Fisher and Lindenmayer, 2000). This surge of interest is due to the prediction that some species will not survive in the wild without reintroduction programmes and the many additional spin-offs that can follow such a programme, for example, national and international increased awareness of conservation issues (Stuart, 1991). As a consequence there has been an estimated 300% increase in the number of vertebrate and invertebrate reintroduction programmes that have occurred world wide between 1993 and 1997 (Seddon and Soorae, 1999). The increasing interest in this approach to wildlife management was the main reason for the creation of an IUCN (The World Conservation Union) Species Survival Commission (SSC) Reintroduction Specialist Group in 1988. The group was established to collect and disseminate information on all reintroduction programmes (animal and plant) and to provide a set of guidelines to assist in the process (IUCN, 1995, 1998).

The latest release of the IUCN Red List of Threatened Species (Hilton-Taylor, 2000) highlighted that the largest increase of threatened and endangered species were within the order Primate. This is partly due to revised taxonomy but in many cases there have been genuine changes as a result of habitat loss and hunting pressures. The IUCN African Primate Action Plan (Oates, 1996) did not once recommend reintroduction as a future conservation action plan for any primate species regardless of taxa status, however, the number of primate reintroduction programmes has, and continues to increase. As a direct consequence, recently the IUCN Reintroduction Specialist Group developed a set of specific policy guidelines for primates 'Guidelines for Nonhuman Primate Re-introductions' (2002).

The new guidelines provide a refinement of terminology. Previously the term reintroduction, introduction and translocation were used interchangeably by some authors and led to confusion. The definition of terms indicates the approach, whether the release occurs within the species original geographic range and if a pre-existing free ranging population occurs at the site (Table 1.1). The term reintroduction is used generally in the guidelines to refer to all approaches except translocation and those motivated by rescue and/or welfare. The movement of primates motivated by the aim to rescue or improve primate welfare is not recognised as reintroduction because the goals are other than conservation of a taxon. However, motives may be inter-linked and programmes motivated by rescue or welfare may contribute to conservation issues and vice versa.

The guidelines state that the main aim of any primate reintroduction or translocation should be to re-establish self-sustaining populations and to maintain the viability of those populations. The principal objective of a reintroduction should be conservation; to enhance the long-term survival of a taxon. Secondary objectives may include re-establishing a keystone species, maintaining or restoring natural biodiversity, enhancing genetic variation of a taxon and promoting conservation awareness.

The guidelines also define 'release stock type' and 'release strategies'. The release stock type, for example, if an animal is wild-born versus captive-bred, will determine the different release strategy employed (see Table 1.1).

Table 1.1 Terms and definitions of primate reintroduction extracted from the IUCN Guidelines for Nonhuman Primate Re-introductions (2002)

Term	Definition
RE-INTRODUCTION APPROACHES	
Re-introduction	The re-introduction of a primate taxon in an area from which it has been extirpated or become extinct ("re-establishment" is used to indicate that the re-introduction has been successful)
Reinforcement/ Supplementation	The addition of individuals to an existing population of conspecifics ("re-stocking" is a synonym)
Conservation Introduction	The introduction of a primate taxon, for the purpose of conservation, outside its recorded known distribution, but within an appropriate habitat and eco-geographical area. This is a feasible conservation tool only when there is no suitable area remaining within a primate's historic range. Because of the risks associated with introducing a non-native species into a habitat, this approach should be considered a last resort
Substitution	The introduction of a primate closely related to another taxon that has become extinct in the wild and in captivity. The introduction occurs in suitable habitat within the extinct taxon's historic range
Translocation	The deliberate movement of wild primates from one natural habitat to another for the purpose of conservation or management
Rescue/Welfare	The movement of wild primates from one area to another with the aim to rescue them from a hazardous situation or to resolve human-primate conflicts, or the release of captive primates, such as orphaned or surplus animals, with the aim to improve their welfare. (*Rescue/welfare is not considered a reintroduction or conservation approach because the aim is motivated by goals other than conservation of the taxon, and so it is not specifically addressed in the IUCN document*)
RELEASE STRATEGIES	
Soft	Animals held in enclosures at or near the re-introduction site prior to release to allow them to adjust to their new environment. Post-release support, such as supplemental feeding and protection from predators, may be provided
Hard	Animals not held in enclosures prior to release, except during transport. Animals are immediately released at the re-introduction site, and generally there is no post-release support, such as supplemental feeding
RELEASE STOCK TYPES	
Captive-born	Animals born in captivity
Wild-born	Animals born in the wild (natural habitat). In a translocation or rescue effort, wild-born primates are often held in enclosures for brief periods during transport and prior to release. They are not considered captive animals as a result
Captive	Animals held in captivity, such as in enclosures or semi-wild environments, for a prolonged period. Captive stock can be wild-born or captive-born. In general, because of their association with and reliance on humans during captivity, captive primates have diminished capacity to survive in the wild after re-introduction
Mixed wild/captive	Captive social groups that comprise both wild-born and captive-born primates. The aim is usually to promote survival of the captive-born animals after re-introduction

The process of planning a reintroduction

Planning a reintroduction is a complex process. The basic programme should consist of four stages; a feasibility study, preparation phase, release phase and follow-up (and maintenance) phase (Stuart, 1991). Within the feasibility and preparation phase, programme aims and objectives need to be defined, economic and political constraints addressed, suitability of a species (and then individuals) for reintroduction reviewed, methodology (veterinary protocol, quarantine, capture, transfer and release) explored and established, potential release sites surveyed and definition of success defined. This list is not exhaustive as every aspect and eventuality (within the preparation, release and follow-up phases) should be addressed. Chapter 4 provides an example of the factors involved and describes the process of reintroducing chimpanzees. In some cases inadequate planning can cause a reintroduction to fail. The failure to successfully reintroduce golden langurs *Trachypithecus phayrei* was attributed to a lack of planning, scientific procedure and follow-up monitoring (Gupta, 2002). The following sections will outline some of the major points with examples from reintroduction programmes where appropriate.

Species and stock to be reintroduced

Some species may be more difficult to reintroduce than other species. For example, the Arabian oryx (*Oryx leucoryx*) has a single social unit (a mixed male-female herd with long-term bonds that moves as a self-contained unit), lives in a relatively simple desert environment, and consumes a relatively small number of trees, plants and shrubs (Stanley-Price and Gordon, 1989). In contrast, the orang-utan (*Pongo* sp.) has a diverse diet and its environment the rain forest, is comparatively complex. Furthermore, adult male orang-utans and adolescents are primarily solitary, they only associate with females to mate, and females live with dependant offspring. Infrequent interaction and wide dietary breadth complicates the reintroduction of orang-utans. Reintroduced orang-utans generally do not range far due to the aggressive behaviour of wild conspecifics and this greatly reduces their chances of self-sufficiency (Stanley-Price and Gordon, 1989). Furthermore, the oryx becomes sexually mature much earlier and reproduces much more frequently than orang-utans, whose low rate of increase hinders the establishment of a viable population unless vast numbers are released. However, despite such disadvantages this has not prevented hundreds of orang-utans being released (Rijksen and Meijaard, 1999; Rosen, Russon and Byers, 2001) although the success of these projects will be discussed later. Within primates, different social systems, dietary requirements and habitat types will provide indicators of whether a species is suited for reintroduction. If the species is judged suitable then the release stock needs to be assessed medically, genetically and behaviourally. Researchers must consider the age and sex classes most appropriate for reintroduction, and the size and composition of groups to be reintroduced. These decisions require knowledge about the social organisation of the species (or similar species) in the wild. The aim is to select a combination of animals that will survive with the least preparation and cost (Kleiman, 1989).

Training, acclimatisation and post-release support

Species are likely to differ in the amount of pre-release training (or exposure to a training environment), acclimatisation to habitat and climatic conditions and post-release training required. Even closely related species vary considerably in the characteristic ways that they respond (behaviourally and physiologically) to their environments and to the changes and challenges that occur within them (Box, 1991a). Beck, Rapaport, Stanley-Price and Wilson (1994) found that more pre-release training, acclimatisation and post-release training were part of the reintroduction process for mammals than with birds, reptiles and invertebrates. This is probably due to the general assumption that many of the behaviours considered essential for survival are heavily dependent on learning and specific environmental experience in mammals (Beck et al., 1994). Skills needed to survive in the wild have been listed as: orientation and movement in space, foraging, finding a suitable place to rest and sleep, interacting with other species including predator avoidance and interacting with conspecifics (Box, 1991b).

Training can occur pre-release, during an acclimatisation phase and/or post-release. It can take the form of intentional training, for example, environmental manipulation and human observers demonstrating skills, or the provision of a suitable pre-release training environment. Pre-release, golden lion tamarins *Leontopithecus rosalia* were exposed to increasingly complex three-dimensional environments that were regularly dismantled and reconstructed to improve locomotor ability and spatial orientation (Kleiman, Beck, Dietz, Dietz, Ballou, Coimbra-Filho, 1986). Later protocols incorporated free ranging experience in wooded habitats pre-release (Kierulff, Beck, Kleiman and Procopio, 2002). Pre- and post-release, Brewer (1978) actively demonstrated which foods to eat and how to use tools to obtain some fruits and insects to released chimpanzees. Post-release food was exclusively provided in trees to encourage orang-utans to climb (Rijksen, 1978 cited in Peters, 1995). Hannah and McGrew (1991) provided chimpanzees with nesting materials pre-release to facilitate the development of this behaviour post-release, and both Brewer (1978) and Carter (1981) actively demonstrated how to make nests to released chimpanzees. The pairing of naive with experienced animals has been used to supplement post-release training in golden lion tamarins (Kleiman, 1989), chimpanzees (Hannah and McGrew, 1991) and orang-utans (Irwin, 2001).

The life history and stock type will influence whether a soft (supported) or hard approach to release is taken (see Table 1.1, p.7). Black and white ruffed lemurs *Varecia variegata variegata* captive bred in the USA were initially placed in a cage for three weeks in the Betampona Reserve (Madagascar) before being released (Britt, Welch and Katz, 1999). During this time they were able to adapt to climatic variables and were exposed to edible forest foods. These animals were initially provisioned on a daily basis but this was stopped after eight weeks when the supplementary food was being ignored. Likewise, wild-born western lowland gorillas *Gorilla gorilla gorilla* reintroduced to the Lesio-Louna Reserve (Republic of Congo) were initially placed in a cage at the release site to acclimatise them to the new surroundings and then they were gradually introduced to the forest whilst provisioning was continued (personal observation). A recent study compared the survival rates of golden lion tamarins according to different pre-release training protocols and soft or hard post-release support strategies (Beck, Castro, Stoinski and Ballou, in press). The authors found that pre-release training conferred no advantage on survival, although Stoinski (2000) proposed that this was probably because it did not occur for long enough or early enough in life. Beck et al. (in press) found that tamarins given intensive post-release management were more likely to survive in comparison to those released under a harder strategy of minimal post-release management. Minimal post-release management involved food provision for one week, twice weekly monitoring and treatment if ill. Intensive post-release monitoring involved daily provision of food and water for several months after release and then for two or three times a week for up to two years. Furthermore, because monitoring was more frequent, there was an increased likelihood of detecting illness and injury.

Post-release monitoring, evaluation and publication

The study by Beck et al. (in press) on golden lion tamarins illustrates the importance of long-term monitoring of released animals and evaluation of the reintroduction process as a crucial component of any reintroduction programme. By recording as much relevant information on release candidates it may be possible to model the efficiency of different release strategies (Sarrazin and Barbault, 1996). Understanding the factors contributing to the success or failure of reintroduction is essential to progress reintroduction biology as a conservation tool (Fischer and Lindenmayer, 2000; Kierulff, Procopio de Oliveira, Beck and Martins, in press). Failed reintroductions and knowing why animals died provides the opportunity to improve methods both immediately and long-term (Stanley-Price and Gordon, 1989).

The golden lion tamarin project is recognised as one of the few (if not only) primate reintroduction projects that has been precisely designed and well documented. The scientific approach taken to the reintroduction provided the opportunity to systematically evaluate and assess the status and development of the tamarins in their pre- and post-release environments. As a consequence, analyses revealed that the success of the programme (defined as survival of animals and their rate of reproduction) was attributable to the intensive post-release monitoring and the provision of critical resources (Kierulff et al., in press).

A planned reintroduction that is monitored and data systematically collected provides the opportunity to make such an evaluation. However, there are no established criteria for calling any given reintroduction a success. In a review of reintroduction programmes, Beck et al. (1994) found that the successful programmes (successful defined as a population of 500 individuals free of provisioning and other human support) were longer, released more animals, and provided local employment and community education programmes. Furthermore, and perhaps surprisingly, more successful programmes used medical screening and post-release provisioning less (in contrast to the results found by Kierulff et al. in press, with golden lion tamarins) than unsuccessful programmes. The stringent definition of success applied by Beck et al. (1994) may not be applicable for large bodied mammals that cannot be reintroduced in large numbers and reproduce slowly. Therefore the number of surviving animals may not always be the most appropriate measure of success. From an ecological perspective, the establishment of a viable self-sustaining population is a key measure (Fischer and Lindenmayer, 2000). Even if every reintroduced individual dies the reintroduction may still be judged successful if it was planned within a broader conservation programme and results in greater habitat protection. Reintroduction may serve to focus attention on wider conservation issues and improve protection and management as with the golden lion tamarin reintroduction programme (Kleiman, et al., 1986). The specific goals of a reintroduction and criteria by which success is evaluated is dependent on the status of the species (in the wild and captivity), variations in life history/reproductive parameters and the political and social conditions in the region.

In contrast to the golden lion tamarin project many reintroduction programmes are not documented at all or only in unpublished reports (although these can be useful) and with little or no follow-up. Struhsaker and Siex (1998) reported that it was not possible to define what factors had led to both successes and failures in red colobus *Procolobus kirkii* translocation and introduction in Zanzibar. This was a consequence of inadequate details of the actual methodology employed and lack of follow-up. Likewise, exact records of the number of orang-utans received and reintroduced, methods employed, numbers surviving, successes and failures etc., at rehabilitation centres in Malaysia and Indonesia (the number of centres continually fluctuates) have been poorly documented (Warren and Swan, 2002). However, there are two papers presently being prepared that aim to supply this vital yet previously missing information (Leiman, in prep; Russon, in prep).

Even if reintroduction programmes do not document their results it may be possible by comparing different projects to extract factors associated with survival and success. A recent study comparing gibbon *Hylobates* sp., reintroduction programmes illustrates this point (Cullen and Swan, 2001). Three species of gibbon from four different projects in three countries were released using 11 different release methodologies during 1966-1997 to eight release sites. Cullen and Swan (2001) highlighted various factors associated with success, defined as individuals surviving more than one year post-release. They found that the following contributed to successful reintroduction: (a) selecting a release site of high quality habitat, free from logging or poaching (b) releasing juveniles rather than adults (c) the provision of large cages pre-release to facilitate social behaviour and exercise (d) regularly exposing the gibbons to the rain forest from an early age (e) long-term supplementary feeding post-release and (f) gaining the support and involvement of the local people.

1.5 African ape reintroduction

In comparison to orang-utan projects, there have been fewer attempts to reintroduce African apes, indeed there have been no attempts to reintroduce bonobos *Pan paniscus*. This is probably a reflection of lower numbers of bonobos, chimpanzees and gorillas *Gorilla gorilla* sp., in need of refuge. In 1991, Hannah and McGrew summarised information for five in-situ chimpanzee projects and compared number, age and background of chimpanzees released, pre-release preparation, post-release support, adaptive behaviour and outcome. A similar method is employed here; Table 1.2 provides up-to-date information on the in-situ projects that Hannah and McGrew (1991) compared and includes four additional projects. Gorilla reintroduction projects are included as they were previously excluded from discussion but orang-utan projects are not included due to a paucity of readily available information (Warren and Swan, 2002). All projects in Table 1.2 are described and salient points discussed.

In 1966, 17 wild-born chimpanzees from zoos and laboratories in Germany were released onto Rubondo Island in Tanzania (Grzimek, 1971; Borner, 1985). No form of pre-release training or acclimatisation was provided despite many of the chimpanzees having spent long periods of time in captivity. A small amount of post-release provisioning was provided but due to aggression displayed towards observers there was little follow-up. Adaptive behaviours consisted of eating wild foods and nest building (Hannah and McGrew, 1991). A surge in interest of the fate of these chimpanzees has provoked surveys based on nest counts, and has revealed a population of at least 40 chimpanzees and two original founders (Pusey, 1998; Huffman, 2000). A recent report attributes the continued survival of these chimpanzees (although it is not known who did and did not survive) to five main factors. The factors are: the size of island, low density of chimpanzees and other fauna, high degree of forest cover and the abundance of fruiting species also found at other wild chimpanzee sites (Moscovice and Huffman, 2001).

From 1968-1972 eight wild-born chimpanzees from a laboratory in Gabon were released onto Ipassa Island in Gabon (Hladik, 1973, 1974, 1977). The chimpanzees were not provided with pre-release training but provisioning accounted for approximately 30% of their annual diet. Follow-up was provided and detailed data were collected on diet and has provided the most comprehensive nutritional analysis of chimpanzee diet to date (see Chapter 8). Adaptive responses consisted of eating wild foods, nest building, ant-dipping and predatory behaviour. However, one male chimpanzee that was latterly introduced to the group disappeared following an aggressive attack by a female, and when water levels were low the chimpanzees waded from the island to the mainland. Most of the group were captured and returned to the laboratory (McGrew, 1983a) although at least two or three individuals escaped to the mainland; one female who escaped was later observed with an

Table 1.2 Projects that have attempted to reintroduce (and introduce) African apes in-situ

Release site	Reference	Aim	Site type/size	Date	Number (m : f)	Age range (years)	Background	Release Methodology		Outcome
CHIMPANZEE								**Pre-release**	**Post-release**	
Rudondo Island, Tanzania	Grzimek, 1971; Borner, 1985	Welfare	Island of 24, 000ha. No wild conspecifics	1966-1969	7 : 10	4 - 12	Wild-born. Taken from zoo and laboratory in Germany	None	PRV for 2 months	1-2 males shot dead. First offspring in 1968. Nutritionally self-sufficient. Recent surveys indicate 40± individuals (at least 2 original founders) Habituation started
Ipassa, Gabon	Hladik, 1973, 1974, 1977	Research	Island of 65ha. No wild conspecifics	1968-1972	3 : 5	4 - 8	Wild-born. Taken from laboratory in Gabon	None	PRV 30% of annual diet. PRM	1 disappeared in 1971. Others escaped and returned to lab in 1978. One lost after escape
Niokola Koba National Park, Senegal	Brewer, 1978; Marsden née Brewer, 1998	Welfare	Mainland forest reserve. Wild conspecifics present	1972-1979	8 : 4	2 - 10	Wild- and captive-born	Intensive PRT	PRV, Intensive PSRT, PRM, MI	4 males disappeared. Others moved to islands (see below) in 1979 due to aggression from wild conspecifics
River Gambia National Park, The Gambia	Carter, 1981; Marsden née Brewer, 1998	Welfare	3 islands; 43, 168, 425ha. No wild conspecifics present	1979	7 : 10	1 - 13	Wild- and captive-born	Intensive PRT	PRV, Intensive PSRT, PRM, MI	Presently 59 chimpanzees (33:26) on islands, 39 were born on the islands Nutritionally self-sufficient. Monitoring from exterior of island

Release site	Reference	Aim	Site type/size	Date	Number (m : f)	Age range (years)	Background	Release Methodology		Outcome
								Pre-release	Post-release	
VILAB, Bandama River, nr Azagny National Park, Ivory Coast	Teleki, 2001; Chonghaile, 2002; Carter, 2002	Welfare	1 island; 169ha. No wild conspecifics	1983	10:10	7 - 11	Wild-born in Liberia. From lab in Liberia	Not known	Not known	8 disappeared or died in the first 3 weeks, and 3 more died in following months. After 1 year the remainder were transferred to another island. In 2002, 4 still alive, two founders & two offspring. All require provisioning
VILAB, Little Bassa River, Liberia	Hannah and McGrew, 1991	Welfare	3 islands; 6, 27, 28ha. No wild conspecifics	1978, 1983, 1985 & 1990	90 total (10:12 main study group)	5 - 20+	Wild-born. From lab in Liberia	PRT	PRST, PRV, PRM, MI,	Of the study group 3 ran away, 5 returned to lab due to illness, 1 male killed by chimps on another island and remainder removed to lab when water levels fell. By 1990, 90 chimps living on five islands, all required provisioning. Majority moved back to lab in war. Recently 18 chimps moved to 2 islands, all require provisioning
Kibale, Uganda	Treves and Naughton-Treves, 1994, 1997	Welfare & data collection on reintroduction process	Mainland forest, north-west Kibale, protected area. Wild conspecifics present	1994	1 named Bahati	4 - 6	Wild-born, 6 months in captivity in Uganda	PRT, PRE, PRV, MS	Introduced to wild group PRST, PRM.	After 10 days found in a village looking for food. Entered villages 5 times in 3 weeks. Placed in local zoo after 45 days post-release
Isinga Island, Lake Edward Uganda	Manning, 1996	Welfare	Island of 5ha. No wild conspecifics	1995	4 : 7	Infants - adults	Wild-born	Not known	Not known	Provisioned. Moved to Ngamba Island in 1998 as Isinga sparsely forested
Ngamba Island, Lake Victoria Uganda	Cox, 1998; Schoene, 2001	Welfare	Island of 40 ha. No wild conspecifics	1998	4 : 7	Infants - adults	Wild-born	PRE (Isinga Island)	PRM, PRV	Now 27 on island (additional ones added). Provisioned

Release site	Reference	Aim	Site type/size	Date	Number (m : f)	Age range (years)	Background	Release Methodology		Outcome
								Pre-release	Post-release	
Afi River Forest Reserve, Nigeria	L. Gadsby, Co-director, Pandrillus, pers. comm., 2001	Escape from sanctuary (not planned)	Mainland forest. Protected area of 38,300ha. Wild conspecifics in reserve but far away	2000	3 : 1	5 – 12	Wild-born. Escaped from sanctuary	PRE (large 30 acre forested enclosure in sanctuary)	None	2 recaptured; one next day, other after 3 months in good condition. 1 possibly killed by hunters after 1 year. Status unknown of other
Tacugama Forest Reserve, Sierra Leone	B. Amarasekaran, Director of Tacugama Chimpanzee Sanctuary, pers. comm., 2001	Escape from sanctuary (not planned)	Mainland forest. Protected area of 17,000ha. Wild conspecifics present	1998, 2000	1 : 3	3 - 4	Wild-born. Escaped from sanctuary	PRE (forested enclosure)	None	All joined nearby wild female during forest walks. 1 returned after one year and two after 5 months all in good condition. Fourth chimp, last seen, 1 year post-release in good health
GORILLA										
Kahuzi-Biega National Park, Democratic Republic of Congo	Lyon, 1976; Mensink, 1986	Conservation and welfare	Mainland forest in protected area. Wild conspecifics present	1976	1 named Julie	8 months	Wild-born. In family home for 2 months	PRT	Introduced to wild group. No PRV, PRST, PRM	Lived with wild group for 10 days and then died. No lactating females in wild group
Parc Nationale des Volcans, Rwanda	Fossey, 1983	Conservation and welfare	Mainland forest in protected area. Wild conspecifics present	1980	1 named Bonne Année	3 years	Wild-born. 6 weeks in captivity before arriving at Karisoke Research Centre	PRT	Introduced to wild group. No PRV, PRST, PRM	Travelled with group for one year but then died from pneumonia

Release site	Reference	Aim	Site type/size	Date	Number (m : f)	Age range (years)	Background	Release Methodology		Outcome
								Pre-release	Post-release	
La Reserve Natural des Gorilles de Lesio-Louna, Republic of Congo	Attwater, Blake, Hudson and Kopf, 1991	Conservation and welfare	Mainland forest. Protected area of 45,000ha. No wild conspecifics	1993 - ongoing	11 : 8	1-13	Wild-born	ACC, MS, PRT,	ACC, PRM, PRV, MI, PRST	4 returned to cage due to ranging near villages and aggression towards humans. 1 gorilla killed by another. All nutritionally self-sufficient except the youngest
Mpassa Reserve, Gabon	L. Pearson, Manager of Projet Protection des Gorilles (PPG) pers. comm., 2001	Conservation and welfare	Main land forest, protected area, 171,800ha. No wild conspecifics	1998 - ongoing	8 : 9	1 - 6	Wild- and captive-born	ACC, MS, PRT,	PRM, PRV, PRST, MI	Almost nutritionally self-sufficient. Eat wild foods but receive small amount of supplementary food
Parc Nationale des Volcans, Rwanda	Primfocus email list 14.05.02 & 21.05.02	Conservation and welfare	Mainland forest in protected area. Wild conspecifics present	May 2002	1 named Ubuzima	12-13 months	Wild-born	Found with mother 2 days after she had been killed. Given fluids for dehydration but spent no time in captivity	Introduced to original wild group immediately following re-hydration	A non-dominant male seen carrying infant. Infant seen eating remains of food dropped by adults. Still alive 2 weeks after reintroduction.

Key: MS medical screening, PRT pre-release training, PRE pre-release environment, ACC acclimatisation, PRST post-release training, PRM post-release monitoring, PRV provisioning, MI medical intervention

Background is divided into two categories; wild- and captive-born. However, wild-born apes arrived to the respective projects having experienced a variety of backgrounds including varying periods of time in captivity and different types of captive environments and care infant (Gautier-Hion, cited in Hannah, 1989). The island did not have a resident wild chimpanzee population.

Brewer (1978) was the first and last (until the present project) to attempt to reintroduce chimpanzees back to mainland forest, except for the attempted reintroduction of a single individual in Uganda (see page 22). In the early 1970's Brewer reintroduced both wild- and captive-born chimpanzees to mainland forest (in Mount Asserik, Senegal) inhabited by wild chimpanzees following two years of intensive pre-release training. Although Brewer did not systemically collect data, she did however, describe the process in some detail and her results have guided other projects including the present one. Initial provisioning was provided, as was post-release support. Brewer initially hoped that her group of released chimpanzees would become integrated into the wild population, however, she finally conceded that the best she could hope for was that they would form an independent group. During the study she found that naive chimpanzees could be encouraged to try new foods by watching more experienced individuals. Furthermore, she found that chimpanzees introduced to an already established larger group were less emotionally dependent on their human caretakers in comparison to chimpanzees introduced to smaller groups. Adaptive behaviours included eating wild foods, nest building, termite fishing, use of stone hammers to crack nuts and predatory behaviour (Hannah and McGrew, 1991). However, due to ecological pressures, the wild population in the area became increasingly aggressive to the reintroduced chimpanzees and they were moved onto three islands on the River Gambia that were devoid of wild conspecifics. Carter (1981) likewise released a group of chimpanzees onto the same islands following intensive pre-release training and post-release support. The chimpanzees that now reside on the three islands are all nutritionally self-sufficient (Marsden née Brewer, 1998). It has not been possible for people to enter the islands for many years due to aggression directed to caretakers and so information is limited. However, it is known that there are now 59 chimpanzees on the islands, 39 of which were born there (Marsden née Brewer, Co-director of Chimpanzee Rehabilitation Centre, personal communication, 2001).

In 1983, 20 wild-born chimpanzees from a laboratory in Liberia were taken to the Ivory Coast with the aim of reintroducing them to mainland forest. The possibility of reintroduction ended when the wildlife officials denied access to the park due to the fear of disease transmission to wild populations and attacks on villagers and tourists. Consequently they were placed onto an island in the Bandama River near Azagny National Park (Teleki, 2001). During the first three weeks after release, eight chimpanzees died or disappeared, and a further three died in the following months (Carter, 2002). Severe diarrhoea due to a shigella outbreak was suspected as the cause of death. One year after the initial release, the nine survivors were transferred to a smaller island. In 2002, four chimpanzees are known to live on the island, two are original founders, and two are offspring (Chonghaile, 2002).

Hannah and McGrew (1991) provided the most detailed account of chimpanzee introduction to island habitat; they systematically collected data on the procedure and results that they employed when introducing wild-born chimpanzees from a laboratory in Liberia to nearby islands. The chimpanzees received pre-release preparation and some acclimatisation. Provisioned food was gradually reduced to a maintenance level; the islands were not sufficiently large enough to allow nutritional self-sufficiency. Follow-up support comprised of follows by radio telemetry and post-release training. Adaptive behaviour included eating wild foods, nest building, ant-eating (without tools) and nut cracking with stone tools. Of the 22 chimpanzees released, three immediately ran away from the release site and were never seen again, four were returned to the laboratory at different times due to illness and one was returned as he seemed physically incapable of looking after himself. The remaining chimpanzees on the islands were returned to the laboratory due to low water levels during the dry season that facilitated access between neighbouring islands. Two females and a male waded across to another island; the male died as a result of injuries inflicted by another group of released chimpanzees.

Hannah and McGrew (1991) examined the characteristics of chimpanzees that did not survive or were returned to the laboratory in contrast to those that remained and successfully adapted to island life. A higher proportion of females successfully adapted than males and suggestions as to why focused on the females learning foraging techniques more readily than males, although a subsequent study showed the reverse trend. Over half of the 'failures' were in the first subgroup as were all three that immediately disappeared. They, like Brewer, found that chimpanzees latterly released benefited from the acquired knowledge of island geography, what to eat and how to eat it from previously released individuals. They also found that radio collars were particularly useful and improved chances of survival. Survival rate was at 95% when the whole group was collared but only 50% when no collars were used. Furthermore, they compared the results of their study to other chimpanzee reintroduction (and introduction) projects. They concluded that the ideal chimpanzee candidates for release were wild-born females, captured late from the wild (three to four years), having experienced only a short period of time in captivity with access to other chimpanzees, and remained in the country of origin. They further concluded that pre-release training, post-release support and monitoring in an area without wild conspecifics and human habitation improved chances of survival.

Subsequently more chimpanzees were introduced to the islands in Liberia, by 1990 approximately 90 chimpanzees were living on five islands. However, during the war they were moved back to the laboratory where approximately half died. Only a small number that were impossible to catch stayed on one island during the war and only one survived. Recently two groups have been introduced to two islands. None of these islands are large enough or have sufficient natural vegetation to allow nutritional independence. Normally within a short period of time it becomes too dangerous for observers to enter the islands preventing long-term post-release monitoring.

The aggression that was directed to the released chimpanzees in the Marsden (née Brewer, 1998) project guided subsequent programmes. The majority of subsequent projects have focused on introducing chimpanzees to island sites devoid of wild conspecifics, ecological competition and human habitation. However, in 1994 an attempt was made to reintroduce a single individual back to mainland forest with conspecifics (Treves and Naughton-Treves, 1994, 1997). The young female was seemingly an ideal candidate according to the criteria of Hannah and McGrew (1991) in that she was wild-born and had spent only three to six months in captivity. She was given pre-release training, gradually reduced provisioning and a small amount of post-release monitoring. Adaptive behaviours included eating wild foods, nest building and eating insects. However, although the initial reaction of the wild group was favourable and she appeared to initially adapt to moving with them, the downfall proved to be the site and its location to human habitation. The chimpanzee was found begging for food in villages on several occasions and was subsequently placed in a local zoo. It was suggested that her departures from the forest coincided with a decline in fruit availability and that she may have had trouble in finding food or keeping up with the wide-ranging wild group.

In 1995, 11 wild-born chimpanzees were moved from the Ugandan Wildlife Education Centre (former Entebbe Zoo) to Isinga Island on Lake Edward in Uganda (Manning, 1996). The island was sparsely forested and constant provisioning was necessary from the start. The chimpanzees slept on constructed platforms and in trees immediately post-release. Two chimpanzees drowned and in 1998 the chimpanzees were moved to the larger and more densely forested Ngamba Island on Lake Victoria. There are presently 27 chimpanzees on Ngamba Island and although there are small amounts of wild chimpanzee foods naturally occurring on the island, it is not sufficient to allow nutritional independence. An unpublished survey of Ngamba Island found that the vegetation could only optimistically sustain a maximum of five adult chimpanzees if their diet was 100% provisioned (Schoene, 2001, unpublished report). As a consequence of this and new arrivals, a second nearby island (Nsadzi) has recently been leased so that some chimpanzees can be transferred and as with Ngamba Island, the chimpanzees will require provisioning.

Two sanctuaries have inadvertently participated in reintroduction following the escape of chimpanzees to mainland forest. Four wild-born chimpanzees escaped from the Pandrillus sanctuary located in the Afi River Forest Reserve in Nigeria (L. Gadsby, Co-director Pandrillus, personal communication, 2001). One was re-captured the next day and another after three months in good health. The two remaining 'free' males had been at the sanctuary for several years but despite this managed to be immediately nutritionally self-sufficient without apparent problem for a minimum 3-12 months. They did not once crop-raid or cause any disturbance to people despite being in close proximity. The status of both chimpanzees remains unknown although it is thought that hunters killed one. Young chimpanzees were taken for walks in an area of forest adjacent to the Tacugama chimpanzee sanctuary in Sierra Leone. However, five chimpanzees (all recent arrivals to the sanctuary) did not return. Apparently a wild female that was frequently seen in this forest block may have acted as a surrogate mother to some of the escapees (B. Amarasekaran, Director of Tacugama Chimpanzee Sanctuary, personal communication, 2001). Three chimpanzees were re-captured but apparently all remained in good health during the 5-12 months that they ranged free. The status of one, a female, remains unknown, but she was last seen one year post-escape in good health.

If we examine all the planned chimpanzee reintroduction projects, only two involved reintroduction to mainland forest and both were primarily conducted with a view to improving the welfare of the chimpanzees and therefore according to the IUCN Guidelines for Nonhuman Primate Re-introductions (2002) should not be classified as reintroduction. All remaining projects that introduced chimpanzees onto islands were welfare motivated and two have resulted in nutritionally self-sufficient populations. The islands were all devoid of wild conspecifics, human habitation and in some cases ecological competition. In all cases of island release it normally becomes too dangerous for observers to enter the islands after a short time; this time period is age dependent, but with adolescent and adult chimpanzees it can be a matter of days or weeks. However, attempts to re-habituate chimpanzees on Rubondo Island are underway and apparently the chimpanzees are shy to human presence. These chimpanzees have not had contact with humans for many years and it is likely that the majority will be offspring and not original founders.

There have been five attempts to reintroduce gorillas. All have involved reintroduction to mainland forest and based on a combination of welfare and conservation rationale. There have been three attempts to reintroduce individual gorillas to wild groups, and two attempts to reintroduce groups of gorillas to areas devoid of wild conspecifics. A young wild-born female Grauer gorilla, *Gorilla beringei graueri,* aged six months was reintroduced to a wild group in Democratic Republic of Congo. She had been taken into the forest and shown wild plant foods pre-release but she died soon after being released. She could not have survived nutritionally without a lactating female in the wild group and there were none present (Beck and Russon, unpublished manuscript). Another young female mountain gorilla *Gorilla beringei beringeri*, aged three years, was reintroduced to a wild group in Rwanda and managed to survive for ten months (Fossey, 1983). She had been provided with some pre-release training, however, she later died of pneumonia. It is possible that the transfer into a new group suppressed her immune system and made her susceptible, however, infant gorilla mortality is high in the wild (Parnell, in prep). Recently an attempt was made to reintroduce a wild-born young male mountain gorilla (12 months old) in Rwanda in the hope that he might be adopted by a nursing female (Environment News Service, 14.05.02, http://ens-news.com/ens/may2002/2002L-05-14-04.html). The infant was found beside its mother who had been killed two days earlier by hunters. He was administered fluids for dehydration and reunited with the original group. Apparently a non-dominant male has started to carry the infant, and the infant has been seen eating solid food dropped by adult gorillas (Primfocus email list, 21.05.02).

There have been no data collected and there has been little detailed published literature from the two projects that have attempted to reintroduce groups of western lowland gorillas in the Republic of Congo and Gabon. However, it is known that at the Lesio-Louna Reserve (Republic of Congo) gorillas were provided with a pre-release environment facilitating development of locomotor, social and foraging skills, a cage in which to acclimatise at the release site, post-release support and provisioning with some follow-up (Attwater, Blake, Hudson and Kopf, 1991). The majority of the reintroduced gorillas have shown nutritional independence but there have been problems with some individuals showing an attraction towards local villages, stealing food and aggression towards humans. A search for a more suitable site far from human habitation is underway. Furthermore, the project has experienced some problems of aggression between gorillas. A solitary blackback gorilla is thought to have killed a female (10 years old) and a blackback died as a result of injuries inflicted by another blackback. The height of the aggression from male gorillas is apparently more acute when females are in oestrous (J. Buchan, former Head of Gorillas, PPG Congo, personal communication, 2001).

Through a process of trial and error this project has now changed its methodology and influenced tactics employed by its sister project in Gabon whose release site is far from human habitation. A 'soft' approach to reintroduction is still taken but longevity of support is reduced. Gorillas are now placed immediately at the release site to remove the stress of the transfer to the release site that resulted in the death of three gorillas in the Congo. The gorillas are introduced as groups to the forest as quickly as possible, provisioning is withdrawn as soon as the gorillas are old enough to cope nutritionally without milk supplements and human contact is kept to a minimum. All reintroduced gorillas except two were wild-born. Two gorillas reintroduced in Gabon were captive-bred and one died soon after release. Both sites are devoid of wild conspecifics.

Published data on precise methodology, background history of reintroduced apes, and cross comparison to adaptation and survival are lacking. In most cases of chimpanzee introduction, adaptation has been less of an issue as the release sites have been islands where nutritional independence was never expected. Overall that there is very little to add to the conclusions reached by Hannah and McGrew (1991) although the additional projects included here do support their findings. Reintroduction in its true sense (not introduction to island habitat where animals are generally not nutritionally self-sufficient) does seem to be more successful if groups of apes are reintroduced as opposed to single individuals which is not surprisingly considering the social nature of the African apes. A recent comparison of social learning publications in primates found that great apes showed elevated positive social learning effects and the authors concluded that candidates for reintroduction would likely benefit from social learning in skill training programmes (Custance, Whiten and Fredman, 2002). Furthermore, reintroduction sites should ideally be devoid of wild conspecifics or be low in number, have sufficient natural vegetation on which the animals can feed (in all seasons) without inflicting adverse competition on resident fauna, and located away from human habitation. A 'soft' approach to reintroduction seems preferable to a 'hard' one, as there is adequate opportunity to acquire and practice skills necessary to survive in the wild in a suitable environment with conspecifics. The type of relationship that is established between human caretaker and ape from a young age is important as it can promote long-term psychological reliance. Chapter 4 will discuss those points salient to the present project in more detail.

1.6 Aims

This chapter has provided background information on chimpanzee behaviour, status, threats and issues surrounding the reintroduction process. All the ape reintroduction projects described lack long-term systematically collected data although they have provided examples and valuable lessons that can be transferred to future reintroduction projects. Since 1996 the non-governmental organisation Habitat Ecologique et Liberté des Primates (HELP) have been releasing chimpanzees from an island sanctuary (pre-release training environment) to mainland forest. It is a major aim of this thesis to describe and review the reintroduction process employed by HELP to highlight factors that contribute to both success and failure to facilitate the design and implementation of future ape reintroduction. Furthermore by presenting the results of a long-term systematically collected data set, it is hoped that those considering reintroduction will likewise view data collection as central to the process. Documenting the methods employed (detailing successes and failures) is vital if the process of reintroduction is to advance on anything other than a trial and error basis.

The main aims of this thesis are:

- To document the scale of the African ape sanctuary problem by presenting an overview of the number of sanctuaries, their location, the background history of the animals being cared for and the range of activities that they are involved in (Chapter 2)
- To describe the rationale, process and results of the present chimpanzee reintroduction project (Chapter 4)
- To describe the activity budgets of the reintroduced chimpanzees and to investigate the influence of sex, age, pre-release environment, ecology and diurnal hour on behaviour in comparison to wild populations. To examine the influence of time post-release on activity budgets (Chapter 6)
- To describe the vertical stratification of activity of the reintroduced chimpanzees and investigate the influence of sex, age, pre-release environment and ecological variables in comparison to wild chimpanzees. To examine the influence of time post-release on height of activity (Chapter 7)
- To describe the diet of the reintroduced chimpanzees in comparison to wild populations and investigate the influence of sex, age, pre-release environment, diurnal hour, ecology and time post-release on diet (Chapter 8)
- To examine the characteristics of nests built by reintroduced chimpanzees in comparison to wild conspecifics (Chapter 9)
- To discuss the implications of this study for future reintroduction projects (Chapter 10)

Chapter 2

African ape sanctuaries

2.1 Introduction

Chapter 1 highlighted the threats facing African wildlife and predictions are that all three taxa of African ape; bonobo, chimpanzee and gorilla will become extinct in the wild if causal factors are not effectively addressed (Butynski, 2001). As pressures escalate so do the number of orphaned primates needing refuge (Teleki, 2001). When adult female primates are killed, their clinging infants can easily be taken by the hunter and sold. Poachers may even intentionally kill a female just to retrieve an infant (Beck and Russon, unpublished manuscript). It has been claimed that the recent killing of two female mountain gorillas were in order to obtain their infants for sale on the illegal market (Environment News Service 14.05.04, http://ensnews.com/ens/may2002/2002L-05-14-04.html). Four wild-born infant gorillas were recently shipped from Nigeria to a Malaysian Zoo with false papers proclaiming captive-birth. Their price tag was 1.6 million US dollars and four wild-born infant chimpanzees were offered for 500,000 US dollars (IPPL News, April 2002).

Pan African Sanctuary Alliance

Escalating environmental and socio-economic pressures have led to an increasing number of orphaned apes needing refuge and sanctuaries have been created in response. They too have steadily increased in number since the first was established in the early 1970's. As a direct consequence, in May 2000 a workshop organised by the Primate Specialist Group and the Conservation Breeding Specialist Group (SSC/IUCN) gathered managers of African chimpanzee sanctuaries to discuss experiences with the aim of formulating universal guidelines and objectives. An umbrella organisation called the Pan African Sanctuary Alliance (PASA) was formed and was extended to include all African primate sanctuaries at the 2001 meeting. PASA was developed to support, assist and encourage sanctuaries in their efforts to save apes and other primates. It proposed to do this by campaigning locally and globally against the threats that face species in the wild, promoting the highest standards of captive animal husbandry and by acting as a forum where sanctuaries can share information and discuss issues of mutual concern. PASA proposed a working definition applicable to in-situ African primate sanctuaries as until this time no official definition existed, and had led to confusion about projects that differed in methodology and long-term goals.

"*A PASA sanctuary provides a safe and secure home for African apes and other primates in need. The welfare of the individual and the preservation of the species are of prime importance and are considered equally. The sanctuary operates in the context of an integrated approach to conservation, which can include rehabilitation and re-introduction*" (Rosen, Seal, Cox, Montgomery and Boardman, 2001, p.13).

Arguments for and against sanctuaries

Arguments in favour of African and Asian sanctuaries are primarily based on the solution they offer to government agents who confiscate illegally held animals. Confiscation of animals held as a result of trafficking and illegal ownership are vital to international law enforcement, and where there are no sanctuaries, there is little or no confiscation (Teleki, 2001). Furthermore, with an understanding of local attitudes, properly managed sanctuaries can play an important role in public education and in nurturing respect for animals and their environment (Karesh, 1995). This form of localised education may have more practical conservation potential than zoos in countries that do not have indigenous populations (Plate 2.1). It has also been argued that in addition to the preservation and management of critical habitats, conserving threatened species will require captive breeding programmes (Kleiman et al., 1986). Although zoos may take primary responsibility for this, sanctuaries within range countries may also play a role by extending numbers and genetic diversity. A prime example is the Drill Breeding and Rehabilitation

Centre in Nigeria that holds the largest captive population of the endangered *Mandrillus leucophaeus* (n=120), half of which are captive-bred (Gadsby, 2002).

Plate 2.1
Ateh Wilson, education officer at the Limbe Wildlife Centre visiting a school

(Source: Limbe Wildlife Centre)

However, although sanctuaries attract some public sympathy and small amounts of funding their popularity does not often translate into active, particularly financial, international support. Nearly every project claims to be perpetually short of funds, and simply finding sufficient money to feed the animals and pay the salaries of local staff can be a major problem. Sanctuary facilities are wide ranging, as are ideologies, and conducted on an individual ad-hoc basis with little or no published evaluation. Consequently some wildlife biologists argue that sanctuaries contribute little to species survival and are a waste of money that could be better spent on habitat protection (Mackinnon, 1977, Soave, 1982). It has been suggested that sanctuaries may even exacerbate the trade in live animals if local populations mis-interpret project goals (Karesh, 1995) by hunting apes with the aim of selling them to the sanctuaries or by viewing them as private collections. Furthermore, resentment may cause friction if more concern appears to be shown for animals than people in areas where there is limited access to good housing, adequate food, and proper medical care.

The debate concerning the role of sanctuaries continues largely in the absence of solid information from the sanctuaries themselves, and may serve to further alienate the sanctuaries from the conservation community and potential donors who know little about what they do and how they do it. The development of PASA may address some sanctuary critics and is clearly a step forward in facilitating international support. Teleki (2001) suggested that an action plan was needed to highlight areas of Africa where future sanctuaries should be located. He suggested that before an action plan could be drafted a survey of the current status of sanctuary projects was necessary. Clearly there remains a need for accurate and detailed information on sanctuaries and this chapter aims to supply it by analysing responses from a questionnaire administered to sanctuary managers.

2.2 Aims

- To present an overview of the current status of African ape sanctuaries
- To describe their range of activities

2.3 Methodology

A sanctuary as defined by PASA considers welfare and conservation equally, and can involve rehabilitation and reintroduction. Therefore, throughout this chapter the term sanctuary is used to apply to all the African projects that include the rescue, rehabilitation and reintroduction of apes, as one of their goals, or main focus.

2.3.1 The questionnaire

The aim of the questionnaire was to ask a series of questions that would produce an overview of the present status of African ape sanctuaries. Questions were formulated to provide information on the following areas:

- Project history, location and emphasis
- Numbers, age, sex, background history, health, reproduction, housing, diet and daily routine of apes

- Additional sanctuary activities
- Running costs and sources of financial support
- Staff numbers

Studies on questionnaire design have highlighted the influence that question wording and type, for example open versus closed questions, can have on the reliability of respondents answers' (Foddy, 1995). In the present questionnaire closed questions were primarily utilised to facilitate coding and analysis. The questionnaire consisted of 10 main sections with sub-categories (see Appendix A for a copy of the questionnaire).

The closed format questions required varying responses from providing a numerical figure, answering yes or no, marking one of several categorical boxes provided or rating using a scale. Age categories rather than age classes were used to provide detail for the reader and to avoid confusion from alternative age classification systems employed. Categories relating to background history and health of apes, sanctuary activities, and sources of financial support were selected due to my prior experience of working in African primate sanctuaries. However, in all instances a category of 'Other' requiring further specification was provided to accommodate additional areas. Some questions required the respondents to provide more individual descriptive detail. Potential criticisms of the design of this questionnaire are addressed in the discussion.

2.3.2 Specifics of individual projects

Data were collected separately for the Ugandan Wildlife Education Centre and Ngamba Island despite both coming under the umbrella of The Jane Goodall Institute (Uganda). Analyses have combined the two sets of figures (except for sanctuary costs) and they have been counted as one project. Sodepal (Gabon), a project that primarily started as a game farm to offer alternative sources of protein to local populations, for example, fish, rodent and wild pig, now has 11 chimpanzees in its care. For the purposes of this chapter it is classified as a sanctuary. Sixty-eight percent of the chimpanzees at the Sweetwater sanctuary in Kenya were transferred from a sanctuary in Burundi during a period of civil unrest whilst the remainder were acquired from within Kenya. However, analyses combine the two sets of figures.

2.3.3 Analyses

The majority of analyses throughout this chapter are descriptive as it was considered the most appropriate way to summarise the responses from a questionnaire distributed to a small number of participants (n=18). Only two statistical tests were performed. As a result of the small data set showing a wide spread of scores, medians, inter-quartile range (IQR shown in brackets) and non-parametric tests were used.

When subjects were required to specify the number of apes falling within various categories, for example with background history and method of arrival (see Appendix A) averages were obtained for each sanctuary. Averages were obtained by comparing the figure in each category against the total number of all apes to produce a percentage. Then for each section, the average score for each sanctuary was compared and the middle percentage (the median) was taken as the overall median score. Numbers were converted into averages because not all participants could provide accurate numbers and some provided averages. However, where subjects were asked to rate according to a scale, within each category, numbers (not percentages) were compared and overall median obtained.

Representatives from 17 of the sanctuaries attended at least one of the PASA meetings. Sodepal (Gabon) was not represented at either meeting and was sent a questionnaire by surface mail. These 18 facilities represent all the current known projects in Africa that hold apes in captivity under the guise of a sanctuary as loosely defined by PASA. Analyses are based on completed and returned questionnaires for 18 African ape sanctuaries. In the majority of cases, the questions were answered by all projects. However, only 16 sanctuaries contributed data to mortality rates and 16 answered questions concerning annual budget and funding sources. Sanctuaries holding non-ape species (n=8) were also asked to provide an estimated annual figure associated with holding apes only; three out of the eight sanctuaries falling into this category provided an estimation.

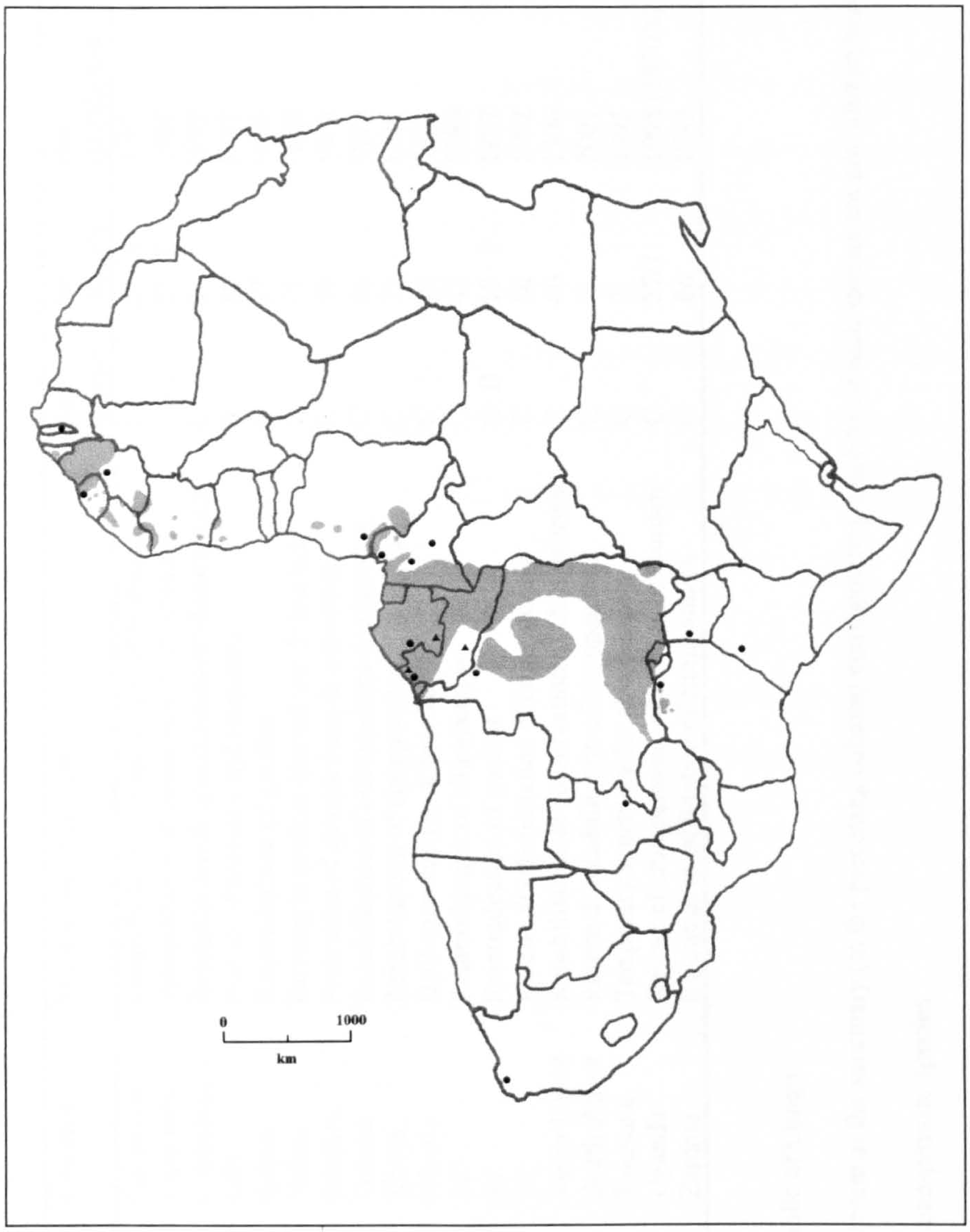
2.4 Results

2.4.1 Overview

There are presently 18 sanctuaries that are known to hold apes, across 13 African countries; Cameroon (3), Republic of Congo (3), Gabon (2) and one in each of the following countries; Gambia, Guinea, Sierra Leone, Nigeria, Democratic Republic of Congo (DRC), Kenya, Uganda, Tanzania, Zambia and South Africa (Figure 2.1). Table 2.1 details the sanctuary name, country, main focus, numbers of apes held and year established. The first was established in the early 1970's and the most recent in 2001. The 18 sanctuaries contain a total of 560 great apes; 490 chimpanzees (241 ♂: 249 ♀), 49 gorillas (25 ♂: 24 ♀) and 21 bonobos (11 ♂: 10 ♀). The numbers of males to females in all species is similar. Within each project, the number of animals varies and ranges from three to 86. When a Spearman's rho correlation was performed on the year that the sanctuary opened and the number of animals within it, a significant negative correlation was found ($r = -0.64$, $n = 18$, $p=0.004$) indicating that the longer the project had been open the more apes it contained.

Thirteen projects solely care for chimpanzees, one for gorillas and one for bonobos. Two projects have gorillas and chimpanzees, and one gorillas and bonobos. Eight sanctuaries also hold other primate and non-primate species on site that may dominate or share the primary focus. Three sanctuaries (one chimpanzee and two gorilla) primary focus is on reintroduction. PPG Congo primary focus is gorilla reintroduction with the long-term aim of transferring the small number of bonobos that they care for to DRC. One project, Sodepal (Gabon), started life as a fish and game farm to provide alternative sources of protein to bushmeat, but has in recent years started to rescue orphaned chimpanzees and mandrills. Some sanctuaries also list conservation, protection, education and tourism as part of their main focus, in addition to the rescue and rehabilitation of apes.

Figure 2.1 Map of African ape distribution and sanctuary location



Source: Adapted from IUCN/SSC Primate Specialist Group (Oates, 1996)
Key: Grey areas represent distribution of African apes; • = sanctuaries, ▲= sanctuaries with a reintroduction component

Six sanctuaries are no longer accepting apes primarily because they are over capacity. Kitwe in Tanzania plans to close and transfer their three chimpanzees possibly to a zoo in South Africa and does not wish to make additions to the group. One sanctuary is continuing to accept chimpanzees (Tchimpounga) despite having twice the number of animals it originally identified as its maximum carrying capacity. A further six are three-quarters full to maximum carrying capacity.

Table 2.1 Sanctuary name, country, ape species, number of apes and date established

Project name	Country	Main focus of project	Ape species	No. of apes	Date established
Cameroon Wildlife Aid Fund (CWAF)*	Cameroon	Rehabilitation & conservation of primates	C: G	25 : 6	1997
Limbe Wildlife Centre (LWC)*	Cameroon	Rehabilitation & conservation of primates	C: G	27 : 7	1994
Sanaga-Yong Chimpanzee Rescue Centre	Cameroon	Rehabilitation & conservation of chimpanzees	C	8	1999
Sanctuaire des Bonobos de Kinshasha	DRC	Rescue of bonobos and education	B	18	1998
Projet de Protection des Gorilles (PPG)	Gabon	Reintroduction of gorillas	G	17	1998
Sodepal*	Gabon	Farming of protein alternatives & tourism	C	11	1999
Chimpanzee Rehabilitation Project	Gambia	Protection of chimpanzees & education	C	59	1974
Chimpanzee Conservation Centre	Guinea	Rehabilitation of chimpanzees & education	C	26	1996
Sweetwaters Chimpanzee Sanctuary (JGI)	Kenya	Rehabilitation of chimpanzees & tourism	C	25	1994
Drill Rehabilitation & Breeding Centre (DRBC)*	Nigeria	Drill conservation & breeding	C	16	1988
Habitat Ecologique et Liberté des Primates (HELP)	RC	Reintroduction of chimpanzees	C	43	1989
Projet de Protection des Gorilles (PPG)	RC	Reintroduction of gorillas	G: B	19 : 3	1987
Tchimpounga Chimpanzee Sanctuary & Reserve (JGI)	RC	Rescue & rehabilitation of chimpanzees	C	80	1992
Tacugama Chimpanzee Sanctuary*	Sierra Leone	Rehabilitation & conservation of chimpanzees	C	40	1996
David Greybeard Sanctuary (JGI)*	South Africa	Rescue & rehabilitation of chimpanzees	C	7	2001
Kitwe Point Sanctuary (JGI)	Tanzania	Temporary sanctuary for chimpanzees	C	3	1995
Ngamba Island/ Entebbe Wildlife Education Centre (JGI)*#	Uganda	Rescue of chimpanzees, education, & tourism	C	27/7	1998 (1970's)
Chimfunshi Wildlife Orphanage*	Zambia	Rescue & rehabilitation of chimpanzees	C	86	1983

Notes:
Country: DRC = Democratic Republic of Congo; RC = Republic of Congo
Ape species: C = chimpanzee; G = gorilla; B = bonobo
Number of apes = when two ape species are listed as being present at the sanctuary (in the preceding column) corresponding numbers of each species are provided separated by a colon.
* Indicates those sanctuaries that also look after non-ape and non-primate species
JGI = Jane Goodall Institute sanctuary
#Ngamba Island was established in 1998 and the Entebbe Wildlife Education Centre (previously Entebbe Zoo) in the early 1970's.

2.4.2 Age of apes: present day and on arrival to sanctuary

Managers at each respective sanctuary were asked to estimate the present age of apes using their experience as a guide. Table 2.2 presents the numbers of apes that fall into each age category. The majority of chimpanzees were aged two years and above when the questionnaire was distributed. Gorillas and bonobos were aged primarily between 2-7 years. Approximately 14% (n=78) of chimpanzees were aged above 16 years and although they were distributed within 11 sanctuaries over half (n=45) were held at the two longest established sanctuaries; Chimpanzee Rehabilitation Project in Gambia and Chimfunshi in Zambia, established in 1974 and 1983 respectively. No gorillas or bonobos fell into this category.

Likewise, sanctuary managers were also asked to estimate the age of apes upon arrival to the sanctuary. Table 2.2 also shows that over a quarter of chimpanzees arrived when they were less than a year old and that overall over two-thirds arrived when they were aged four years or younger. All gorillas and bonobos were aged less than four years upon arrival.

Table 2.2 Estimated age of apes: present age in 2001 and age at arrival

	Age categories						
	0-12 mths	**13-23 mths**	**2-4 yrs**	**5-7 yrs**	**8-11 yrs**	**12-15 yrs**	**16+ yrs**
Number of apes							
Present age:							
Bonobo	0	1	10	7	2	1	0
Chimpanzee	26	31	99	75	100	81	78
Gorilla	1	7	23	9	5	4	0
Age on arrival:							
Bonobo	1	5	15	0	0	0	0
Chimpanzee	143*	60	132	57	13	5	11
Gorilla	18*	13	17	0	0	0	0

* These figures do not include the 69 chimpanzees and 1 gorilla that were born on-site

2.4.3 Early history: origin and background history

Table 2.3 shows that over half of all apes arriving at the sanctuaries were confiscated. Over a quarter were donated although sources were not identified. Six chimpanzees fell into a category of 'other' and they comprised one escaped pet, one already on site, and four animals that were "surrendered", implying forcibly donated.

Table 2.3 Origin of apes held in sanctuaries

	Bonobo		Chimpanzee		Gorilla		Total %
	n	%	n	%	n	%	
Confiscated	15	71	259	53	30	61	54
Donated	4	19	124	25	17	35	26
Born on-site	0	0	69	14	1	2	12
Transfer	2	10	32	7	1	2	6
Other	0	0	6	1	0	0	1

Overall, the apes were found either awaiting sale (and/or transportation) or had been kept as pets (Table 2.4). The category of 'other' consisted of four chimpanzees that been used as props by photographers at Spanish beach resorts, one chimpanzee and one gorilla from a laboratory, two chimpanzees from a circus, and one gorilla born in and transferred from an English zoo.

Table 2.4 Early history of apes prior to arrival at the sanctuaries

	Bonobo		Chimpanzee		Gorilla		Total %
	n	%	n	%	n	%	
Awaiting sale	15	71	199	41	32	65	44
Pet	4	19	156	32	12	25	31
Born on-site	0	0	69	14	1	2	12
Attraction	2	10	59	12	2	4	11
Other	0	0	7	1	2	4	2

In only five of the 18 sanctuaries were all the apes known to originate from the country in which the sanctuary was based. The remaining sanctuaries received apes from neighbouring countries as well as from Europe and USA.

2.4.4 Health and reproduction

Sanctuary managers were asked to estimate the state of health when apes had first arrived at the sanctuaries and to provide a figure for each category. The number of apes that were rated as having arrived in an excellent condition was low, and consequently a zero median frequency was found (Table 2.5). A higher proportion arrived in fair condition jointly followed by good and poor and lastly very poor.

Table 2.5 Median frequency of health status of apes upon arrival to the sanctuaries (highest first)

Health category	Median frequency	IQR
Fair	22	37
Good	19	38
Poor	19	25
Very poor	15	16
Excellent	0	-

Sanctuary managers were asked to rate the frequency of health problems that apes presented with on arrival, according to nine categories on a scale of zero to ten (where zero represents never and ten always). Table 2.6 shows the most frequently reported health problems that apes presented with. Conditions rated as occurring most frequently were internal parasites, behavioural abnormalities and malnutrition. Wounds due to wire or chains (normally around the lumbar region), infected wounds and external parasites also occurred, but less frequently, as did cases of arrival with broken bones, bullet wounds and suspected malaria. Respondents also stated that apes had presented with the following problems upon arrival: hair loss, pneumonia, skin problems (fungal/bacterial), ulcers, physical handicap (e.g., missing digits, lameness, limb dysfunction), self-mutilation, dehydration, diarrhoea, teeth grinding and chest infections.

Table 2.6 Median frequency of condition in animals arriving to sanctuaries (highest first)

Condition	Median frequency	IQR
Internal parasites	9	4
Behavioural abnormalities	8	4
Malnutrition	8	6
Infected wound	5	5
Wire wound	5	7
External parasites	5	6
Bullet wound	1	3
Broken bones	1	0.3
Suspected malaria	1	1

A total of 45 apes died as a direct result of their poor condition upon arrival, a median of two apes per project. It was reported that in one case a gorilla died within 20 minutes of arriving. Overall, 140 apes have died prematurely (i.e., before reaching adulthood) at the sanctuaries. If we add this figure to the number presently existing in the sanctuaries this would account for 20% of the total sanctuary population. It is not known how many of these were born on-site but the figure is likely to be low considering that only two projects have an active breeding population and one of these did not complete this section in the questionnaire.

If mortality rates for each species are compared with present numbers in the sanctuaries a higher percentage of gorillas died. Fifty percent (n=56) of gorillas died in comparison to 42% (n=10) of bonobos and 25 % (n=74) of chimpanzees. If the number of deaths against chance were compared for each ape species a significant association between ape species and mortality rate was found (Chi-Square test; $X^2 = 92.51$, df $= 2$ $p<0.001$). Age at time of death and cause of death was not requested in the questionnaire.

Sanctuary managers were asked if contraception was either in use or planned. Nine sanctuaries presently employ some form of contraceptive protocol ranging from vasectomies for males, to birth control pills and subcutaneous implants for females (Table 2.7). Although CWAF (Cameroon) has an active contraceptive protocol for chimpanzees it does not use or plan to use contraception with gorillas. Of the remaining projects, four presently use no form of contraception; Kitwe Point (Tanzania) only houses males and does not plan to accept more chimpanzees but transfer the remaining ones to another facility. David Greybeard Sanctuary (South Africa) presently only houses infant chimpanzees but plans to implement a contraceptive protocol at a later date. It is not known if Sodepal (Gabon) or Sanctuarie des Bonobos de Kinshasha (Dem. Rep. of Congo) plan to implement contraceptive protocol in the future. The three projects focusing on reintroduction do not use or plan to use contraception; one reintroduced chimpanzee and one gorilla have given birth post-release. The two remaining projects do not employ any kind of contraceptive protocol and have an active breeding population. These two sanctuaries have two of the largest populations: Chimfunshi (Zambia) has 86 chimpanzees, 22% (n=19) of which were born on- site, and the Chimpanzee Rehabilitation Project (The Gambia) holds 59 chimpanzees, and 66% (n=39) being born on-site.

Table 2.7 Contraceptive protocol employed for apes at each sanctuary

	Contraceptive protocol	
Project name	**In use**	**Planned**
Cameroon Wildlife Aid Fund (CWAF)	Vasectomy – for two chimpanzees	Implants - female chimpanzees. No contraception planned for gorillas
Limbe Wildlife Centre (LWC)	Vasectomy – chimpanzees	Vasectomy - chimpanzees Implants/injection - female gorillas
Sanaga-Yong Chimpanzee Rescue Centre	Vasectomy	Vasectomy
Sanctuaire des Bonobos de Kinshasha	No	Not known (no adult females yet)
Projet de Protection des Gorilles (PPG Gabon)	No	No
Sodepal	No	Not known
Chimpanzee Rehabilitation Project	No	No
Chimpanzee Conservation Centre	Birth control pills	Birth control pills
Sweetwaters Chimpanzee Sanctuary (JGI)	Norplant	Norplant
Drill Rehabilitation & Breeding Centre (DRBC)	Vasectomy	Vasectomy
Habitat Ecologique et Liberté des Primates (HELP)	No	No
Projet de Protection des Gorilles (PPG Congo)	No	No
Tchimpounga Chimpanzee Sanctuary & Reserve (JGI)	Birth control pills	Birth control pills
Tacugama Chimpanzee Sanctuary	Vasectomy	Vasectomy
David Greybeard Sanctuary (JGI)	No	Implanon
Kitwe Point Sanctuary (JGI)	No	No – only males
Ngamba Island & Entebbe Wildlife Education Centre (JGI)*	Implanon	Implanon
Chimfunshi Wildlife Orphanage	No	No

Notes: In cases where the same method is in use and planned, this is where contraception is actively employed in older apes but planned for younger apes prior to reaching reproducing age. Likewise, where there is no present contraceptive protocol in use but it is planned, this is because none of the apes are near the age of reproduction. Implanon and Norplant are both forms of subcutaneous implants for females.

2.4.5 Accommodation facilities and daily routines of animals

The three projects focusing on reintroduction are based in mainland forest where the apes are free ranging within large protected areas (Table 2.8). Size of the release site varies from 50,000 ha (PPG, Rep. of Congo) to 504,500 ha (HELP, Rep. of Congo). HELP also holds chimpanzees deemed not suitable for reintroduction on three islands (17, 30 and 50 ha). PPG Congo holds gorillas deemed unsuitable for release and all bonobos full-time in gang and individual cages.

Two additional sanctuaries (plus HELP) use islands as a permanent home for apes; island size ranges from 41ha to 425ha. Chimpanzees at The Chimpanzee Rehabilitation Project (The Gambia) are all nutritionally self-sufficient while chimpanzees on Ngamba Island (Uganda) and at HELP are not. The islands in The Gambia and at HELP are maintained for exclusive use by the chimpanzees. In contrast, two hectares of Ngamba Island have been fenced off (using electric fencing) for a camp, night-time holding facilities and viewing platform for visitors (Plate 2.2).

Plate 2.2 Electric fence on Ngamba Island, Uganda

The remaining projects (n=13) use a combination of cages and enclosures. All use electric fencing but some additionally employ water (n=4) and a wall (n=1) as barriers. None of the apes in these enclosures are nutritionally self-sufficient.

Table 2.8 Sanctuary location and accommodation type/size

Project name	Location (or nearest town/city)	Accommodation type & size
Cameroon Wildlife Aid Fund (CWAF)	Two sites: Yaounde Zoo & Mefou Park	Cages. Enclosures with electric fencing; 0.01ha, 0.1ha, 0.17ha, 0.36ha
Limbe Wildlife Centre (LWC)	Formerly Limbe/Victoria Zoo	Cages. Enclosures with electric fencing; 0.05ha, 0.1ha, 0.3ha
Sanaga-Yong Chimpanzee Rescue Centre	22km from Belabo	Cages. Enclosure with electric fencing; 2ha & small forest area for infants
Sanctuaire des Bonobos de Kinshasha	Kinshasha	Cages. Enclosures with electric fencing; 0.03ha, 0.1ha
Projet de Protection des Gorilles (PPG Gabon)	Mpassa Reserve	Free ranging in 171,800ha forest
Sodepal	7km from Bakoumba	Cages. Enclosures with electric fencing.
Chimpanzee Rehabilitation Project	River Gambia National Park	3 islands; 43ha, 168ha, 425ha
Chimpanzee Conservation Centre	Parc National de Haut Niger	Cages. Enclosure with electric fencing ; 2ha
Sweetwaters Chimpanzee Sanctuary (JGI)	Ol Pejeta Ranch, Nanyuki	Cages. Enclosures with electric fencing & water divide; 86ha
Drill Rehabilitation & Breeding Centre (DRBC)	Two sites: Calabar & Afi River Forest Reserve	Enclosures using electric fencing; 12ha
Habitat Ecologique et Liberté des Primates (HELP)	Two sites: islands and release site in the Conkouati-Douli National Park	Released chimpanzees free ranging in forest; 504,500ha 3 islands for nonreleasable chimpanzees; 15ha, 30ha, 50ha
Projet de Protection des Gorilles (PPG Congo)	La Reserve Natural des Gorilles de Lesio-Louna	Released gorillas free ranging in 50,000ha forest. Cages for non-releaseable gorillas & bonobos
Tchimpounga Chimpanzee Sanctuary & Reserve (JGI)	33km from Pointe-Noire	Cages. Enclosures with electric fencing
Tacugama Chimpanzee Sanctuary	Tacugama Forest Reserve	Cages. Enclosures with electric fencing; 0.2ha, 1ha, 3ha
David Greybeard Sanctuary (JGI)	Johannesburg Zoo	Cages. Enclosures with electric fencing; 16ha
Kitwe Point Sanctuary (JGI)	6km from Kigoma	Enclosure using electric fencing, peninsula and water
Ngamba Island & Entebbe Wildlife Education Centre (EWEC) (JGI)	Two sites: Ngamba Island on Lake Victoria & EWEC (formerly Entebbe Zoo)	Ngamba Island: cages, electric fencing, water; 41ha. EWEC: cages, enclosures with electric fencing and moat; 2x 0.2ha
Chimfunshi Wildlife Orphanage	70km from Chingola	Cages. Enclosures using electric fencing, water & wall; 2ha, 3ha, 6ha, 2x 202ha

Notes: Not all sizes of accommodation are known. All sizes have been converted into hectares (ha)

Five of these projects take young apes into nearby forested areas during the day but they are returned to sleep in cages at night. Four projects provide some supplementary natural vegetation for the apes to feed on. Eight projects accommodate other animals; species and numbers differ for each project. For example, The Limbe Wildlife Centre (Cameroon), Cameroon Wildlife Aid Fund and Ugandan Wildlife Education Centre are all based on previous zoo sites. They inherited some animals (including apes) but also continue to accept many different species.

2.4.6 Additional activities of sanctuaries

Sanctuary managers were asked to describe if and how they were involved in activities that extend beyond the immediate rescue, rehabilitation and reintroduction of primates. Table 2.9 presents the activities in which the sanctuaries report they actively participate.

Table 2.9 Extended activity types that sanctuaries participate

Category	Activities
Local education	Outreach programs to schools, villages, hunting camps On-site visits by school parties, teachers/educators and the general public Nature clubs Education officers Displays and keeper talks Workshops/seminars Radio, television broadcasts Activity packs Ecology courses
Local development	Employment and training Building of schools, latrines, roads and bridges Small business development Sustainable agriculture Health education Reforestation Eco-tourism initiatives for local communities
Habitat protection	On-site conservation education through displays and tours Out-reach programs to schools, villages and hunting camps Project presence in protected areas Employment of eco-guards Establishment and reinforcement of wildlife sanctuary demarcation Assisting with snare removal
Tourism	Dependant upon location (Plate 2.3). None at reintroduction projects
Data collection	Reintroduction projects collect data on the behaviour and ecology of released apes and conduct surveys on native fauna and flora Genetic analysis of released and wild chimpanzee populations through hair and faecal samples Collaboration with biologists Data collection on behaviour and health of sanctuary apes Surveying nearby wild populations

Sixteen of the 18 sanctuaries are involved in local education. The category of 'local development' is broad but generally concerns improvements in 'quality of life', for example in health care, education and housing, employment and training opportunities. Seven sanctuaries specified that they were involved in local development. However, through the provision of employment to locals, all 18 projects to some extent participate by definition in local development. As mentioned earlier one project (Sodepal, Gabon) was originally established to provide alternative sources of protein (from bushmeat) through fish and game farming.

Thirteen sanctuaries are reported to actively participate in habitat protection. The location of the sanctuary influences how this involvement is expressed. For example, the LWC is based in a small coastal town in Cameroon and encourages habitat protection by on-site conservation education out-reach programs. Projects located within remote areas can give rise to more tangible effects, for example, project presence in a protected area can act as a deterrent to hunters and protects habitat (e.g., HELP, Rep. of Congo). All sanctuaries except the three that focus on reintroduction are open to tourists. In all cases there appears to be no active solicitation of tourism, but location is clearly an important factor in whether a site receives tourists. All three projects that focus on reintroduction collect systematic data on released apes and native fauna and flora. Of the remaining sanctuaries, over half (n=9) are involved in data collection.

Plate 2.3 Tourist viewing platform at Ngamba Island

2.4.7 Costs and funding

Sanctuary managers were asked to indicate how much it costs annually to run their respective sanctuaries (total project cost was requested, in addition to cost for apes only in those sanctuaries holding non-ape species). The estimated annual cost (for apes only) ranges from US$15,000-200,000 with a median US$40,000 (IQR74,700) (see Table 2.10 on p.47). The annual cost per ape ranges from US$407-9091 with a median cost of US$3520 (±IQR4134).

Sanctuary managers were also asked to rate on a scale of zero (least important) to ten (most important) according to 11 categories, source of project funding. Table 2.11 shows the median proportion that each category contributed to project finances. Overseas non-governmental organisations were rated highest, followed by overseas individual donations, tourism and zoos. In five categories; local non-governmental organisations, overseas commercial sponsorship, volunteer programmes and government, a large number of 'zero' responses resulted in the median score being shown as zero. The category of 'Other' highlighted that one project has been able to fully fund its activities through an animal adoption scheme (Chimpanzee Rehabilitation Project, The Gambia).

Table 2.11 Median proportion of financial contribution (±IQR)

Funding category	n	Median	IQR	Minimum-maximum
Overseas non-governmental organisation	17	4	7.5	0 – 10
Overseas individual donation	17	2	6	0 – 7
Tourism	17	2	3	0 - 10
Zoo	17	2	4.5	0 – 10
Local individual donation	17	1	2.5	0 – 4
Local non-governmental organisation	17	1	-	0 – 1
Local commercial sponsorship	17	0	2	0 – 5
Overseas commercial sponsorship	17	0	0.5	0 – 5
Personally financed	17	0	3	0 – 10
Volunteer programme	17	0	-	0 – 1
Government	17	0	3	0 – 4

Table 2.10 Annual costs of running a sanctuary and staff numbers

Project name	Annual costs (US$)	Annual cost per ape (US$)	Staff numbers
Cameroon Wildlife Aid Fund (CWAF)*	Up to 50,000	-	29
Limbe Wildlife Centre (LWC)*	40,000	-	22
Sanaga-Yong Chimpanzee Rescue Centre	40,000	5,000	12
Sanctuaire des Bonobos de Kinshasha	40,000	2,222	10
Projet de Protection des Gorilles (PPG Gabon)	100,000	5,882	9
Sodepal*	100,000 (15,000 for chimpanzees)	1,364	5
Chimpanzee Rehabilitation Project	24,000	407	7
Chimpanzee Conservation Centre	18,000	692	5
Sweetwaters Chimpanzee Sanctuary (JGI)	88,000	3,520	14
Drill Rehabilitation & Breeding Centre (DRBC)*	Up to 50,000 (20,000 for chimpanzees)	1,250	42
Habitat Ecologique et Liberté des Primates (HELP)	93,000	2,163	22
Projet de Protection des Gorilles (PPG Congo)	Up to 200,000	9,091	46
Tchimpounga Chimpanzee Sanctuary & Reserve (JGI)	-	-	41
Tacugama Chimpanzee Sanctuary*	25,000	-	9
David Greybeard Sanctuary (JGI)*	-	-	10
Kitwe Point Sanctuary (JGI)	25,000	8,333	6
Ngamba Island/ Entebbe Wildlife Education Centre (JGI)*	100,000/150,000 (30,000 for chimpanzees)	3,704/4,286	10/46
Chimfunshi Wildlife Orphanage*	200,000	-	34

* Indicates projects that also accommodate other primate and non-primate species

\- Information not provided or not available for projects that did not provide an annual cost for apes versus whole project costs

2.4.8 Staff and volunteers

A total of 347 local staff were employed within the 18 projects; a median of 12 (±25) with a minimum of 5 and maximum of 46 local staff at each project (Table 2.10). Staff numbers for Ngamba Island and the Entebbe Wildlife Education Centre have been counted separately. Thirty-two expatriate staff were employed, seven on a voluntary basis. Over 70% of sanctuaries (n=14) accepted volunteers. The majority of sanctuaries arranged the volunteers themselves and only one did this through an official organisation.

2.5 Discussion

2.5.1 The questionnaire

As highlighted on page 32 of this chapter, the wording and structure of questions can greatly influence respondent answers. Although these factors were taken into account when designing the questionnaire and an expert was consulted, any future design should incorporate defining response frameworks. When respondents are left to define a topic in global terms for themselves, for example in the case of health status categories, the researcher cannot be sure that they will all do it in the same way. One sanctuary manager may consider the health status of one chimpanzee as being poor whilst another would consider it to be very poor or conversely fair. When respondents are required to answer in terms of specific dimensions, the dimensions that they are to focus on must also be properly defined.

2.5.2 Overview and numbers

Chapter 1 highlighted the relationship between human population growth and demands for natural resources. As the African human population is expected to double by the year 2025 (Butynski, 2001) the trade in bushmeat will undoubtedly continue to proliferate as will the number of orphaned primates. Consequently, there will be a need for more sanctuaries and existing ones to extend facilities. Eighteen great ape sanctuaries presently operate throughout East, West, Central and South Africa and their numbers have gradually increased since the mid-1980's, an average of one per year. Political instability and poverty in some countries have prevented sanctuaries from being established but if and when political will allows, then their distribution may extend. At the present time a sanctuary is being developed in South Africa to receive orphaned chimpanzees from Angola, but the sanctuary may have a greater impact if located in-situ where the problems and primates originate. In the Central African Republic (CAR) a country ravaged by organised yet illegal poaching campaigns, a similar situation exists. It is estimated that approximately 200 young chimpanzees are being held in poor captive conditions in the east of the country and no sanctuary exists to care for them (Anonymous, 2002). Arrangements to transfer one chimpanzee from CAR, two from the Ivory Coast and one from Ghana to Chimfunshi chimpanzee sanctuary in Zambia are presently underway as no sanctuaries exist in these countries. However, although this addresses the short-term welfare needs of a small number of chimpanzees, this does not provide a long-term solution for the large number of chimpanzees and other primates in these countries or in-situ conservation problems.

The number of apes presently held in African sanctuaries does not represent the total number in need of refuge. During the 2nd PASA workshop when sanctuary managers were asked to present up-to-date figures on numbers of apes, they had increased by almost 100 since the preceding year (Rosen et al., 2001); this year the proportion has risen by approximately a further 70 (Rosen, Cox & Montgomery, in press). This increase is not due to an active solicitation of animals, as most sanctuaries would be unable to accept all the apes being held illegally. An estimate of the number of apes being kept illegally outside of the sanctuaries totalled over 1000 (Rosen et al., 2001). This figure is only an estimate, and it is likely that there are many more throughout those countries with endemic ape populations. In an unpublished survey of African, Asian and Central/South American primate sanctuaries, over 50% said that they had refused to accept primates mostly due to lack of funds and facilities (Taylor, 2000). In the present survey, projects that have not yet reached maximum carrying capacity would probably only be able to accept young apes due to a lack of space/facilities and problems integrating older individuals into already established groups (Bernstein, 2001; Brent, Kessel and Barrera, 1997; Alford, Bloomsmith, Keeling and Beck, 1995). As the majority of animals in the sanctuaries at present are not yet adults, sanctuaries will face increasing financial and logistical pressure as they need to increase and strengthen their captive facilities.

2.5.3 Age of animals and background history

It is not surprising that the majority of apes arriving at sanctuaries are aged less than four years, by this time they have lost their appeal as pets and have become increasingly agile, destructive and potentially dangerous. Most pet chimpanzees face imprisonment or death (Goodall, 1992).

Over half of all apes arriving at the sanctuaries were confiscated. This highlights the important role of sanctuaries in enforcement of wildlife protection. Although confiscation is frequently the only method available of obtaining animals, in particular from owners who hope to make a profit from their sale, encouraging owners to donate animals can be positive if they become supporters of the sanctuary. The present survey found that 36% of apes were donated to the sanctuaries. When possible the LWC encourages owners to part willingly with their animals and to subsequently visit the sanctuary. It is hoped by doing so, the owners will support the sanctuary, its goals and not buy another primate pet. In contrast some animals are happily donated normally because they are past their cute stage and are becoming too much of a handful as a pet. It is very easy for a sanctuary to be seen as an easy solution for owners who want to dispose of their older pets. In an unpublished survey 57% of primate sanctuaries asked owners of ex-pets to donate money for the support of the animal, but it was rarely received (Taylor, 2000). That over 25% of the apes in the present survey had been previously kept as pets indicates how big a problem the pet trade can be. Identifying whether the owners are national or foreign could assist in developing specific campaigns aimed at tackling this problem. Although apes were kept for entertainment purposes and/or as tourist attractions to a lesser extent, such 'exhibitions' legitimise this practise and the often sub-optimal conditions in which the animals are frequently kept (Plate 2.4).

Plate 2.4 A chimpanzee kept outside a hotel as an 'attraction'. She was confiscated and is now at the LWC

Only a small number of projects held apes that came exclusively from the country in which the sanctuary was based. Furthermore, exact origin is frequently not known. The IUCN/SSC Reintroduction Specialist Group recommend that primates whose geographic origin cannot be precisely determined should not be reintroduced (IUCN Guidelines for Nonhuman Primate Re-introductions, 2002). This is one factor that may prevent many sanctuaries from pursuing reintroduction as a future option.

2.5.4 Health of sanctuary apes

A figure often quoted is that for each baby chimpanzee that reaches its final destination alive, at least ten other chimpanzees will have died although the true figure may be nearer 30 (Teleki, 1989). The mothers are shot for food, traditional medicine and/or to capture their infants; if not killed instantly, she may crawl away, and die from her injuries; the infant will die also. Infants may die of the wounds they receive when their mothers are shot, others may die of stress, lack of proper care and cruel treatment during transit on the journey from the forest to point of sale (Goodall, 1992). This highlights the numbers involved in this trade but also the likely physical and psychological effects on the surviving infant. Young wild chimpanzees are dependent on their mothers until about four years of age. Orphan chimpanzees may suffer from many of the same emotional disturbances displayed in human infants when deprived of their mothers (Goodall, 1992). Consequently, few animals arrived in an excellent state of health. Approximately an equal proportion of animals arrived in a good, fair, poor and very poor state of health; it is surprising that more did not arrive in a very poor state. At the Chimpanzee Rehabilitation Centre in The Gambia it was noted that chimpanzees previously kept as pets normally arrived in good physical condition and that chimpanzees previously used by photographers on Spanish beaches as tourist attractions were found to be in poor psychological shape.

The large percentage of animals that die prematurely (20%) in sanctuaries is striking. This survey did not ask about cause of death; a specific diagnosis is unlikely to be available in most cases. Deaths may be a consequence of injuries/illnesses not readily apparent upon arrival, sub-optimal sanctuary facilities (quarantine, cages, hygiene), disease transmission (ape-ape and anthropozoonotic exchange) or sub-standard veterinary facilities and protocols. That over 70% of apes do survive probably reflects the stoic efforts by sanctuary personnel but it is clear however, that sanctuaries need more logistical and financial support to be able to improve standards of care for the health and welfare needs of their animals.

Interestingly, a difference emerged when mortality rates between ape species in sanctuaries were compared; the mortality rate for chimpanzees is substantially lower than bonobos and gorillas. Comparative evidence is sparse on wild (Schaller, 1963; Goodall, 1983; Nishida, Takashaki and Takahata, 1990; Furuichi, Idani, Ihobe, Kuroda, Kitamura, Mori, Enomoto, Okayasu, Hasimoto and Takayoshi, 1998) and captive populations (Courtenay and Santow, 1989; Mace, 1990; Hill, Boesch, Goodall, Pusey, Williams and Wrangham, 2001) but contradicts the rates found in the present study. The details on age and cause of death are necessary to make comparisons between wild, captive and sanctuary ape populations. However, the high mortality found for gorillas in the present study maybe reflect injuries, susceptibility to disease upon arrival following capture, inability to tolerate and digest food provided in captive conditions and/or emotional disposition. Infant gorillas appear more psychologically and physically fragile than the comparatively resilient chimpanzee (personal observation). The development of PASA may help to promote dissemination of information regarding successful protocols that will ultimately lower mortality rates.

Medical conditions that animals arrive with include internal parasites, behavioural abnormalities, malnutrition and to a lesser extent infected wounds, wounds due to chains and rope, and external parasites. Wounds due to chains and ropes are from tethering; the rope or chain chafes and can even become embedded in the skin. The frequent need for veterinary intervention emphasises the importance of having experienced medical personnel on site, personnel that the majority of sanctuaries cannot afford.

Over 70 % of the sanctuaries used or plan to use some method of contraceptive. Those who did not focused primarily on reintroduction or perceived no need. The principal aim of reintroduction is generally to establish a viable self-sustaining population (IUCN Guidelines for Nonhuman Primate Re-introductions, 2002) and a frequently used measure of reintroduction is successful reproduction (Beck et al., 1994). Where contraception in captivity is not used, the primary motive is normally to allow a more natural group composition to be established. However, in the future, contraception may have to be considered as captive populations grow but the environment does not.

2.5.5 Housing of sanctuary apes

The majority of sanctuaries use a combination of enclosures and cages to accommodate their animals. The preferred method of securing an enclosure is electric fencing (refer to Noon, 1997 for a review of electric fencing as a barrier for chimpanzee enclosures).
The size of enclosure varies from project to project and depends on its location and available space. Electric fencing can allow for large areas to be enclosed; the largest are over 200 hectares (Chimfunshi and Sweetwaters) and greater than many island sanctuaries. Satellite cages within fenced areas offer the opportunity to separate animals and intervene

in medical emergencies. However, electric fences are not infallible and protocols for escape need to be developed.

Islands can offer a practical means of providing a secure, sometimes spacious and semi-natural captive environment, but unfortunately suitable islands are scarce. Islands used vary in size from less than 0.25 to over 200 hectares. As highlighted in Chapter 1, most release sites for chimpanzees have been islands and there have been some cases of chimpanzees drowning (S. Marsden née Brewer, personal communication, 2001; F. Prince, personal communication, 2001) and escaping (Hladik, 1974: Hannah and McGrew, 1991). However, no chimpanzees have drowned at the HELP sanctuary in spite of chimpanzees wading, frequently to chest height, to receive tins of Cerelac (a commercial baby food mixture) at feeding time (see Chapter 3, p.60). Furthermore as animals mature access onto islands becomes reduced and consequently so do the possibilities to intervene when medical problems arise (S. Marsden née Brewer, personal communication, 2001). The three projects that focus on reintroduction have either used islands or mainland forest as training grounds prior to full release. Less than half of the sanctuaries are able to take their apes into a forest area during the day. Due to increasing levels of aggression in older apes it is usual that only young apes can be taken for forest excursions.

2.5.6 Additional activities of sanctuaries

All of the sanctuaries to some extent are involved in activities that may directly or indirectly impact on the conservation of wild populations and their habitats. Some are more pro-active than others, for example, the employment of eco-guards compared to the presence of the project alone as a means of protecting habitat. Conservation education in particular, ranging from information boards outside of enclosures to outreach programmes, seem ideally suited to sanctuaries (Farmer, 1996). The great apes are large charismatic mammals and can make powerful flagship species for conservation projects of all sorts. The extent to which sanctuaries are pro-active is probably dependent upon finance and resources rather than will. This contradicts the widely held belief that sanctuaries can and do only contribute to the welfare of individual animals. However, a systematic assessment of the impact of conservation education programmes on the attitudes of the local population would clarify what is and is not working. Any data collected needs to be published to illustrate trends. If a sanctuary argues it is protecting habitat by its presence then this needs to be quantified. Sanctuaries may require logistical and financial help to establish such assessment procedures. Interestingly, a recent book publication 'Primate Conservation Biology' (Cowlishaw and Dunbar, 2000) that includes reviews on conservation strategies and management practises delivers less than 100 words on the topic of 'ethical rehabilitation projects' (i.e., projects established for long-term captive care and not reintroduction). This is probably a consequence of the paucity of published articles about sanctuaries other than in the popular press, which often describes the rescue of individual animals accompanied by an illustration of a primate clinging to a human.

2.5.7 The costs of operating a sanctuary and funding sources

In-situ sanctuaries have received a great deal of criticism in the past, and have been accused of being a waste of money that could be better spent on habitat protection (Mackinnon, 1977; Soave, 1982). However, over half of all sanctuaries cost less than US$100,000 per annum to operate. The average annual cost of maintaining a chimpanzee in an American sanctuary has been quoted as US$3650 based on a per diem of US$10 (Dyke, 2001). This amount is approximately the same required to maintain an ape in some African sanctuaries. However, there is wide variation in the minimum-maximum figures calculated per ape in the present study, and they include the cost of additional activities as described in the previous section. These figures indicate that some African sanctuaries can be cost affective in relation to the possible positive impact that they can have on wildlife, people, and the environment. The most costly projects are those focusing on reintroduction, that employ expatriates and with the largest captive populations. The high percentage of projects that accept volunteers may help to keep costs down. The majority of sanctuaries gain funding from overseas sources; non-governmental organisations, individual donations, zoos and tourists. Multi-national companies, for example Elf

Petroleum, British American Tobacco, and logging concessions are potential sources of in-situ funding that could be exploited.

2.6 Conclusions

- African ape sanctuaries will undoubtedly increase as will the number of animals within them as the destruction of natural habitat and wild populations continues.
- The high proportion of apes in sanctuaries that are confiscated provides evidence of the role that sanctuaries play in facilitating wildlife law enforcement.
- A large number of apes in sanctuaries had been previously kept as pets. Future research should consider identifying ownership characteristics as this could assist in the development of specific campaigns aimed at reducing this problem.
- The welfare of the apes is clearly compromised as indicated by the range of medical conditions that are presented when the apes arrive at the sanctuaries.
- The preferred method of containing apes in captivity is electrified fencing which allows large areas to be enclosed.
- All sanctuaries are to some extent involved in activities that can contribute directly or indirectly to conservation issues. However, an assessment of conservation education programmes is needed to highlight what is and is not working.
- Costs associated with running sanctuaries are wide-ranging but overall lower than sanctuary critics might imagine. In-situ multi-national companies as sources of funding have yet to be exploited.
- Although habitat protection should be central to conservation thinking, sanctuaries should not be seen as a threat to limited financial resources in conservation. They can compliment protected area management by facilitating law enforcement, are ideally placed to nurture respect in the local population for animals and their environment, and may be able to supply stock for reintroduction projects.

The following chapter will describe the site of the HELP sanctuary whose primary focus is reintroducing chimpanzees to the natural environment in the Republic of Congo.

Chapter 3

Study site

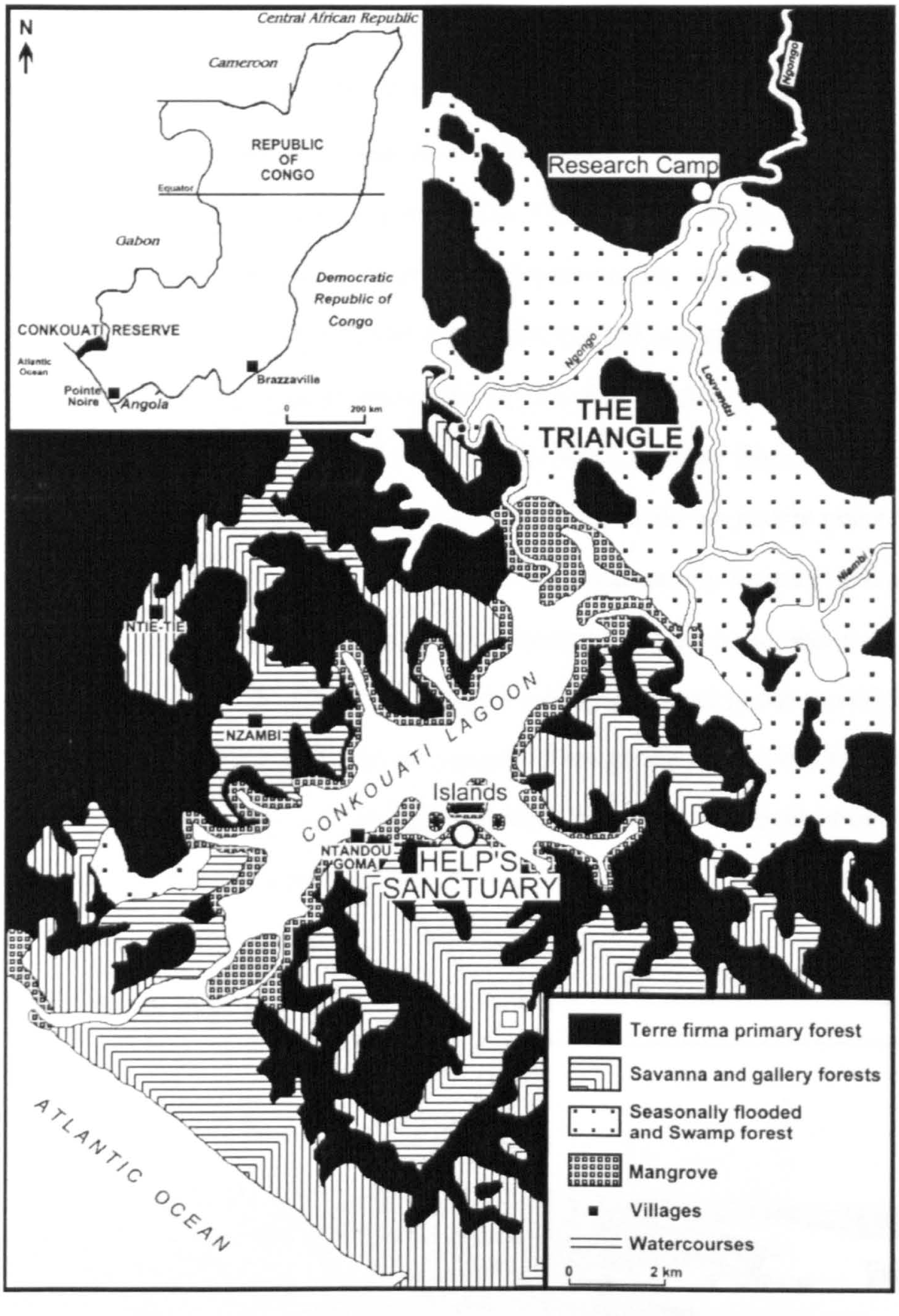
3.1 Overview

In 1991 an association named 'Habitat Ecologique et Liberté des Primates' (HELP) was created under Congolese law (Association law 1901, registered under No. 068/91) in the Republic of Congo. The association had the stated aim of contributing to the protection of threatened primates by (a) undertaking reintroduction projects to return captive primates to their natural environment, (b) helping with conservation education, and (c) assisting the country's wildlife service (Ministry of Water and Forests) with anti-poaching activities (Tutin, 1994).

The HELP project is split between two sites; the reintroduction site and the sanctuary. The reintroduction site known as the 'Triangle' is an area of approximately 21km² within the Conkouati-Douli National Park (previously known as the Conkouati Faunal Reserve). The park (longitude 11°, 10' - 11°, 40' E; latitude: 3° 33' - 4° 02' S) is located in the south-west corner of the Republic of Congo (Congo-Brazzaville), limited by the Gabonese border to the north and west, and by the Atlantic Ocean to the south-west (Figure 3.1). In its present form the park covers 5045km² and falls within the administrative region of Kouilou.

The Triangle resembles an island; it is limited to the west by the Ngongo River, to the east by the Louvandzi River, to the north where these two rivers meet, and the south by the river that joins Lake Tchivoka and Conkouati Lagoon itself. However, crossing canopy and fallen tree trunks provide access to and from the rest of the park for a variety of species. The longest distance in a straight line from north to south of the Triangle is 5.7km, and from west to east 5.2km (Paredes, 1997). The altitude varies from 60-100m (Paredes, 1997).

Figure 3.1 Map depicting the location of the Conkouati-Douli National Park, reintroduction site, sanctuary, villages and geographical features



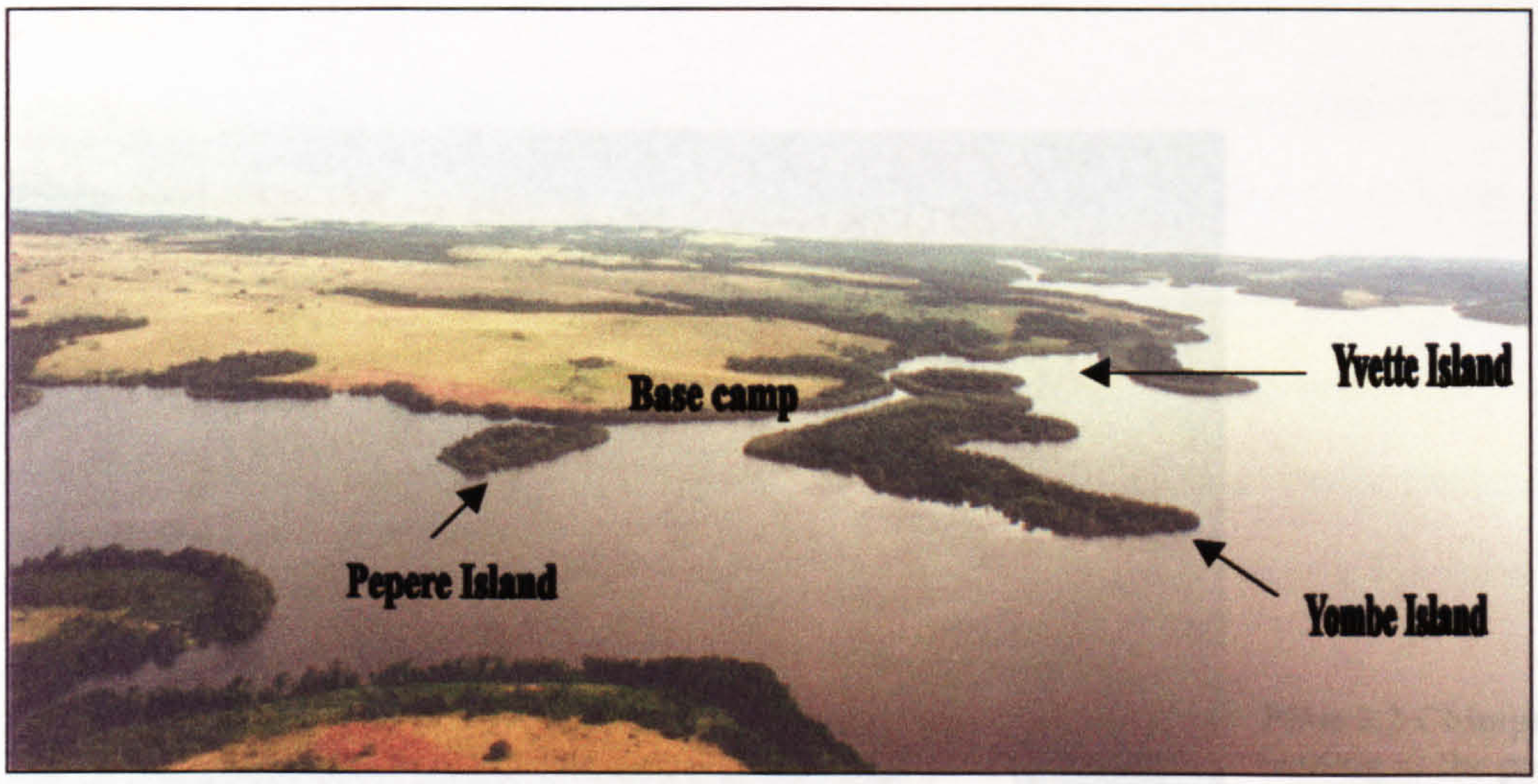
(Source: M. Vacher-Vallas, 2001)

The closest village to the Triangle release zone is Ntié-tié, a distance of 12km separated by lakes and rivers that are impassable by chimpanzees (M. Vacher-Vallas, former HELP Manager, personal communication, 2001). There are major water barriers between the Triangle and all villages except perhaps Cotovindou that is at least 100km to the north-east

(F. Maisels, Scientific Director, Wildlife Conservation Society (WCS), Republic of Congo, personal communication, 2001).

The HELP sanctuary consists of three forested islands on the Conkouati Lagoon that fall just outside of the park's official boundaries (Plate 3.1). Distance between sanctuary and reintroduction site is approximately 12km. The only way to get from the sanctuary to the Triangle is by boat and the journey takes approximately two hours but this can vary dependent upon season and water levels. The closest human settlement to the sanctuary is the village Ntandou Ngoma approximately 2.5km from the mainland base camp. The sanctuary is only accessible by road and the 180km journey from Pointe-Noire, the nearest major town, takes approximately eight hours. The roads are poorly maintained and at certain times of the year, the journey time can substantially increase and occasionally the roads are impassable. The only public transport to and from the region consists of a 'foula-foula'; a truck that sporadically transports local people and goods to and from Point-Noire. No public system of communication exists although the project has recently acquired a short-wave radio connecting the project sites (islands and reintroduction site) with one another and Pointe-Noire.

Plate 3.1 Aerial view of islands



(Source: Adapted from HELP)

The island sanctuary is where the chimpanzees are based prior to release, and for the non-releasable individuals a place of permanent residence. The largest of the islands at the sanctuary has a surface area of approximately 50 hectares (Yombe Island), the second 30 hectares (Yvette Island), and the third approximately 17 hectares (Pepere Island). Until 1996 very young chimpanzees were kept on the mainland and taken for walks in nearby forested areas. However, following the first release they were all moved onto Yvette Island. All three islands are forested (varying densities) and surrounded by mangroves. Although it is no longer possible to enter Yombe Island due to the aggressive nature of some chimpanzees, from the periphery of the island the trees appear taller and vegetation denser in comparison to Yvette and Pepere Island. None of the islands are sufficiently large enough for the chimpanzees to be nutritionally self-sufficient although they are able to harvest some wild foods. Consequently twice a day the chimpanzees are provisioned; in the morning with Cerelac (a commercial baby food preparation high in vitamins) and fruits (bananas, pineapples, mangoes as and when available) in the late afternoon. The chimpanzees on Yombe Island wade into the water surrounding the island to receive the tins of Cerelac (Plate 3.2). This behaviour is only possible on Yombe Island due to the shallow gradient from the edge of the island to the water. Wading was never actively encouraged, but from a very young age the chimpanzees witnessed the human caretakers wading in the water to get to and from the boat.

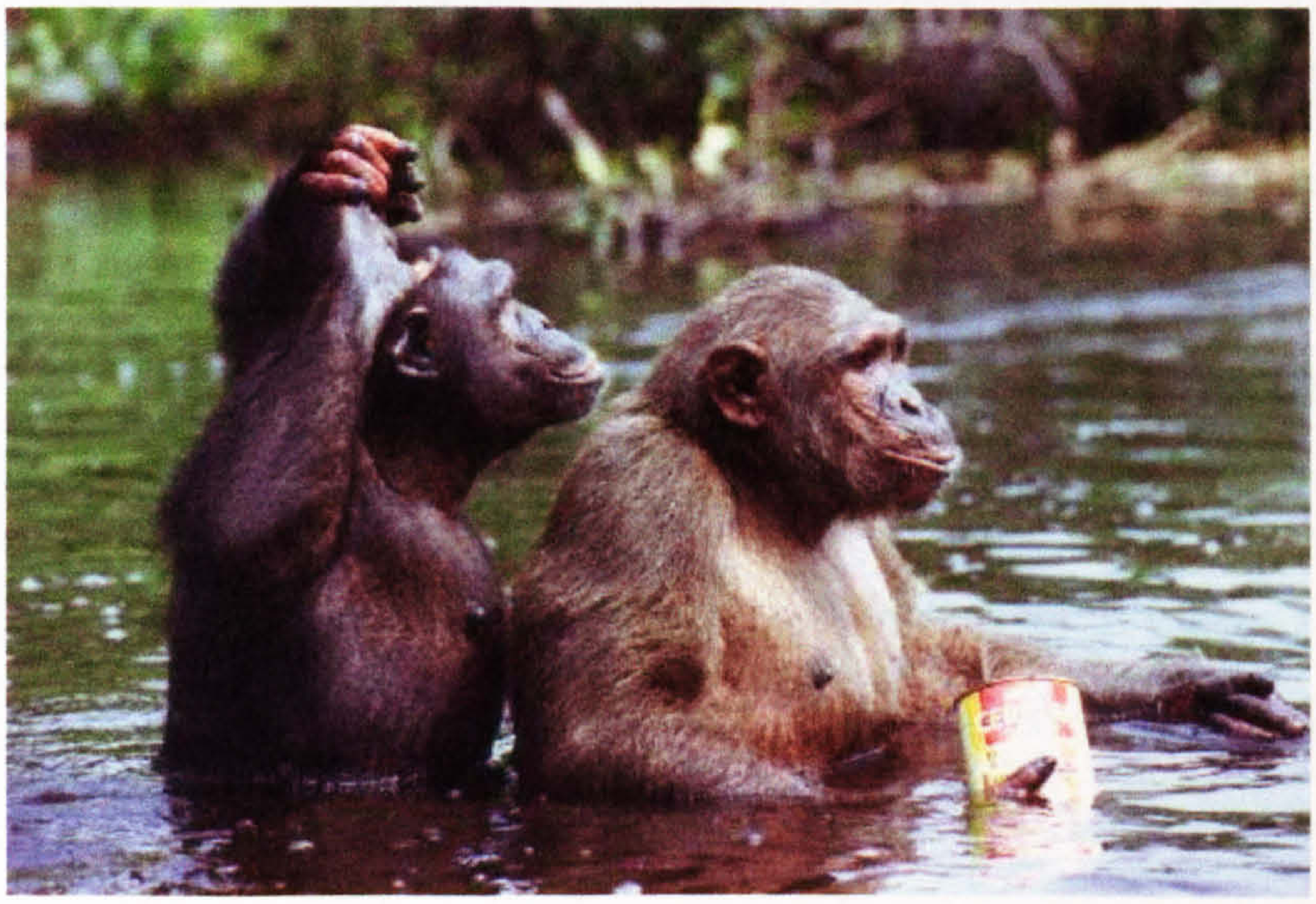


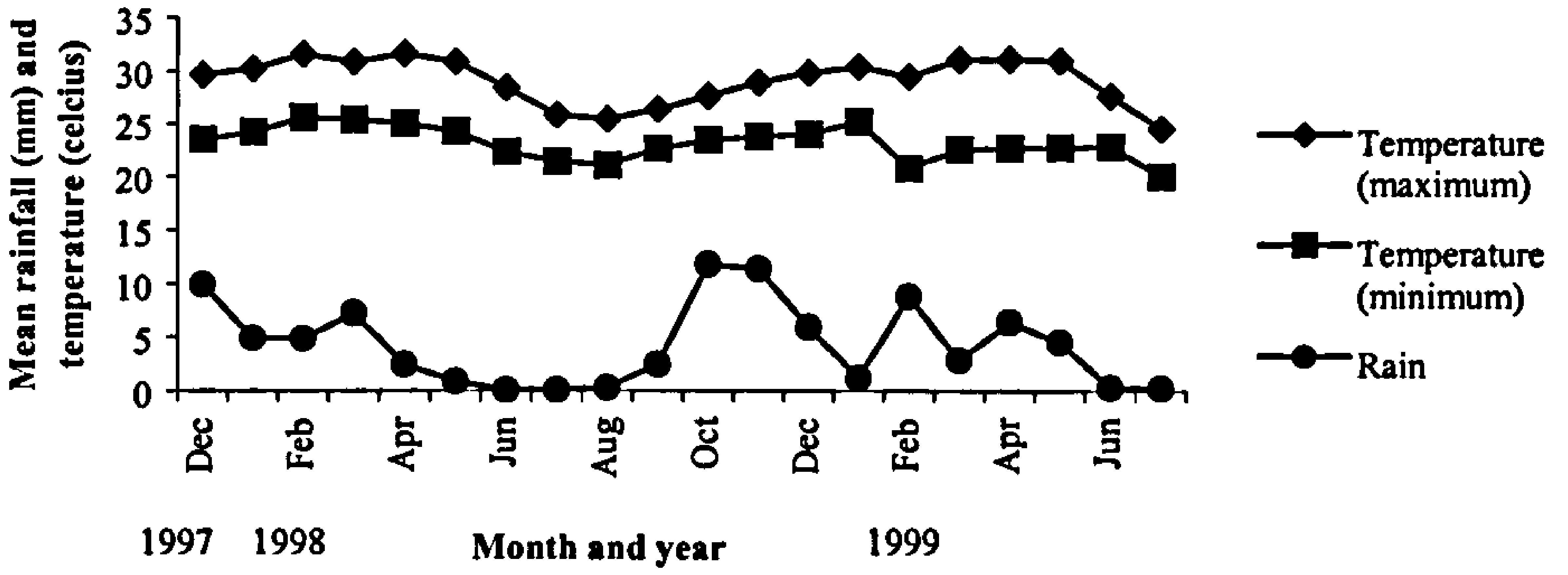
Plate 3.2 Chimpanzees wading at the periphery of Yombe Island at feeding time

3.2 Climate of the region

Rainfall

The climate is tropical and generally characterised by a dry season that falls between mid May and the end of September, and a rainy season between October and the beginning of May (Dowsett, 1991; Hecketsweiler and Ikonga, 1991; Doumenge, 1992). Only during the year of 1998 were climate data reliably collected at the Triangle (Figure 3.2). The total yearly rainfall for 1998 was 1609.90mm (for actual monthly levels see Figure 6.2, p.135). This yearly precipitation level is slightly higher than found in previous years measured at Pointe-Noire (Dowsett, 1991; Sita, 1996).

Figure 3.2 Comparison of the average daily level (for each month) of rainfall (mm) and minimum/maximum temperature (°c) in the Triangle (December 1997-July 1999)



During the dry season there is very little sunshine. The daily average number of hours of sunshine in Pointe-Noire ranges from five in the rainy season to four (3.6) hours in the dry season (Hecketsweiler and Ikonga, 1991). In the forest the dry season is also frequently characterised by cloud and mist in the mornings. There also exists a smaller dry season that falls within the main rainy season, a period of approximately three weeks starting late December through to mid January, when there is not a great deal of rain but many hours of sunshine.

Temperature and humidity

The average annual temperatures in southern Congo vary from 25°c in Pointe-Noire to 23°c in Dimonka, the mountainous region of Mayombe that has an altitude of 411m (Hecketsweiler and Ikonga, 1991). The pattern of a cooler dry season followed by an increase of temperature into the rains likely pertains throughout southern Congo, with local variations resulting from altitude and distance from the coast (Figure 3.2).

The overall level of humidity in the southern Congo is approximately 88%. However, during the dry season humidity levels are higher with a mean daily range of 88-90% and in the rainy season a range of 83-87% (Hecketsweiler and Ikonga, 1991). Despite the cooler temperatures in the dry season, the mist and drizzle during this period maintain forest humidity.

3.3 Flora

The Triangle

The Triangle has been categorised into three main forest types (refer back to Figure 3.1):

1. **Primary forest** is limited to three main slightly elevated areas that are situated on the central, western, and southern parts of the Triangle (Paredes, 1997).
2. **Seasonally inundated forest** covers the majority of the northern part of the Triangle. During the rainy season some of these areas can get up to 1.60m metres deep (Paredes, 1997).
3. **Swamp forest** surrounds the three patches of primary forest. During the rainy season these areas can get up to 1.40m deep on the western and eastern sides of the Triangle (Paredes, 1997).

As shown on Figure 3.1 areas of mangrove are restricted to the southern edge of the Triangle, particularly on the edge of the Conkouati Lagoon. Raphias are present along the Louvandzi and Ngongo river edges and in some areas form mixed vegetation with bamboo.

Within the Triangle, non-inundated forests constitute approximately 400 hectares, the largest of which is centrally located and corresponds to primary forest. Within inundated forest some areas are periodically flooded for approximately three months each year and are rich in *Marantaceae* sp. (310 hectares). Areas flooded for more than three months each year are primarily located in the southern region of the Triangle (920 hectares) and consist of swamp forest (600 hectares) and raphia (320 hectares) (Vacher-Vallas, Goossens, Farmer, Vallas, Ancrenaz, Paredes, Vidal and Jamart, in prep).

The Conkouati-Douli National Park

Details of the vegetation of the Conkouati-Douli National Park can be found in Doumenge, 1992; Dowsett and Dowsett-Lemaire, 1991; Maisels and Cruickshank, 1996; Maisels and Onononga, 2000; Moutsambe, 1997 and Sita, 1996. The park runs from the Atlantic Ocean to the Niari Plain, and includes lagoons, freshwater lakes, littoral forests, littoral and inland savannahs, sublittoral forests on dry ground, marsh forests and closed tropical forests (Maisels and Cruickshank, 1996). The northern two-thirds of the park are mostly Mayombian Forest and the southern third is a mosaic of savannah, marshes, lakes and lagoons. The Mayombian and sublittoral forest account for most of the forested area of the reserve (Doumenge, 1992).

3.4 Fauna

Direct observations of 19 mammal species have been recorded (Paredes, 1997) and signs (prints and faeces) of a further four (Paredes, 1998) specifically within the Triangle. Refer to Appendix B (p.372) for a list of species.

Inventories of mammals within the Conkouati National Park (Maisels and Cruickshank, 1996; Maisels and Onononga, 2000); the south-west (Doumenge, 1992) and south-east region of the park (Hecketsweiler and Ikonga, 1991), and the Kouliou Basin (Dowsett and Dowsett-Lemaire, 1991) have been conducted. In summary, Doumenge (1992) identified 24 mammal species and local hunters confirmed a further 20 within the south-west region.

More recent inventories have identified 37 (Maisels and Cruickshank, 1996) and 17 (Maisels and Ononga, 2000) large mammal species within the park. Species on the Red Data list include Endangered species such as elephant (*Loxodonta africana cyclotis*), gorilla (*Gorilla gorilla gorilla*), chimpanzee (*Pan troglodytes troglodytes*) and vulnerable species such as manatee (*Trichurus senegalensis*) and several species of marine turtle which use the Conkouati coastline for nesting (Maisels and Ononga, 2000).

3.5 Human presence and activity in the park

There are no human settlements specifically within the Triangle but the population living in around the park totals approximately 3000 people (Maisels and Ononga, 2000). As in many parts of Africa a dramatic exodus from rural areas has marked the last 40 years. The urban population of Pointe-Noire increased from 84,643 to 297,392 during 1964-1984 (Doumenge, 1992). In the last 14 years the population in the zone around Conkouati has fluctuated up and down as a consequence of economic opportunities associated with lumber, oil and mineral companies. However, the recent economic recession and armed conflict between opposing political groups has reversed the earlier pattern of migration from country to town and has increased the number of young men resident in the area (Doumenge, 1992; Tutin, Ancrenaz, Paredes, Vidal, Goossens, Bruford and Jamart, 2001). One solution to decreased employment opportunities in Pointe-Noire is to return to rural life where money can be earned by commercial fishing or hunting. Hunting with snares is common and shotguns are also regularly used. Manioc and bananas are the major agriculture crop. Surplus food (both plant and animal) is exported to Pointe-Noire. Pointe-Noire and Man Fai Tai (Chinese logging company) are the main markets for bushmeat coming from the east of the protected area, and hunters can get a lift from the logging company vehicles to Pointe-Noire to sell their goods (Maisels and Ononga, 2000).

Forestry exploitation in the region expanded rapidly during the 50 years that followed the building of the railway in 1934 and the recession of the Second World War. Following a period of recession from the mid-seventies, the late eighties has seen selective logging rapidly expanding in the Kouliou region (Dowsett-Lemaire, 1991). In 1989 the Congolese Government designated concessions to three main commercial logging companies within the then named Conkouati Reserve, and two are presently active.

3.6 History of park management

In 1980 the Conkouati Faunal Reserve was created by the Congolese Government to protect both wildlife resources and the frontier with neighbouring Gabon. As well as being rich in fauna and flora the Conkouati area contained significant timber and mineral resources. Prior to 1980, prospections were made by oil and logging companies but activity in the area was limited due to lack of access. Consequently, the area was relatively commercially unexploited (A. Jamart, Director of HELP, personal communication, 2001). However, a bridge built at Madingo Kayes connected Pointe-Noire with Conkouati and facilitated access to the area. The original reserve decreed in 1980 covered 300,000 hectares (3000km^2) but in 1989 its limits were redefined and reduced by half in order to allow a number of logging concessions (Chinese, French and Congolese), entry into the area. The local population was not involved in the creation of the reserve nor was anything done to create any reserve management or administrative structure following its creation, and therefore it existed on paper only without implementation (Clay, 1998).

Surveys conducted in the early nineties (Doumenge, 1992; Hecketsweiller and Mokoko Ikonga, 1991) highlighted the biological importance of the Conkouati Reserve and the growing threats from increased human use. At this time although laws existed to protect the reserve there was a lack of authority and presence in the area. This led to the IUCN (The World Conservation Union) implementing an Integrated Conservation and Development Project (ICDP) and gaining funding from the World Bank Global Environment Fund (GEF) in 1994. The objectives of the ICDP (Project Conkouati) were to introduce sustainable activities and local management to the park with the aim of improving living conditions of the residents while reducing threats to biodiversity. However, the eruption of civil war in June 1997 severely disrupted the work of Project

Conkouati. Brazzaville, the political and administrative centre for the Congo, was severely affected by the war. The instability meant that the normal conduit for project funds was held up for months. As a consequence of continuing instability in 1999 all GEF funding was withdrawn from the Congo. This resulted in the closure of Project Conkouati and financial difficulties for HELP who also received funding from GEF for three years. The HELP project is now primarily funded by grants from non-governmental animal welfare and conservation organisations.

The boundaries of the reserve have again been recently modified and the newly named Conkouati-Douli National Park (2000) is the most recent incarnation of a protected area with the highest habitat diversity in the Congo (Maisels and Ononongа, 2000). In its present form it covers 5045km^2. Presently the Wildlife Conservation Society is managing the park. The following chapter will describe the process that HELP used to reintroduce chimpanzees into the Conkouati-Douli National Park.

Chapter 4

Review of the reintroduction process

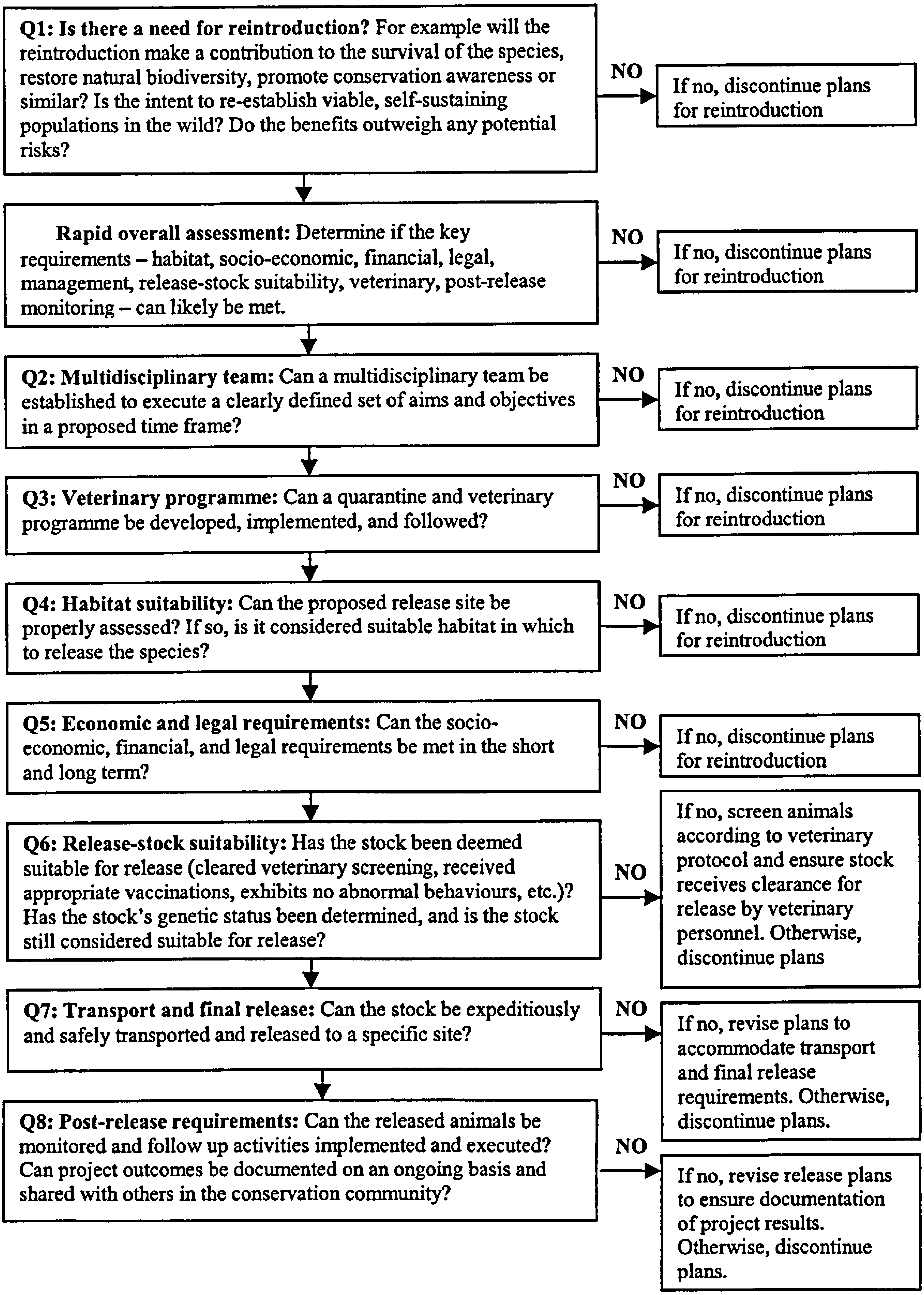
4.1 Introduction

Chapter 1 outlined the considerations and processes involved in reintroduction and factors associated with success from previous reintroduction projects. The aim of the present chapter is to describe the rationale and methodology of a chimpanzee reintroduction programme to provide guidelines for future attempts by highlighting and discussing salient aspects of the process that may facilitate or hinder survivorship. The rationale and methodology for the present reintroduction was guided by the IUCN Guidelines for Re-introductions (1995, 1998) (see Figure 4.1) and previous attempts to reintroduce apes as described in Chapter 1, and these will be commented on throughout this chapter where applicable.

4.2 Background and rationale for the reintroduction

Chapter 1 highlighted that reintroduction is a complex process and involves a great deal of planning and preparation. Figure 4.1 summarises the decisions involved if contemplating a reintroduction (IUCN Guidelines for Nonhuman Primate Re-introductions, 2002). The first question the decision tree asks is if there is a need for the reintroduction, and the suitability of release stock and habitat. Chapter 3 highlighted that biological and socio-economic surveys of the Conkouati area (Doumenge, 1992; Hecketsweiller and Mokoko Ikonga, 1991) had revealed its biological importance. As a consequence, the park was one of five sites selected for GEF funding, a fund administered by the World Bank and established to protect significant natural resources. In 1994 the IUCN began the implementation of an ICDP at Conkouati under the auspices of the World Bank. The objectives of the IUCN 'Project Conkouati' were to introduce sustainable activities and local management

Figure 4.1 Decision tree for nonhuman primate reintroduction



Q1: Is there a need for reintroduction? For example will the reintroduction make a contribution to the survival of the species, restore natural biodiversity, promote conservation awareness or similar? Is the intent to re-establish viable, self-sustaining populations in the wild? Do the benefits outweigh any potential risks?

If no, discontinue plans for reintroduction

Rapid overall assessment: Determine if the key requirements – habitat, socio-economic, financial, legal, management, release-stock suitability, veterinary, post-release monitoring – can likely be met.

If no, discontinue plans for reintroduction

Q2: Multidisciplinary team: Can a multidisciplinary team be established to execute a clearly defined set of aims and objectives in a proposed time frame?

If no, discontinue plans for reintroduction

Q3: Veterinary programme: Can a quarantine and veterinary programme be developed, implemented, and followed?

If no, discontinue plans for reintroduction

Q4: Habitat suitability: Can the proposed release site be properly assessed? If so, is it considered suitable habitat in which to release the species?

If no, discontinue plans for reintroduction

Q5: Economic and legal requirements: Can the socio-economic, financial, and legal requirements be met in the short and long term?

If no, discontinue plans for reintroduction

Q6: Release-stock suitability: Has the stock been deemed suitable for release (cleared veterinary screening, received appropriate vaccinations, exhibits no abnormal behaviours, etc.)? Has the stock's genetic status been determined, and is the stock still considered suitable for release?

If no, screen animals according to veterinary protocol and ensure stock receives clearance for release by veterinary personnel. Otherwise, discontinue plans

Q7: Transport and final release: Can the stock be expeditiously and safely transported and released to a specific site?

If no, revise plans to accommodate transport and final release requirements. Otherwise, discontinue plans.

Q8: Post-release requirements: Can the released animals be monitored and follow up activities implemented and executed? Can project outcomes be documented on an ongoing basis and shared with others in the conservation community?

If no, revise release plans to ensure documentation of project results. Otherwise, discontinue plans.

(Source: IUCN Guidelines for Nonhuman Primate Re-introductions, 2002)

to the park with the aim of improving living conditions of the residents while reducing threats to biodiversity. The problem of hunting and effective protection was an integral part of the ICDP's planned activities and of vital importance to the reintroduction. It was suggested that the risk of releasing chimpanzees could be addressed as part of the ongoing and planned conservation activities of the ICDP in the reserve and that the release project could make a significant contribution to conservation (see Figure 4.1, question 1). Dr Caroline Tutin (affiliated to Centre International de Recherché Medicales de Franceville, Station d'Etudes des Gorilles et Chimpanzes, Gabon) was asked to assess the reintroduction potential of the chimpanzees and to find a suitable release site (Tutin, 1994, 1996).

4.2.1 Assessment of the chimpanzees

Table 4.1 details the background history and current status of the chimpanzees at the HELP project; both those remaining on the islands and at the release site. Presently 37 chimpanzees have been reintroduced and 12 remain on the three islands. The information on this table will be referred to throughout this chapter and sections summarised where applicable to assist the reader. Precise background history for each reintroduced chimpanzee is not available. However, HELP were asked to complete the questionnaire for Chapter 2, and provided estimations on the percentage of chimpanzees (includes all chimpanzees released or not) that had been kept as pets or in a zoo and whether they had been confiscated, donated, born on-site etc. Thirty-nine percent of chimpanzees prior to arriving at the sanctuary were found awaiting sale and/or transportation, 33% had been kept as pets, 19% were from a zoo (Pointe-Noire or Brazzaville) and 9% were born on-site. Over half of the chimpanzees (55%) had been confiscated by government officials, 36% were donated, 2% transferred from other facilities and the remainder born on the islands.

Concerning just the reintroduced chimpanzees, of those whose physical condition upon arrival were recorded, 18 of the reintroduced chimpanzees were described as arriving in a poor or bad condition and 14 in fair or good physical condition. Knowledge of background

Table 4.1 Background history and current status of the chimpanzees at the HELP project

Name	Sex	Origin	Time in captivity (pre-HELP)	Condition upon arrival/early history	Age at arrival	Island location	Time at HELP pre-release	Date of release	Age at release	Present age (Jan 2002)	Time post-release (Jan 2002)	Present status and miscellaneous comments
Bougnoule	F	Niari (or Mossendjo)	2 years +	?	5 yrs	Yvette	4¾ yrs	24.11.96	9¾ yrs	16 yrs	5¼ yrs	Alive and well. Slight aggressive tendencies towards observers. No collar when released
Yvette	F	Kouilou	5 yrs	Bad condition, high parasite load	5¼ yrs	Yvette	4¾ yrs	24.11.96	10 yrs	16 yrs	5¼ yrs	Alive and well
Mekoutou	M	Democratic Republic of Congo	1 yr	Good but developed eczema	3 yrs	Yvette and nursery	4¾ yrs	24.11.96	7¾ yrs	12½ yrs	5¼ yrs	Alive and well. Father to Choupettes infant. People orientated
Jeanette	F	Sounda (Kouilou)	2 mths	Bad - dehydrated	1 yr	Yombe	8½ yrs	24.11.96	9½ yrs	14¾ yrs	5¼ yrs	Alive and well. Often with Choupette. No collar when released
Choupette	F	Kouilou	?	Poor – dehydrated and diarrhoea. Came from Brazzaville Zoo	1 yr	Yombe	6 yrs	26.11.96	7 yrs	12¼ yrs	5¼ yrs	Alive and well. Gave birth to male infant October 2001, father Mekoutou. Often with Jeanette
Andreas	M	Conkouati	Born at release site	?	Born on-site	-	-	-	-	3 mths	3 mths	Infant of Choupette and Mekoutou born post-release
Rosette	F	Lekoumou	Days	?	16-17 mths	Yvette	6¾ yrs	25.1.97	8 yrs	13 yrs	5 yrs	Alive and well
Fanny	F	Kouilou	2 yrs	Good	2 yrs	Yvette	5 yrs	25.1.97	7 yrs	-	-	Status unknown: radio signal disappeared after first day
Nyasha	F	Kouilou	2-3 mths	Bad	1 yr	Yvette	5 yrs	19.11.97	6 yrs	-	-	Status unknown: disappeared immediate post-release. Removed collar
Kaka-moeka	F	Kakamoeka	1-3 wks	Good	7 mths	Yvette	5¾ yrs	19.11.97	6¼ yrs	-	-	Status unknown: disappeared immediate post-release
Massabi	F	Massabi	3 wks	Good	1 yr	Yvette	5¼ yrs	28.11.97	6¼ yrs	10½ yrs	4¼ yrs	Alive and well. Often with Mossendjo
Cabinda	F	Saisie (Cabinda)	4 mths	Poor – hairless and swollen abdomen	2 yrs	Yvette	5¾ yrs	28.11.97	7¾ yrs	12 yrs	4¼ yrs	Alive and well
Mossendjo	F	Mossendjo	?	Good	1 yr	Yvette	5¼ yrs	28.11.97	6¼ yrs	10½ yrs	4¼ yrs	Alive and well. Often with Massabi
Hinda	M	Hinda (Kouilou)	6 mths	Good – quite fat	8 mths	Yvette	6 yrs	28.11.97	6¾ yrs	-	-	Dead: killed by WC 24.7.00. Previously badly injured by WC in 1999
Caline	F	Saisie (Cabinda)	4 mths	Poor – had several infected wounds	2 yrs	Yvette	4¾ yrs	28.11.97	6¾ yrs	10¾ yrs	4¼ yrs	Status unknown: last seen in October 1999 with no collar

Name	Sex	Origin	Time in captivity (pre-HELP)	Condition upon arrival/early history	Age at arrival	Island location	Time at HELP pre-release	Date of release	Age at release	Present age (Jan 2002)	Time post-release (Jan 2002)	Present status and miscellaneous comments
Dolisie	M	Niari (or Loubomo)	2 mths	Fair	1 yr	Yvette	5¾ yrs	28.11.97	6¾ yrs	-	-	Dead: Skull and collar found, either killed by WC or hunters
David	M	Kouilou	3 mths	Anorexic and apathetic	1 yr	Yombe	10 yrs	1.2.99	11 yrs	13 yrs	2 yrs	Status unknown: disappeared 22.5.99. No collar
Agathe	F	Kouilou	2 mths	Very thin	6-8 mths	Yombe	8½ yrs	1.2.99	9¼ yrs	11¼ yrs	2 yrs	Alive and well. Timid nature
Sophie	F	Kouilou	2 mths	Good	1 yr	Yombe	8½ yrs	1.2.99	9½ yrs	11½ yrs	2 yrs	Status unknown: last seen 17.11.00. Collar not working
Valentine	F	Born on Yombe island	1½ mths	Fair	Born on site	Yombe	1½ mths	1.2.99	1½ mths	-	-	Mother Sophie, father Yombe. Presumed dead: disappeared 22.5.99. No collar
Koutou	M	Madingo-Kayes (Kouilou)	7 days	Good	5 mths	Yombe	9 yrs	1.2.99	9½ yrs	11½ yrs	2 yrs	Alive and well. People orientated
Chinois	M	Nkola (Kouilou)	1-2 mths	Very thin – full of parasites and fleas	7 mths	Yombe	11½ yrs	2.6.00	12 yrs	13¾ yrs	1¾ yrs	Alive and well. Shy
Matalila	F	Makabana (Niari)	2 mths	?	5 mths	Yombe	11¼ yrs	19.6.00	11¾ yrs	12¼ yrs	1¾ yrs	Alive and well. Pregnant when released, later miscarried
Perlette	F	Kouilou	Days	Suffering from mycoses	7-8 mths	Yombe	9½ yrs	19.6.00	10 yrs	11¾ yrs	1¾yrs	Alive and well
Lucie	F	?	1 wk	Thin	1 mth	Yombe	9¾ yrs	5.7.00	10 yrs	11¾ yrs	1¾yrs	Alive and well
Louzolo	M	Mayombe	Few mths	Thin and infected wounds	18 mths	None	None	17.9.00	18 mths	3¾ yrs	2¼ yrs	Alive and well. Taken direct to the Triangle and reintroduced into a group. No collar
Emilie	F	Kouilou	3 mths	Poor – high parasite load and malnourished	1 yr	Yvette and nursery	6½ yrs	4.7.01	7½ yrs	8 yrs	6 mths	Alive and well
Tessie	F	Kouilou	6 mths	Fair	2-3 yrs	Yvette and nursery	8 yrs	4.7.01	10½ yrs	11 yrs	6 mths	Alive and well
Bateko	M	Kouilou	4 mths	Fair	2 yrs	Yvette and nursery	7 yrs	9.7.01	9 yrs	9½ yrs	6 mths	Alive and well. Aggressive to observers pre-release
Mfoubou	F	Mfoubou (Kouilou)	Few days	Poor – several gunshot wounds on hands and feet	3 mths	Yvette and nursery	8 yrs	9.7.01	8¼ yrs	8¾ yrs	6 mths	Alive and well
Makabana	F	Makabana (Niari)	3 mths	Poor- dehydrated, no teeth and stayed in a foetal position for 1 wk	1 yr	Yvette and nursery	7½ yrs	15.7.01	8½ yrs	9 yrs	6 mths	Alive and well. Pregnant on release. Gave birth to female infant 28.11.01 – infant died a few days after being born

Name	Sex	Origin	Time in captivity (pre-HELP)	Condition upon arrival/early history	Age at arrival	Island location	Time at HELP pre-release	Date of release	Age at release	Present age (Jan 2002)	Time post-release (Jan 2002)	Present status and miscellaneous comments
Dimonika	F	Kouilou	Few days	Good	1 yr	Yvette and nursery	6¼ yrs	15.7.01	7¼ yrs	7¾ yrs	6 mths	Alive and well
Karine	F	Kouilou	Few days	?	5-6 mths	Yvette and nursery	6¼ yrs	15.7.01	6¾ yrs	7¼ yrs	6 mths	Alive and well
Derek	M	Kouilou	2 mths	?	7 mths	Yvette and nursery	6¼ yrs	20.7.01	6¾ yrs	7¼ yrs	6 mths	Alive and well
Kouilou	F	Kouilou	Few days	Poor – no hair	2 yrs	Yvette and nursery	7¾ yrs	13.9.01	9¾ yrs	10 yrs	3-4 mths	Alive and well
Cheyenne	F	Kouilou	3 mths	Poor – very thin	1 yr	Yvette and nursery	6½ yrs	13.9.01	7½ yrs	7¾ yrs	3-4 mths	Alive and well
Bilinga	M	Bilinga (Kouilou)	Few days	Poor – very little hair and dehydrated	4-5 mths	Yvette and nursery	7½ yrs	5.11.01	8 yrs	8¼ yrs	2 mths	Alive and well. Bilinga was originally reintroduced with Derek on 20.7.01. He was taken back to the island to accompany Sibiti who was apparently distressed at being alone and difficult to capture
Sibiti	F	Sibiti (Lekoumou)	Few days	Good	2 mths	Yvette and nursery	10½ yrs	5.11.01	10¾ yrs	11 yrs	2 mths	Difficult to capture from island. Status unknown: disappeared 2nd day post-release
Yombe	M	Mayombe (Kouilou)	15 days	Chronic leg infection led to amputation from knee joint down	3½ yrs	Yombe	-	-	-	15¾ yrs	-	Permanent resident on Yombe island. Dominant male. Not considered suitable candidate for reintroduction due to age, physical handicap and temperament
Yoko	F	Kouilou	5 yrs	Good	5-6 yrs	Yombe	-	-	-	15¾ yrs	-	Permanent resident on Yombe island. Dominant female. Not considered suitable candidate for reintroduction due to age and temperament
Younsala	F	Yombe Island	Born on island	?	Born on island	Yombe	-	-	-	5 mths	-	Born 4.11.01 to Yoko. Father Yombe

Name	Sex	Origin	Time in captivity (pre-HELP)	Condition upon arrival/early history	Age at arrival	Island location	Time at HELP pre-release	Date of release	Age at release	Present age (Jan 2002)	Time post-release (Jan 2002)	Present status and miscellaneous comments
🟪 **Charlotte**	F	Kouilou	4-5 yrs	Handicapped leg Kept in bar and Brazzville Zoo	5 yrs	Yombe	-	-	-	18 yrs	-	Permanent resident on Yombe island. Not considered suitable candidate for reintroduction due to physical handicap
🟪 **Micky**	M	Brazzaville	2yrs	?	2 yrs	Yombe	-	-	-	13½ yrs		Permanent resident on Yombe island. Not considered suitable candidate for reintroduction due to temperament. Given a vasectomy in 1999
🟦 **Olga**	F	Kouilou	15 days	Wire around lumber region	5-6 mths	Yombe	-	-	-	14 yrs		Gave birth to male infant 1.3.99. Attempts to capture for reintroduction have so far failed
🟦 **Oyo**	M	Yombe Island	Born on island	?	Born on island	Yombe	-	-	-	2 yrs		Born 1.3.99 to Olga. Father either Chinois, David, Koutou or Yombe
🟦 **Emmanu-elle**	F	Kouliou	1 mth	Very thin	4 yrs	Yombe	-	-	-	15½ yrs		Attempts to capture for reintroduction have so far failed
🟦 **Ewo**	M	Yombe Island	Born on island	?	Born on island	Yombe	-	-	-	2 yrs		Born 12.5.99 to Emmanuelle. Father either Chinois, David, Koutou or Yombe
🟪 **Pepere**	M	?	8-9 yrs	Good physical health. From Pointe-Noire Zoo	9 yrs	Pepere	-	-	-	19 yrs		Permanent resident on Pepere island. Not considered suitable candidate for reintroduction
🟪 **Gina**	F	?	13 yrs +	Good physical health. From Pointe-Noire Zoo	12 yrs	Pepere	-	-	-	22 yrs		Permanent resident on Pepere island. Not considered suitable candidate for reintroduction
🟪 **Banane**	M	?	20 yrs +	Good physical health. Kept in a hotel and then Brazzaville Zoo	20 yrs	Pepere	-	-	-	24½ yrs		Permanent resident on Pepere island. Not considered suitable candidate for reintroduction

Notes: F = female, M = male; ? = not known, - not applicable; WC = wild chimpanzees; Origin = area thought to be from originally; yrs =years, mths = months. Unless otherwise stated, the chimpanzees were released wearing radio collars.

The following colour codes represent present status:

🟩	Released: alive and well	🟦	On island: candidate for release
🟨	Released: status unknown	🟪	On island: permanent resident
🟥	Released: dead		

history is important, as it will impact on physical, behavioural and psychological suitability for reintroduction and influence survivorship. The IUCN Guidelines for Nonhuman Primate Re-introductions (2002) recommend that animals are assessed for any behavioural abnormalities that may make them unsuitable for release (Figure 4.1, p.68, question 6). Despite varying backgrounds all the chimpanzees on Yombe and Yvette Island were found to be in good physical condition (even those with physical handicaps), and psychologically and behaviourally well adapted. They were able to harvest some wild foods, build night nests and the majority spent most of their time in a cohesive group. The assessment concluded that these two groups (with some exceptions see Table 4.1) could not have been better prepared. The chimpanzees on Pepere Island had spent many years in a zoo and were judged to be less well balanced than the younger chimpanzees arriving at the HELP sanctuary that had benefited from a human surrogate mother during their early years. They had never been seen building nests or eating wild foods and hence were not judged to be suitable candidates for reintroduction.

The IUCN guidelines (1995, 1998) recommend that there needs to be appropriate health (free from infectious or contagious pathogens and parasites) and genetic screening of stock before release and that any vaccinations should be administered during preparation stages to allow sufficient time for the development of required immunity. The recent guidelines specific to primate reintroduction are much more detailed in their recommendations for quarantine and veterinary requirements. In May 1992 and April 1996, all the chimpanzees held at the HELP sanctuary were physically examined and screened for a variety of diseases (Table 4.2) (Tutin, et al., 2001). Each chimpanzee regardless of whether they were destined for reintroduction in the immediate future, at a later date or not at all, underwent routine monitoring and pre-release screening (Table 4.2). Those destined for reintroduction underwent a third phase before capture and immediately pre-release (Table 4.2). Furthermore, to facilitate post-release monitoring, radio collars were fitted on all chimpanzees immediately prior to release unless otherwise stated. No precise post-release veterinary protocol was established to describe if and when medical intervention should or should not occur. However, if medical assistance was necessary to maintain the health of the chimpanzees and their survival then intervention was deemed acceptable.

Identification of animal origin is important to avoid genetic pollution of subspecies (IUCN, 1998). The majority of the chimpanzees are thought to have originated from forests in the Kouilou Department, the administrative district that includes the Conkouati-Douli National Reserve. Furthermore, genetic analyses of hair samples have revealed that none were related (Goossens, Funk, Vidal, Latour, Jamart, Ancrenaz, Wickings, Tutin and Bruford, in press).

Table 4.2 Summary of veterinary procedures prior to and during the reintroduction process

Routine monitoring	**Pre-release screening (May 1992 and April 1996)**	**Release preparation**
• Assess body condition • Dental formula • Weight and measurements • Clinical examination • Examination of stool for intestinal parasites • Intra-dermal tuberculin test • Behavioural and psychological assessments	**Routine monitoring plus:** • Hematological and blood chemistry analysis • Serological screening for retroviruses, filoviruses, Hepatitis A and B, blood parasites • Hair samples for genetic analysis and individual identification (since January 1999) Vaccination against polio and tetanus	**Pre-release:** • De-worming • Behavioural assessments **At capture immediate pre-release:** Routine monitoring plus: • Repeat serological screening • Booster vaccinations if needed • Injection of vitamins and antibiotics as preventative measure against stress-related vulnerability to infection • Measured and weighed (Plate 4.1) • Fitting of radio collar (Plate 4.2)

Plate 4.1 Dr M. Ancrenaz and K. Farmer measuring a chimpanzee

Plate 4.2 Dr J. Paredes adjusting a radio collar

4.2.2 Identifying a release site

A release can only be contemplated if a suitable site is available. To be suitable, the site must be able to provide sufficient resources for the released individuals without negatively impinging on the requirements of species already present either by depletion or over exploitation of key resources. Additionally, the site must offer adequate protection from threats such as logging and hunting, and not expose the released chimpanzees to situations of conflict with humans by being located to close to villages and plantations (Tutin et al., 2001). Previous attempts to release chimpanzees (see Chapter 1) and densities of wild chimpanzee communities were taken into account when a site for the reintroduction was being sought. It was concluded that an area of approximately 50 hectares per chimpanzee (for a maximum population density of two individuals per square kilometre) of suitable habitat (botanically diverse forest) containing no wild chimpanzees was needed (Tutin, 1994). Even the largest of the islands at the sanctuary (Yombe Island) that had an approximate area of 50 hectares was found to be too small to allow nutritional independence for even a small group of chimpanzees, as much of it was mangrove forest and provided no food. There were no larger islands in the reserve, and although forest blocks close to villages in the area may have been devoid of wild chimpanzees, they were not considered suitable release sites due to the conflict that may arise if crop raiding occurred and the subsequent risk of hunting. Analyses of vegetation maps of the Conkouati-Douli National Park (Doumenge, 1992) guided selection of two potential release sites. The eastern Tchibinda forest block and the Triangle both appeared promising based on ecological (mosaic of vegetation types) and practical (relative ease of access, absence of villages) criteria. Ground surveys were made of each site and data were collected on vegetation and particular attention was paid to the presence and absence of plant species that are known to provide food for chimpanzees. Signs of wild chimpanzees were noted (nests, trail, vocalisations), other large mammals (nests, prints, faeces, vocalisations), and of human activity (villages, hunting camps, plantations, paths, felled trees, snares, cartridge cases) and supplemented by interviews with residents of neighbouring villages. The Triangle was considered the better release site in comparison to the eastern Tchibinda forest block due to its greater size, diversity of plant species, and distinct geographical boundaries. Descriptions and results from the Triangle survey that led to this decision are as follows.

The Triangle is water bound on all sides but natural bridges (e.g., crossing canopy, fallen trees) provide access to this area to and from the park for some animal species. It was hoped that these natural boundaries would be an asset, as they would allow clear identification of the site and patrolling to prevent illegal use. Additionally, it was hoped that the rivers may discourage the chimpanzees from dispersing immediately post-release, and the fringe of inhospitable swamp forest discourage penetration by people. Elsewhere in the Triangle there were few signs of human activity, and surveys revealed a diversity of mammal tracks indicating the health of the ecosystem in that area. The majority of the Triangle was composed of wet forest types due to the high water table. Normally such a wet environment would not make this site an ideal habitat due to the species normal aversion to water. However, as Chapter 3 (p.60) highlighted, the chimpanzees from the HELP islands have had extensive contact with both water and wet forest types, and do not show the same hydrophobia as their wild counterparts. Wild chimpanzees are known to have an aversion to water. They have been found to cross even shallow streams on bridges of fallen or standing trees (Goodall, 1968; Tutin, Fernandez, Rogers, Williamson and McGrew, 1991) and do not forage in marshes or swamps unlike their cousins the lowland gorilla (Parnell, 2001). However, due to the natural bridges, the river barriers had not kept wild chimpanzees out of the area; both chimpanzees and gorillas used the area although neither were seen directly - only their nests. The density of wild chimpanzees were calculated from nest counts along transect lines; local population density was estimated at 0.17-0.33 individuals/km^2, equivalent to an average of three to seven wild chimpanzees using the site. As a comparison Teleki (1989) found that wild chimpanzee densities range from a low 0.1 to a high 6.8 chimpanzees per square kilometre, with an average of 0.3 in rain forest habitat. Wild chimpanzees (and many other mammals) were found to move between the Triangle and the extensive forest to the north using the natural bridges. The presence of wild chimpanzees complicates the reintroduction because as highlighted in Chapter 1 (p.1), wild resident chimpanzees are likely to react aggressively to strangers. The HELP project had already experienced such a reaction. In 1995 when a group of young chimpanzees were still kept on the mainland and taken for walks in a nearby forest area, a young female (approximately three years old) was snatched by a solitary wild adult male and never seen again (L. Penn, former volunteer, personal communication, 2002).

However, the survey concluded that particularities of the HELP/Conkouati situation would reduce the risk of highly aggressive encounters. Firstly, it was argued that hunting had undoubtedly reduced the population density of wild chimpanzees in the surrounding area. Secondly, if it was confirmed that wild chimpanzees used the area sporadically during the dry season, then the chimpanzees should be released at the end of this season to ensure that they settled into their new environment before any such encounters occurred. Thirdly, the female biased sex ratio of the HELP chimpanzees restricts the risk of highly aggressive encounters. In general, it is adult males or suckling infants that are targeted in inter-community attacks (White and Tutin, 2001) and at the time neither existed on either island. Young females are less likely to be severely attacked as transfer into a new community is a normal pattern during adolescence. There is an increased risk for the males. However, an adult female reintroduced in Senegal was severely attacked by three wild male chimpanzees and probably would not have survived without medical intervention (Marsden née Brewer, 1998). She was however, carrying a small infant and it was possible that the attack was an attempt at infanticide, a behaviour that has been reported from several studies of wild chimpanzees (Goodall 1977; Goodall, Bandora, Bergmann, Busse, Matama and Mpongo, 1979; Kawanaka, 1981). It was concluded that no release is without risks but that these could be substantially reduced with careful preparation. Additionally it was suggested that the release could benefit remaining wild populations by stopping poaching and incorporating new females into the wild population.

Botanical surveys conducted in the Triangle concluded that the area supported a wide diversity of plant species. Sita (1996) identified over 605 species of higher plants, 100 of which were known wild chimpanzee foods. The density of certain 'fallback' foods that sustain chimpanzee populations during periods of food scarcity were calculated in different habitat types by counts in quadrats. Densities of the sampled plants were found to be greater than those found at four wild chimpanzee study sites (Tutin et al., 2001).

4.3 The release process

Acceptance of the conclusions and recommendations by Dr Tutin and the IUCN by HELP ensured full financial support for the reintroduction project from GEF for three years (October 1996-June 1999). Consequently between November 1996 and 2001, 37 chimpanzees at HELP have been reintroduced during nine separate periods. Table 4.3 summarises the information from Table 4.1 and presents basic information on the number, sex and the name of chimpanzees released at each stage.

Table 4.3 Date, number, sex and name of chimpanzees reintroduced

Release number	Month/year	Number	Sex (M:F)	Name of chimpanzee (M:F)
1	November 1996	5	1:4	*Mekoutou*: Bougnoule, Yvette, Jeanette, Choupette
2	January 1997	2	0:2	Rosette, Fanny
3	November 1997	8	2:6	*Hinda, Dolisie*: Nyasha, Kakamoeka, Massabi, Cabinda, Mossendjo, Caline,
4	February 1999	5	2:3	*David, Koutou*: Agathe, Sophie, Valentine
5	June/July 2000	4	1:3	*Chinois*: Matalila, Perlette, Lucie
6	September 2000	1	1:0	*Louzolo*
7	July 2001	8	2:6	*Bateko, Derek*: Emilie, Tessie, Mfoubou, Makabana, Dimonika, Karine
8	September 2001	2	0:2	Kouilou, Cheyenne
9	November 2001	2	1:1	*Bilinga*: Sibiti

NB: Males identified by *italics*

This thesis focuses on the chimpanzees from Release 1-4 and Figures 4.1- 4.4 present an overview of the most salient points from these four releases; only these releases are discussed as detailed information was unavailable for Releases 5-9. Description of techniques employed for Release 1-3 were taken from two HELP reports (Paredes, 1997, 1998) whereas I directly observed the techniques employed for Release 4.

Figure 4. 1 Reintroduction process; chimpanzees released in November 1996

	RELEASE 1
ISLAND	**3 from Yvette and 2 from Yombe Island**
SEX	**4♀1♂**
MEAN TIME ON ISLAND (training environment)	**5¾ years**
RELEASE SITE	**Grid location B0 – (see Figure 4.5)**
MEAN AGE AT RELEASE	**8¾ years**
RADIO COLLARS	**3 collared (2 ♀ 1 ♂)**
CAPTURE/RELEASE/ ACCLIMATISATION	**4 captured on first day; 3 released together same day, 1 released following day and taken to other 3 chimpanzees. 5th chimpanzee caught two days later, released same day and taken to other 4 already released**
INITIAL REACTION POST-RELEASE	**2 climbed a tree and made all movements above ground for the first day. 2 ran away and lost for 4 hours (1 found outside of Triangle). 1 stayed on ground and did not move for 4 hours**
SIGNIFICANT EVENTS POST-RELEASE	**1 serious attack (♂) by WC that required vital treatment and provisioning for 1 month. Subsequently there were 3 less serious encounter's (2♀ 1♂) that required minor treatment. 1 serious parasitic infection (♀) that required removal from forest for 1 week and vital treatment. 1 birth of male infant in October 2001, father identified as male in release group**
PRESENT STATUS (as of March 2002)	**All alive and well**

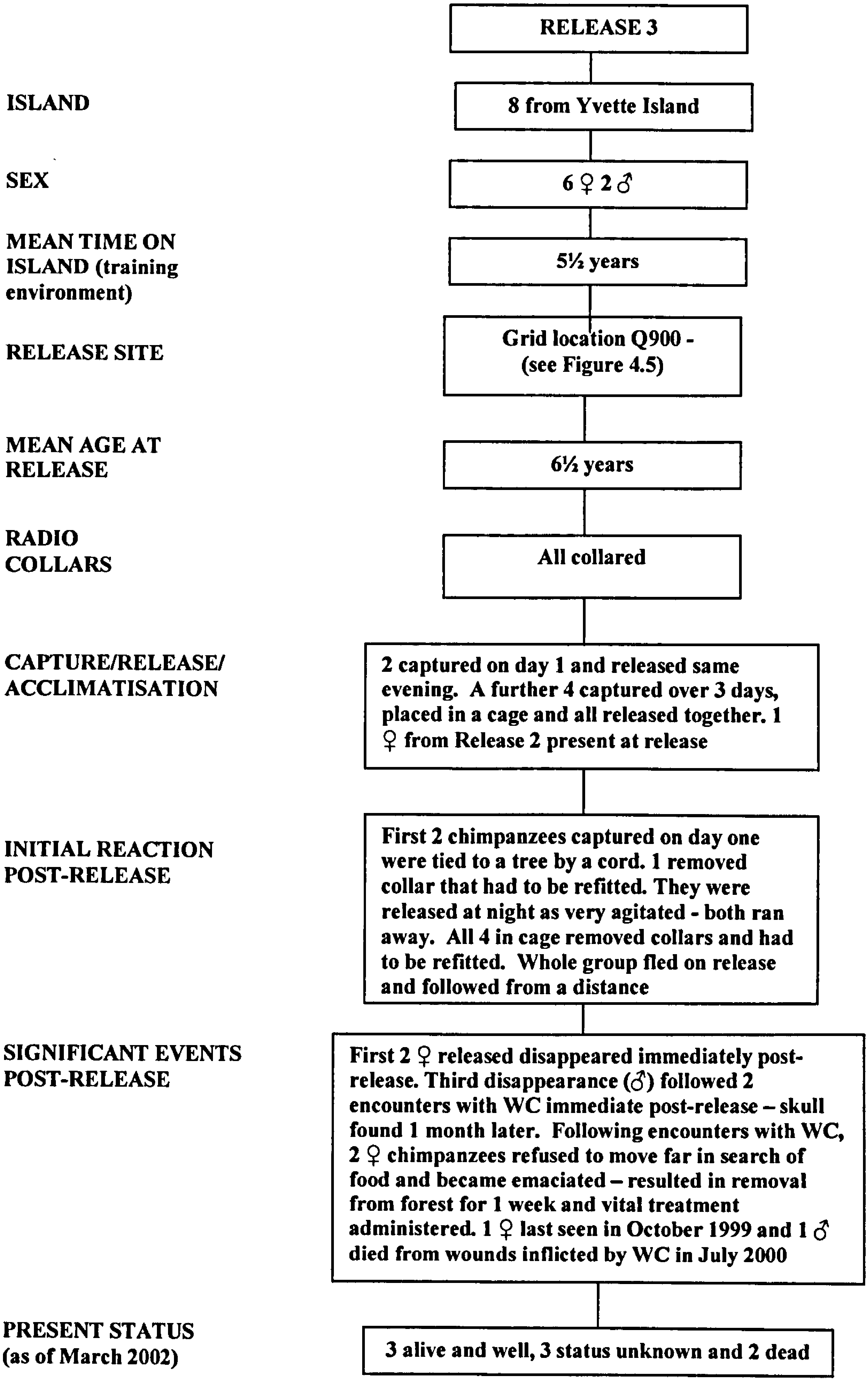
Key: WC = wild chimpanzees

Figure 4. 2 Reintroduction process; chimpanzees released in January 1997

	RELEASE 2
ISLAND	2 from Yvette Island
SEX	2 ♀
MEAN TIME ON ISLAND (training environment)	5¾ years
RELEASE SITE	Grid location 5L200 – (see Figure 4.5)
MEAN AGE AT RELEASE	7½ years
RADIO COLLARS	Both collared
CAPTURE/RELEASE/ ACCLIMATISATION	Both captured and released on same day. Chimpanzees from Release 1 were present at release
INITIAL REACTION POST-RELEASE	Both ran away. 1 relocated 500m away and led back to group. 1 continued to run away whenever an observer was seen, radio signal was lost and she was not seen again after the first day
SIGNIFICANT EVENTS POST-RELEASE	2 minor attacks by WC to remaining ♀
PRESENT STATUS (as of March 2002)	1 alive and well, 1 status unknown

Key: WC = wild chimpanzees

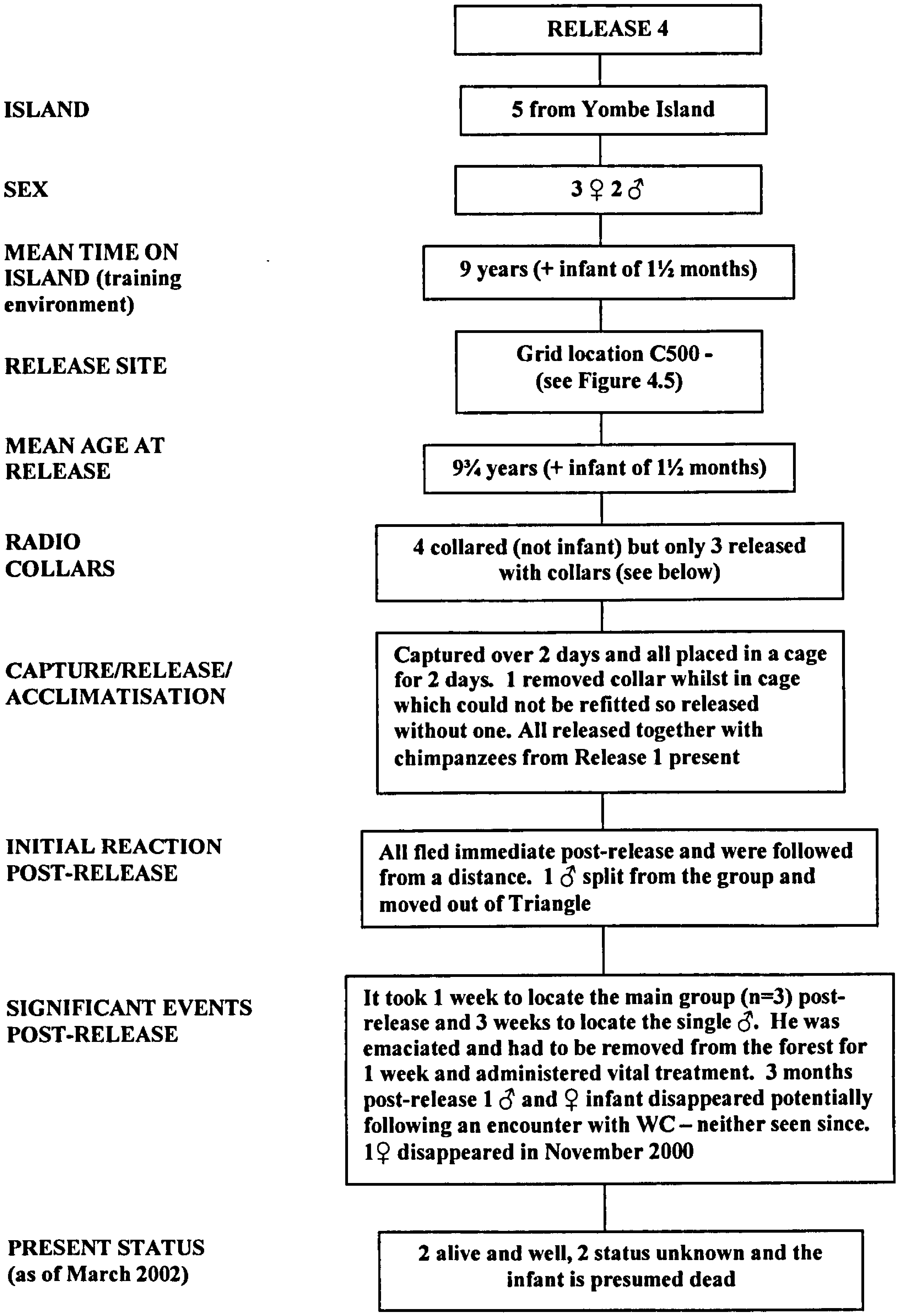
Figure 4. 3 Reintroduction process; chimpanzees released in November 1997



	RELEASE 3
ISLAND	8 from Yvette Island
SEX	6 ♀ 2 ♂
MEAN TIME ON ISLAND (training environment)	5½ years
RELEASE SITE	Grid location Q900 - (see Figure 4.5)
MEAN AGE AT RELEASE	6½ years
RADIO COLLARS	All collared
CAPTURE/RELEASE/ ACCLIMATISATION	2 captured on day 1 and released same evening. A further 4 captured over 3 days, placed in a cage and all released together. 1 ♀ from Release 2 present at release
INITIAL REACTION POST-RELEASE	First 2 chimpanzees captured on day one were tied to a tree by a cord. 1 removed collar that had to be refitted. They were released at night as very agitated - both ran away. All 4 in cage removed collars and had to be refitted. Whole group fled on release and followed from a distance
SIGNIFICANT EVENTS POST-RELEASE	First 2 ♀ released disappeared immediately post-release. Third disappearance (♂) followed 2 encounters with WC immediate post-release – skull found 1 month later. Following encounters with WC, 2 ♀ chimpanzees refused to move far in search of food and became emaciated – resulted in removal from forest for 1 week and vital treatment administered. 1 ♀ last seen in October 1999 and 1 ♂ died from wounds inflicted by WC in July 2000
PRESENT STATUS (as of March 2002)	3 alive and well, 3 status unknown and 2 dead

Key: WC = wild chimpanzees

Figure 4. 4 Reintroduction process; chimpanzees released in February 1999



	RELEASE 4
ISLAND	5 from Yombe Island
SEX	3♀2♂
MEAN TIME ON ISLAND (training environment)	9 years (+ infant of 1½ months)
RELEASE SITE	Grid location C500 - (see Figure 4.5)
MEAN AGE AT RELEASE	9¾ years (+ infant of 1½ months)
RADIO COLLARS	4 collared (not infant) but only 3 released with collars (see below)
CAPTURE/RELEASE/ ACCLIMATISATION	Captured over 2 days and all placed in a cage for 2 days. 1 removed collar whilst in cage which could not be refitted so released without one. All released together with chimpanzees from Release 1 present
INITIAL REACTION POST-RELEASE	All fled immediate post-release and were followed from a distance. 1 ♂ split from the group and moved out of Triangle
SIGNIFICANT EVENTS POST-RELEASE	It took 1 week to locate the main group (n=3) post-release and 3 weeks to locate the single ♂. He was emaciated and had to be removed from the forest for 1 week and administered vital treatment. 3 months post-release 1 ♂ and ♀ infant disappeared potentially following an encounter with WC – neither seen since. 1♀ disappeared in November 2000
PRESENT STATUS (as of March 2002)	2 alive and well, 2 status unknown and the infant is presumed dead

Key: WC = wild chimpanzees

Chapter 1 outlined some of the major points in the reintroduction process. The following section discusses these in relation to this specific project. The HELP project has experienced both successes and failures in its attempt to reintroduce chimpanzees. One of the main problems that confronted the project was the initial fear reaction of the chimpanzees to run away after being released. Of the chimpanzees that have either disappeared or died, half ran away immediately after being reintroduced. It is possible that the chimpanzees were trying to locate a familiar landmark. However, there may be something about the procedure itself that is stressful. The following issues are cumulatively highly relevant in the reintroduction process and for alleviating immediate post-release stress.

The pre-release training islands

Brewer (1978) and Carter (1981) actively taught their chimpanzees how to build nests and what foods to eat, and the young female Bahati was shown by researchers how to remove snares (Treves and Naughton-Treves, 1997). Hannah and McGrew (1991) reviewed ape release projects and concluded that pre-release training and post-release support improved chances of survival. Recent studies on the golden lion tamarin suggest that it is post-release support and not pre-release training that is the key to successful reintroduction (Beck et al., in press). However, some kind of training is thought to be necessary for animals, especially mammals and birds, to survive since many critical behaviours are learnt (Box, 1991b). The IUCN Guidelines for Nonhuman Primate Re-introductions (2002) recommends that prior to release, primates should be given the opportunity to acquire the necessary skills to enable survival in the wild, and be provided with training environments such as islands or semi-wild enclosures to test adaptation skills to the natural environment. Chapter 2 highlighted that the three sanctuaries focusing on reintroduction have used forested islands or excursions into nearby forests to practise skills necessary to survive in the natural environment. In the present study the islands provided micro-habitats of natural vegetation in which the chimpanzees were able to forage, build nests and live in groups with very little human interference for a mean seven years pre-release. Data chapters 6, 7, 8 and 9 in conjunction with survivorship detailed later in this chapter indicate that the islands did provide an environment that facilitated adaptation post-release although no pre-release data on chimpanzees not exposed to the pre-release islands exist to substantiate this.

Selection of candidates

By comparing the background of chimpanzees that have survived, disappeared or died it may be possible to highlight important points to be considered for future reintroduction projects. Table 4.4 presents the mean amount of time spent in captivity prior to arrival at the HELP sanctuary, at the HELP sanctuary, age on arrival to the sanctuary and age at release for the study group (Release 1-4). The details of Valentine have been excluded from Table 4.4 as she was born on-site and released with her mother when newly born but her assumed death (Figure 4.4, p.84) indicates that females with suckling young do not make ideal candidates for reintroduction. Table 4.5 presents comparable descriptive statistics for all the chimpanzees that have been reintroduced by HELP (except Louzolo, see Table 4.1, p.70). The survivors were, on average, older when captured from the wild, had spent longer in captivity (pre-HELP) than chimpanzees that have died or whose status remains unknown. They were older at capture, on arrival to HELP, and at release (Table 4.4). This supports the recommendation by Hannah and McGrew (1991) that chimpanzees captured late from the wild make suitable candidates for reintroduction (Chapter 1, p.21). Also when all the chimpanzees reintroduced were compared, those that had died had spent less time at the sanctuary than chimpanzees that had either survived or disappeared (Table 4.5). However, these small differences may simply reflect the large difference in sample size between categories and some of the chimpanzees were only released at the end of 2001. Once all the chimpanzees have been released for one year it will be interesting to reassess survivorship and review these factors once again.

Table 4.4 Mean (±SD) age at capture from the wild, time in captivity (pre-HELP), time at HELP, age at arrival and release in relation to status of reintroduced chimpanzees (study group only)

Status	Age at capture (yrs/mths)		Time in captivity pre-HELP (yrs/mths)		Age at arrival to HELP (yrs/mths)		Time spent at HELP (yrs/mths)		Age at release (yrs/mths)	
	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n
Alive	1.2 (0.9)	9	0.9 (1.6)	10	2.1 (1.7)	11	6.4 (1.6)	11	8.4 (1.4)	11
Unknown	0.8 (0.5)	2	0.5 (0.7)	6	1.3 (0.6)	6	6.6 (2.2)	6	7.8 (2.0)	6
Dead	0.8 (0.6)	6	0.4 (0.3)	2	0.9 (0.1)	2	6.0 (0.1)	2	6.9 (0)	2

NB: Mean and SD are shown in years/months. The differences in sample size (n) are due to not all information being available for each chimpanzee. The infants Valentine and Louzolo are not included in these figures. Age at capture was calculated from estimated age at arrival minus time in captivity pre-HELP.

Table 4.5 Mean (±SD) age at capture from the wild, time in captivity (pre-HELP), time at HELP, age at arrival and release in relation to status of reintroduced chimpanzees (all reintroduced chimpanzees)

Status	Age at capture (yrs/mths)		Time in captivity pre-HELP (yrs/mths)		Age at arrival to HELP (yrs/mths)		Time spent at HELP (yrs/mths)		Age at release (yrs/mths)	
	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n
Alive	1 (0.8)	24	0.7 (1.2)	16	1.8 (1.6)	27	7.3 (1.9)	26	8.8 (1.6)	25
Unknown	0.5 (0.5)	2	0.6 (0.7)	6	1.1 (0.7)	7	7.1 (2.5)	7	8.2 (2.2)	7
Dead	0.7 (0.6)	7	0.4 (0.3)	2	0.9 (0.1)	2	6.0 (0.1)	2	7.0 (0)	2

NB: Mean and SD are shown in years/months. The differences in sample size (n) are due to not all information being available for each chimpanzee. The infants Valentine and Louzolo are not included in these figures. Age at capture was calculated from estimated age at arrival minus time in captivity pre-HELP.

The present project knew the risks of releasing males into areas where wild conspecifics lived; in wild communities it is generally males and infants that are targeted in inter-community attacks. As mentioned earlier (p.78) a young female chimpanzee (3 years old) was snatched by a wild adult male chimpanzee during a forest walk at the Conkouati mainland sanctuary and never seen again. However, it was hoped that due to the small number of males, their near normal behavioural repertoire, together with the strategic planning of when and where to release, that risks would be kept to a minimum. As expected, the reintroduced male chimpanzees have received more serious wounds inflicted by wild chimpanzees than females. This prompted daily nest to nest follows regardless of time post-release on all males. Normally the project policy is that new reintroduced chimpanzees are followed from nest to nest daily for the first year but then subsequently as and when possible dependent upon staff availability. However, it was a reintroduced female chimpanzee that fared worse and required sutures following a recent interaction with wild conspecifics and not the two males that were also present (HELP-INFO, April, 2002). Whether projects should reintroduce males into areas where wild chimpanzees cohabit can only be judged on an individual basis, but regardless, mortality rates should approximate and not exceed those of wild conspecifics (recommended by the IUCN Guidelines for Nonhuman Primate Re-introductions, 2002). Studies on wild populations suggest that males experience higher mortality than females throughout their life (Hill, Boesch, Goodall, Pusey, Williams and Wrangham, 2001). It was by pure chance and not design that the HELP sanctuary had a significantly higher number of females than males. At Tchimpounga (a Jane Goodall Institute chimpanzee sanctuary also in the Republic of Congo) there are more males than females, making the decision of reintroduction difficult. The increasing number and severity of attacks directed towards the reintroduced males has led HELP to take the recent decision to remove all the reintroduced males from the release site and return them to the relative safety of the island sanctuary (C. Vidal, HELP veterinarian, personal communication, 2002).

Twenty-two percent of reintroduced females have disappeared in comparison to 20% of males (Table 4.6) however, the HELP project is hopeful that the females may have survived and joined with groups of wild chimpanzees. Generally, with one exception (outlined above) encounters between females and wild groups have been more positive and less aggressive in comparison to the males. It is thought (although not confirmed) that some females have periodically left the reintroduced group, sometimes for several weeks and months at a time, may move with wild groups particularly during periods of oestrus. For example, one female (Bougnoule) was absent for six months before returning to her 'known' group. Immediately prior to her disappearance she was observed pursuing a group of wild chimpanzees. However, it is the policy of the project not to pursue the reintroduced chimpanzees if they are attempting to interact with wild conspecifics as this would likely damage the interaction. Consequently it is not known if the reintroduced chimpanzees do remain with wild conspecifics or not. The wild chimpanzees in the area are not habituated and if they see people, they instantly flee. In contrast to the females, the outlook for males if they encounter wild male chimpanzees is bleak (see section 10.3, p.343-346, for further discussion on males versus females as suitable candidates for reintroduction).

Table 4.6 Status of female and male reintroduced chimpanzees

	Females		Males	
Status	**%**	**n**	**%**	**n**
Alive	74	20	70	7
Dead	4	1	10	1
Unknown	22	6	20	2

Previous attempts to reintroduce chimpanzees have emphasised the importance of conspecifics in the process. Marsden (née Brewer, 1998) found that releasing chimpanzees together meant that they could offer one another support rather than turning to human caretakers for emotional support. Hannah and McGrew (1991) also found that conspecifics subsequently released could benefit from the knowledge of others previously reintroduced. Decisions were made pre-release whom to release together from known associations pre-release so that the chimpanzees could provide support for one another post-release. The one exception to this was in 1996 when two chimpanzees from Yombe Island and three chimpanzees from Yvette Island were released together as a consequence of failed attempts to capture more individuals from Yombe Island (see following section). The present project has always released chimpanzees as groups (except in the unusual case of Louzolo, see Table 4.1, p.70) although group size has varied and has been primarily dictated by who could be captured.

Capture

The inability to access Yombe Island has proved to be a significant problem when attempting to capture chimpanzees. For example, the first reintroduction in 1996 was aimed at releasing chimpanzees from Yombe Island as they were older than chimpanzees on Yvette Island. However, it was only possible to catch two individuals; it was not possible to enter this island due to the potentially aggressive nature of some chimpanzees. Attention was then shifted to Yvette Island where a further three chimpanzees were captured comparatively easily. Difficulties were also experienced in 1999 when only four chimpanzees were captured from Yombe Island when eight had been targeted. For several weeks prior to capture, observers had been encouraging the chimpanzees into the mangrove area at feeding time (areas where capture would be facilitated) and engaged in syringe play. Syringes (minus needles) were taken to the island so that the chimpanzees would become familiar with them and not produce a fearful reaction (Plate 4.3). Syringes were filled with water and resembling a real injection, water was squirted onto areas such as the outer thigh where the actual injection might be administered. The chimpanzees were initially fearful but soon appeared to view the syringes as objects of play (personal observation). However, due to a large number of unknown personnel and equipment (a film company and a team of veterinarians) (Plate 4.4) coinciding at a time when some females were in oestrus, resulted in some males becoming aggressive and protective, and all chimpanzees reticent to show themselves.

Over the past few years there have been several attempts to capture Olga and Emmanuelle from Yombe Island as they were both judged suitable candidates for reintroduction (see

Table 4.1, p.73). They have become increasing shy with age and both now have suckling infants which makes their capture more difficult and their suitability for release less likely.

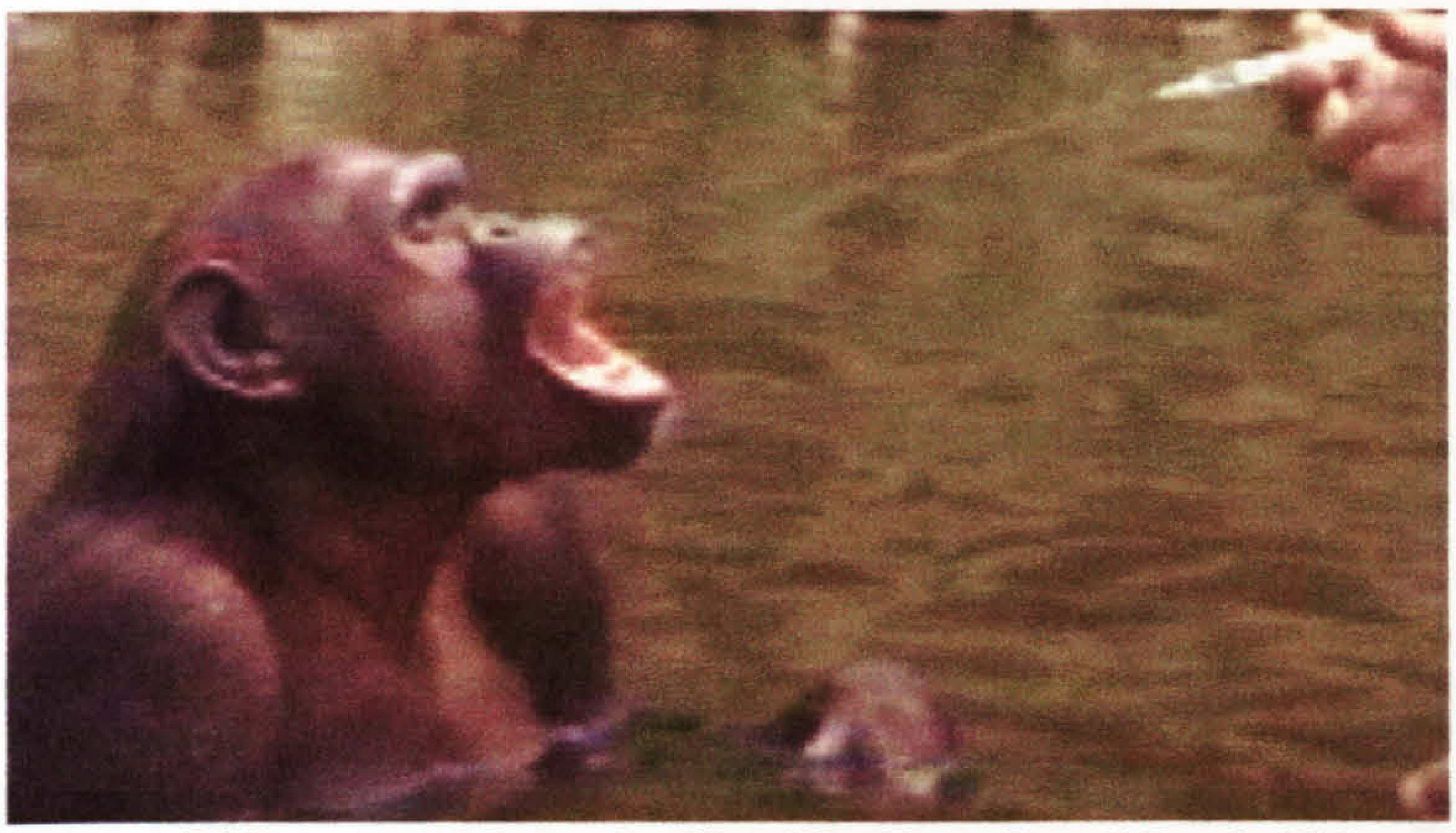


Plate 4.3 Familiarising Charlotte with a syringe

Source: Still captured from the film 'Nes Pour Etre Libre', Gideon (2000)

Plate 4.4 Film crew at Conkouati

Although these problems are specific to the HELP project they do suggest that capture and release should be performed at an age when access to pre-release holding areas and a good relationship with caretakers are possible. As chimpanzees become older and potentially aggressive it becomes increasingly difficult to maintain a close relationship (personal observation). A younger chimpanzee may be more likely to turn to their caretaker for reassurance rather than run away. However, it is also important that the chimpanzees do not rely too heavily on caretakers for emotional support. The chimpanzees that reacted less fearfully to the presence of observers post-release were those reintroduced in 1996. At the time access to the pre-release islands was still possible. Although chimpanzees were also taken from Yvette Island in November 1997, political instability in the Republic of Congo during 1997 meant that the amount of contact that these chimpanzees received was substantially reduced. In 1999, the chimpanzees from Yombe Island had very little contact with caretakers pre-release due to the inaccessibility of the island and they all fled post-release. If access onto the island is possible (or the relationship with caretakers positive) this in turn facilitates capture, which can make the whole procedure less stressful. The capture process needs to be as stress free as possible as this will influence the immediate post-release behaviour of the chimpanzees. Capture can be further facilitated by familiar staff and keeping unknown persons to a minimum.

Anaesthesia and radio collars

Radio collars were used to facilitate post-release monitoring. They have been used on a variety of vertebrate species and proved invaluable in the Hannah and McGrew (1991) study. They found that survival rate increased from 50% when not employed to 95% when the whole group was collared. The present project has also found that radio collars were extremely important and particularly so during the immediate post-release period when the chimpanzees were scared and more likely to flee. Of the seven status unknown cases, three had removed their collars, two had collars that were not working and one was not wearing a collar at the time of disappearance. This emphasises the importance of radio telemetry for post-release monitoring both in the short- and long-term. Beck et al. (in press) found that post-release monitoring was vital for detecting illnesses in golden lion tamarins. The inability to locate the chimpanzees would have resulted in a much higher mortality rate and all chimpanzees should be reintroduced wearing some kind of telemetric device. When it is not possible to get an animal to wear a collar, it may be prudent to have subcutaneous implants ready. For example, in the case of David whose head shape prevented him from wearing a collar, he was released without one and disappeared less than four months post-release. The use of microchips is presently being used in orang-utan reintroduction; a reader is placed over the skin and a specific code identifies the individual ape (G. Shapiro, Vice President of the Orangutan Foundation International, personal communication, 2001). However, it can not be used at a distance to locate apes or telemetrically to send physio-data, so it would (at the present) only allow identification of apes being held, anaesthetised, or found dead. However, the costs of these may be prohibitive as with radio collars. Only three out of five chimpanzees were fitted with collars in Release 1 as each collar cost approximately $US328.00.

The HELP project has found that the signal reception of telemetric devices can vary according to forest type and the animal height in the forest. For example in the primary forest it is possible to get a signal for up to one kilometre in comparison to the closed canopy of seasonally inundated forest which can sometimes be as low as 200m (Paredes, 1998). In the present study, collars used were breakaway collars. These were designed to be expandable if snagged, and after a period of time (approximately one year) the rubber splits, and leaves the animal collar-free. The collars were made with two pieces of rubber to be sufficiently strong for the chimpanzees not to break them, and generally they were. In Release 1 no problems were experienced with the radio collars and only one chimpanzee (Fanny) was able to remove the collar during Release 2. It is not known how she was able to do this but she was obviously frightened having fled the release site and ran away from the other chimpanzees immediately post-release. Perhaps the stress and consequent frequent pulling at the collar split the rubber tubing. Correct collar adjustment is important, the collar should be placed loosely enough so that it will not irritate the animal but not too loose so that it can be removed. Separation between neck and collar is a recommended 4½-5cm (Paredes, 1998) but this may vary slightly according to the age of chimpanzee.

The collars that were used in November 1997 were not the same model as used previously; they were built with only one piece of rubber and were not strong enough. This resulted in five of the eight chimpanzees being able to remove them whilst still in the release cage. The chimpanzees had to be re-anaesthetised (an additional stressor) and the collars modified on-site as there was no time to return them to the manufacturer (Telonics) in the USA. It is normally when the chimpanzees are rousing from anaesthesia that they remove the collar. This is probably due to a combination of stress, hallucinatory effects from some anaesthetics and an analgesic effect from the anaesthetic that may facilitate removal.

One further problem that was experienced with collars in 1997 was channel frequency. The channels were very close together and this resulted in the collars emitting signals of almost the same wavelength. This caused problems in distinguishing between signals for the different chimpanzees.

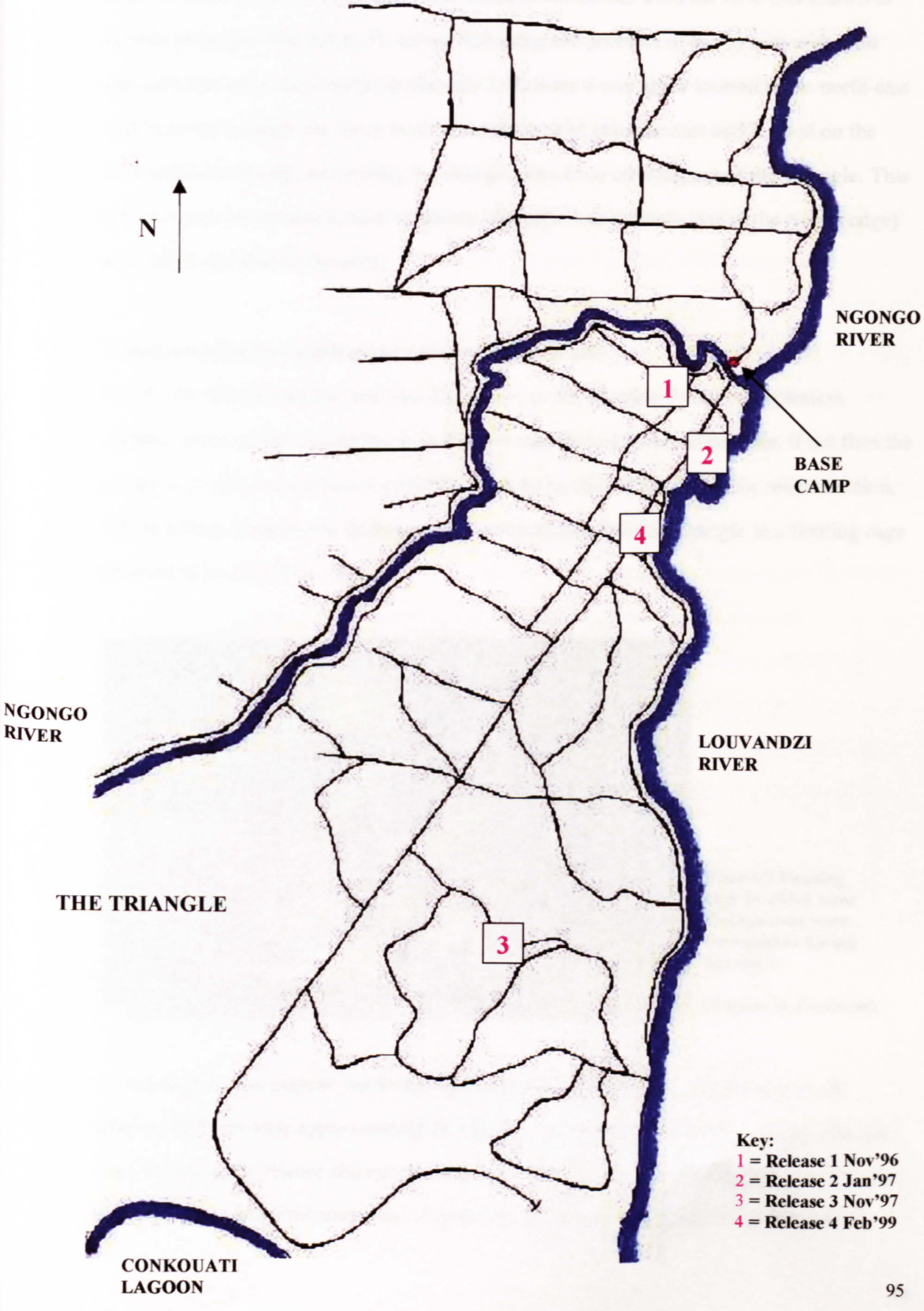
In the present study it has been possible with some chimpanzees to change old collars without using anaesthetic (Paredes, 1998). However, the expense of refurbishing or buying new collars and the practical implications of having to re-anaesthetise some animals (this will undoubtedly become more of an issue with older animals) will force HELP and other such projects to decide how long animals should be fitted with telemetric monitoring devices. Without such monitoring devices, the reintroduced chimpanzees would have to be located and followed in a similar way to wild habituated chimpanzees.

The release site

Earlier in this chapter it was highlighted how and why the Triangle was selected as a suitable site but Figure 4.5 indicates the exact location of each release within the Triangle (Release 1-4). The release point of the first group was in the north of the Triangle close to the Ngongo River. The Triangle base camp is near this point; 300m north-east on the other side of the river. The exact point of release was chosen because it was known to have a high density of plant species consumed by wild chimpanzees particularly so during November and December.

The second release was again located in the northern part of the Triangle but this time on the eastern edge (Louvandzi River side) due to the problem of chimpanzees moving out of the Triangle soon after release (Release 1) hindering post-release monitoring. The Louvandzi River is wider than the Ngongo River and it has no places where the chimpanzees can cross and leave the Triangle; along the western side there are many areas of crossing canopy and fallen tree trunks acting as natural bridges. There were also known plant species fruiting in the area at the time.

Figure 4.1 Specific sites of reintroduction within the Triangle



The site for the third reintroduction in the Triangle was situated in the primary forest (much further south than Release 1 and 2) easily accessible from the river and known to contain principal wild foods. However, following the problem of encounters with wild chimpanzees soon after release in Release 3, Release 4 was again located in the north-east region of the Triangle far away from the resident wild chimpanzees and located on the Louvandzi River edge preventing the chimpanzees from crossing out of the Triangle. This site was also chosen due to ease of access (the cage was located close to the river's edge) and edible ripe fruit in the area.

Transportation and holding procedure at release site

The IUCN (2002) decision tree (see Figure 4.1, p. 68, question 7) asks the question whether stock can be expeditiously and safely transported to the release site, if not then the advice is to either revise plans so that they can be or discontinue plans for reintroduction. The first four chimpanzees in Release 1 were transported to the Triangle in a floating cage attached to a boat (Plate 4.5).

Plate 4.5 Floating cage in which some chimpanzees were transported during Release 1

(Source: B. Goossens)

A veterinarian was present inside the cage with the chimpanzees. The journey up the Louvandzi River took approximately five hours. All chimpanzees were standing once the boat arrived at the release site except one, Jeanette, who became distressed during the trip and received a supplementary dose of anaesthesia. For other releases the chimpanzees were transported by boat fully anaesthetised but without a cage (sometimes requiring supplementary doses of anaesthetic). Minus the weight of the cage, the journey time was reduced from five to less than two hours. Therefore the quickest method of transportation that does not require heavy and lengthy sedation is recommended, concurring with IUCN recommendations.

The floating cage has been subsequently used as a place for recovery from anaesthesia and convalescence from illness/injury post-release. During Release 1 and 2 only one chimpanzee was held in a cage (floating cage) over night before being released the next day and this was because (as mentioned earlier) she became distressed in the floating cage, was re-anaesthetised and was not sufficiently awake to be released. The first two chimpanzees captured in Release 3 were tied to a tree by a piece of cord to prevent them from running away immediately upon waking. As a consequence of their obvious distress to being physically restrained in such a way, a cage was built in the forest for the remaining chimpanzees. Four of the chimpanzees in the cage had to be re-anaesthetised as they removed their collars and they all fled post-release. Likewise, chimpanzees reintroduced in 1999 were also placed in a cage, two removed their collars, and all fled immediately post-release. The cage built in 1999 had partitions to separate the chimpanzees until they recovered from the anaesthetic and was approximately 4.10m in length by 2.10m in width and 1.5m in height with one sliding exit door (55x52cm) (Plate 4.6).

Plate 4.6 Cage built for Release 4 in 1999

On average the chimpanzees spent a mean time of seven years on the pre-release islands. Some of these chimpanzees may have experienced constraint when very young but not for several years. The distress of being tied by a cord seems obvious but was employed to stop the chimpanzees from running away after recovering from the anaesthetic as no cage had been built at this point. There are no descriptions of the cage that was built in 1997 but in 1999 the cage was small, dark and weak in structure. Although the cage in 1999 may have been adequate as a place of recovery from anaesthetic for a brief period of time, the original aim was to keep the chimpanzees within this cage for several days. However, the design of the structure was wholly inadequate for such a function. Studies in captivity have shown that cage size is an important variable for the psychological well being of chimpanzees. Vertical space is very important to apes (National Research Council, 1998) and various studies have shown that following transfer to large enclosures where chimpanzees can see out, incidences of stereotypic behaviour reduce (Berkson, Mason and Saxon, 1963; Pfeiffer and Koebner, 1978; Clarke, June and Maple, 1982). To maintain chimpanzees for more than a brief period of time in between capture and reintroduction, the cage should be strong, provide sufficient space, means of escape from other chimpanzees (Koutou became aggressive towards the other chimpanzees in the release cage) and enable the chimpanzees to see out. This combined with the use of a long-acting tranquilliser may help to reduce stress. If a tranquilliser is used then all the chimpanzees should be fully recovered before the cage doors are opened; the reintroduced chimpanzees should be fully conscious and able to defend themselves in the event of a surprise encounter with previously reintroduced or wild chimpanzees.

The length of time that chimpanzees should be held in the release cage depends upon its function and this in turn dictates its design. If the cage is simply designed to allow chimpanzees to wake in safety from anaesthesia, then the length of stay in the cage should be short. However, if chimpanzees recover close to nightfall (e.g., the first two chimpanzees released in November 1997) then they should be held until the next day; following chimpanzees in the dark particularly during the immediate post-release period when they are scared and can move quickly is not recommended. If the function of the cage is one of acclimatisation to the forest then the stay should be longer. The decision to use either a soft or hard release strategy will be reflected in the type of holding facility and the length of time the animal remains within it. A soft release strategy was employed at PPG in the Republic of Congo. A large and stimulating cage was built for the gorillas to acclimatise to the new environment and they spent two months in the cage before the first guided forest walks began (Chapter 1, p.24-25). However, these gorillas were used accustomed to close contact with people and had already experienced guided forest walks by caretakers at the pre-release site. However, this project now advocates that gorillas are encouraged to live full-time in the forest as quickly as possible as this facilitates behavioural development and emotional independence from caretakers.

It is not possible to provide an exact measure of how much time should be spent acclimatising animals to a new site. There are many factors involved ranging from the origin (country, climate) of the animals and type of prior captive environment to relationship with caretakers and individual differences. Brewer (1978) worked with chimpanzees for two years at Abuko Nature Reserve in The Gambia before transferring them to Senegal. In contrast, chimpanzees that were moved from zoos and laboratories in Germany to Rubondo Island in Tanzania (Grzimek, 1971; Borner, 1985) were not provided with any period to acclimatise to the new environment. A period of acclimatisation may have helped these chimpanzees adjust to the extreme differences in environment, the personnel, and facilitate post-release monitoring which was prevented due to aggression (probably as a result of fear) exhibited by the chimpanzees. In the present project, the three chimpanzees in Release 1 that were awake upon arrival to the release site, and immediately released, reacted the least aversively post-release.

If the animals to be released are from the onset based at the reintroduction site then the potential stress of capture and transfer can be avoided. Gorillas at PPG Gabon (and also now in the Congo) are immediately taken to the release site following confiscation (or any other method of arrival) which negates any problems of capture, transfer and stress of adapting to a new environment. The cause of three gorilla deaths following transfer from Brazzaville Zoo to the Lesio-Louna release site was attributed to the stress of the move (D. Chronopoulos, former PPG Manager, personal communication, 2001).

Provisioning

The policy of the present project was not to provide post-release provisioning with the aim of breaking the association of humans as providers of food. It was hoped that the knowledge of edible plants acquired on the pre-release islands and initial help from observers guiding chimpanzees to areas of known edible species post-release would be sufficient for the chimpanzees to achieve nutritional independence. However, in some cases this was not sufficient, for example in the case of Massabi and Mossendjo (Release 3) and Koutou (Release 4) who were all found emaciated and in need of intravenous fluids and supplementary food. In all three cases the chimpanzees had fled into areas with little food soon after release. This was following interactions between Massabi and Mossendjo and wild chimpanzees who were subsequently too scared to move, and with Koutou, a case of running away due to fear (personal observation). This suggests that post-release provisioning may not be necessary except in extreme circumstances. However, to alleviate some of the immediate stress of release and furthermore to facilitate contact between chimpanzee and observer, some degree of initial provisioning viewed as post-release support may be beneficial, dependent upon the prior experience of animals released. Chimpanzees at Rubondo, Niokola Koba, VILAB and gorillas at PPG Gabon and Congo all received provisioning that was gradually reduced (see Table 1.2, p.15-18).

Post-release veterinary intervention

On several occasions veterinary intervention has been necessary and without it six chimpanzees; Mekoutou and Choupette (Release 1), Massabi and Mossendjo (Release 3) and Koutou (Release 4) would have undoubtedly died. This emphasises the importance of post-release support and monitoring in the reintroduction process.

Encounters with previously reintroduced chimpanzees post-release

Chimpanzees from Release 1 were encouraged to be present for Release 2 and likewise for Release 4. It was hoped that the more experienced individuals would act as guides for the newcomers as with the chimpanzees at VILAB (Hannah and McGrew, 1991) and Niokola-Koba (Brewer, 1978). In some cases this has caused conflict and may have contributed to the chimpanzees fleeing immediately post-release. For example Choupette (Release 1) reacted aggressively towards Fanny (Release 2). However, the chimpanzees did not know one another; Choupette was from Yombe Island and Fanny from Yvette Island. It may be prudent to avoid such contact immediately post-release in what is already a stressful situation.

To date there have been no serious or fatal cases of aggression directed from one reintroduced chimpanzee to another although intimidation and mild aggression has occurred within and between the sexes. This is in contrast to the two gorillas that died as a direct result of wounds inflicted by other reintroduced gorillas at PPG Congo. The two male gorillas that directed the attacks were blackbacks (aged 12 years) and the recipients, a male and a female both aged 10 years. The scenario surrounding the attacks is not known, but in the wild, although inter-group/unit fighting between silverback gorillas can be fatal, gorillas of blackback age would normally still be with the natal group and the resident silverback would intervene in any serious fights. These reintroduced male gorillas are essentially premature solitary silverbacks. In only one case at Karisoke in the 1980's did a male gorilla kill a female and it was thought that she was already dying (L. Williamson, former Director of Karisoke Research Centre, personal communication, 2002).

Encounters with wild chimpanzees

Immediately following Release 3 the reintroduced chimpanzees experienced two encounters with wild conspecifics soon after release. It seems probable that this contributed to Dolisie running away; he was subsequently lost and killed either by wild chimpanzees or hunters. This also resulted in Massabi and Mossendjo (Release 3) fleeing into an area with little food, becoming too scared to move and becoming emaciated as a result. The radio collars enabled the observers to locate most of the disbanded group following these encounters. Such contact at the early stage of a reintroduction should be avoided although obviously it is not always possible to predict the movements of wild chimpanzees. The first two releases were located in the north of the Triangle and one of the reasons was to avoid any contact with the resident group of wild chimpanzees in the south of the Triangle. The release in November 1997 was located much further south in the Triangle nearer wild chimpanzee territory. By conducting detailed surveys of nest counts and seasonal fruit production, it is possible to some extent to predict approximately where wild groups may range. However, in the long-term it is not possible to provide total protection for the reintroduced chimpanzees. Previous attempts to reintroduce chimpanzees into areas of wild conspecifics and knowledge about wild chimpanzee behaviour suggests that the likelihood of aggressive interactions between reintroduced and wild chimpanzees is high and may be fatal, particularly for males. As mentioned earlier on p.88 this has led HELP to take the decision to remove all reintroduced males and return them to the island sanctuary. This knowledge should guide site selection and preferably result in one devoid of wild conspecifics.

Re-habituation

Personnel should be known to the chimpanzees and kept to a minimum not only during capture but also at release and post-release. Observers should all become familiar with the chimpanzees pre-release to be able to recognise the animals post-release but also to facilitate post-release contact. Sufficient numbers of trained personnel should be on standby in case the group splits and each chimpanzee needs to be followed individually. On release, some chimpanzees were initially nervous of human presence, even of very familiar persons, and would flee if approached. In such cases, observers maintained visual contact whilst keeping as far from the chimpanzee as possible. However, by a known observer gradually reducing this distance, it was possible to get within a few metres of most chimpanzees in a few days. The project policy is to follow chimpanzees at a reasonable distance (see Chapter 5, p.114), for example, to be close enough not to lose them but not too close to have physical contact (no exact distance specified). The IUCN recommend a distance of ten metres and the International Gorilla Conservation Programme seven and a half metres for tourists visiting the mountain gorilla (Homsy, 1999). Once the chimpanzees were reassured and no longer fearful, being followed did not seem to cause any distress despite not experiencing this pre-release. However, if practical, following the chimpanzees pre-release could combat any potential problems that this may cause post-release. At the moment, gorillas at PPG Congo and Gabon are not directly followed post-release; if they wander from the group the observer does not follow to see where they are or what they are doing. If the gorillas became habituated to being followed from a young age this could facilitate post-release monitoring and data collection that is presently lacking.

Ape-human-ape interaction

Chapter 1 (p.22) described the case of a young female chimpanzee named Bahati who was reintroduced but found begging for food in nearby villages (Treves and Naughton-Treves, 1997). There are no human settlements within reach of the reintroduced chimpanzees in the present project preventing this problem. Reintroduced gorillas at PPG Congo have also strayed close to villages and more seriously one blackback gorilla attacked two local villagers and others have shown aggression towards staff (D. Chronopoulos, personal communication, 2001). The reason for this aggression from male gorillas of blackback (8-12 years) and young silverback (12-15 years) age may originate from excessive contact between humans and gorillas from a very young age (personal observation). This contact may have blurred the line between gorilla and human and resulted in the gorillas viewing humans as competition or a threat as they would potentially view male gorillas of the same age (personal observation). It will be interesting to see if the new hands off approach adopted at PPG Gabon and now Congo (as described in Chapter 1, p.24-25) will sharpen the line between gorillas and humans and deter the aggressive behaviour displayed by some of the gorillas to humans. A similar although less violent problem has been found with mountain gorillas. In the 1970-1980's groups of gorillas were established as research groups at Karisoke (Rwanda). At this time no rules of distance between humans and gorillas were established and frequently humans would groom and play with the gorillas. Over the years these gorillas have shown no fear of people. Three male gorillas (of blackback and young silverback age) became problems for observers at Karisoke; they would charge, drag people, pull at bags, sit on observers and bite, although not seriously (L. Williamson, personal communication, 2002). One of these gorillas is now a silverback and continues to pose problems. At Mbeli Bai (Republic of Congo) play patterns in juvenile western lowland gorillas such as wrestling, chasing, and display appear increasingly aggressive although not menacing amongst sub-adults and blackbacks and have been described as 'play-agonsim' (Parnell, in prep.). 'Quasi-aggressive behaviour' (Adang, 1984) and 'para-play' (Hayaki, 1985; Mendoza-Granados and Sommer, 1995) have been used to describe similar phenomena in chimpanzees. Female gorillas have not been seen to exhibit the same increasing levels of 'play-agonsim' and have not posed a problem to observers at Karisoke or PPG Congo. There have been a small number of problems reported with wild chimpanzees. There have been incidents of minor harassment (charges, stone throwing) directed by some adolescent chimpanzees to observers and tourists (particularly towards females), apparently at a time they are also attempting to dominate female chimpanzees (Goodall, 1986). More seriously three human infants have been snatched by wild chimpanzees at Gombe and two were partially eaten (Goodall, 1986). Presently there have been no serious problems of aggression reported between chimpanzees and observers at the HELP reintroduction site. This may be a consequence of a small number of males in the released community that primarily originated from Yombe Island where there has been less contact with humans. However, in 2001 three males from Yvette Island aged between seven and nine years were released, two of which had been causing problems to observers on the island. This is a period of early adolescence that Goodall (1986) characterises by increasing levels of aggression in an attempt to dominate females. Consequently only time will tell if these individuals become a problem to staff post-release.

Post-release monitoring

Post-release monitoring has proved invaluable in the present project not only to assess the status of the animals (and intervene when necessary) but has provided the opportunity to collect long-term detailed behavioural and ecological data on a group of reintroduced chimpanzees. These data will be published and will facilitate understanding of the process and provide recommendations for future reintroduction programmes. These groups of habituated chimpanzees that exhibit behaviour not dissimilar from their wild conspecifics (see Chapters 6 to 9) may provide an opportunity for ape researchers to study aspects of behaviour that is difficult to observe in less habituated wild populations. However, post-release monitoring should include data on the impact that the reintroduced animals may be having on the resident fauna and flora and are currently lacking.

4.4 Summary of survivorship

From November 1996 until November 2001, 37 chimpanzees (27 females and 10 males) have been reintroduced, 27 are confirmed to be alive and well (20 females and 7 males) and that includes six that were reintroduced over five years ago. The status of seven chimpanzees remains unknown (6 females and 1 male); four females fled immediately post-release, one male disappeared after five months and two females after two years. There have been three known deaths; one male died as a direct result of injuries inflicted by wild chimpanzees, a second male may also have died in the same way or been killed by hunters. Finally Valentine (the infant from Release 4) disappeared and is presumed dead. Taking all of the above into account overall the reintroduction has a confirmed 73% success rate and a possible 92% if status unknown cases are included. However, this includes all the chimpanzees that have been reintroduced even those only recently released. If chimpanzees from the study group (Release 1-4) only are considered (n=20) the success rate is a confirmed 55% with a possible 70%. All of the aforementioned factors of the reintroduction process that have been discussed throughout this chapter have cumulatively contributed to these statistics of survivorship.

4.5 Conclusions

- Before a reintroduction can be contemplated a suitable site needs to be located; one that provides sufficient food resources, ideally have no or a low density of wild chimpanzees, be situated at a distance from human settlements and adequately protected. Exact location and timing of release should take into account, areas and periods of seasonal food abundance.
- Pre-release chimpanzees need to be provided with an environment that can stimulate natural behaviours such as foraging and nest building and offer group living.
- Candidates need to be physically, behaviourally and psychologically able to survive post-release and should be screened for a variety of illnesses. The release of male chimpanzees into areas where conspecifics cohabit may prove fatal.
- Candidates older when captured from the wild, having spent longer periods of time in suitable pre-release training environments, and older at release, may show elevated rates of survival.
- Capture should be quick and involve the least amount of stress possible by involving known personnel.
- All chimpanzees should be fitted with telemetric devices.
- Transportation to release site should be expeditious and the design of holding cage functional for its purpose dependent upon whether a 'soft' or 'hard' release is being contemplated. If pre-release training took place at the release site then the potential stress of capture and transportation from one site to another would be removed.
- Chimpanzees should be released with other chimpanzees they know so that they can provide support and reassurance for one another post-release. They should be released at an age when there is trust between caretaker and chimpanzee; observers should be able to provide reassurance post-release and this will facilitate post-release support and monitoring.
- Sufficient numbers of trained observers should be on standby at release in case the group splits and each chimpanzee needs to be individually followed.

- It may be necessary to provide provisioning initially post-release but this will depend upon the animal's prior history and experience.
- Post-release veterinary intervention can be imperative for the survival of chimpanzees during initial adaptation and following aggressive encounters with wild conspecifics.
- Interactions between reintroduced and wild chimpanzees during the initial adaptation phase should be avoided. Timing and exact location of release site should take into account seasonal movements of wild conspecifics.
- It may be necessary to gradually re-habituate the chimpanzees to human presence post-release. If so, familiar observers should gradually decrease the distance between observer and chimpanzee.
- Relationships developed with young apes will influence their later response to human presence. Contact between human surrogate mother and the ape should be gradually reduced so that they rely and focus more on one another for support and interaction.
- Post-release support and monitoring is a vital component to reintroduction. Without post-release support in the form of guidance to feeding sites, provisioning when necessary and veterinary intervention, more chimpanzees would have died. In the present study post-release monitoring and data collection are providing a long-term database of behavioural and ecological indices of adaptation and guidelines for future reintroduction programmes. The possibility to easily follow and study reintroduced groups of chimpanzees may also facilitate data collection on behaviours that to date have been difficult to study in wild groups.
- A high survival rate with one post-release birth indicates that chimpanzees reared in semi-captivity can be successfully reintroduced (defined here as the majority surviving) to the natural environment.

The following chapter will outline methods of data collection and present the results of post-release behavioural data to provide a further indication of the adaptation process.

Chapter 5

General methods

5.1 General overview

Originally HELP had planned to capture and release a minimum of eight individuals in 1999, either all at once or between two periods (e.g, February and July 1999) and it was these individuals which were to be the focus of this study. However, it became increasingly difficult to capture chimpanzees on Yombe Island as it was not possible to enter the island due the age and aggressive behaviour of some individuals. A combination of many unknown personnel and equipment (three veterinarians and a three-person film crew in addition to normal staff) at a time when some females were in oestrus causing the males to be protective and aggressive, caused difficulties in capturing the chimpanzees. Furthermore, problems were encountered immediately post-release when all the chimpanzees disappeared and took several days to locate, and Koutou remained lost for over two weeks. Consequently only four chimpanzees and one suckling infant were released with no plans to release any more that year. Due to the resultant small sample size, HELP provided access to data that had been collected on eleven previously released chimpanzees so far not analysed. It was decided to compare behavioural and ecological data for the first 14 months post-release for the 11 previously released chimpanzees and the four adolescents about to be released. The decision to include 14 months post-release data was to allow for the initial post-release period when the monitoring procedure often comes secondary to locating the chimpanzees and ensuring their safety, resulting in fewer observations. Furthermore, 14 months would enable the importance of seasonal fluctuation on dietary and behavioural components to be evaluated. The present data set took nearly a year to enter and due to time constraints within the doctorate it was not possible to include more data even though they were available.

The inclusion of a data set already collected dictated the methodology of the data to be collected as they needed to be directly comparable. The data set, in hard format only, included thousands of check-sheets. In order to be able to enter all the data, I returned from the field earlier than previously expected. Trained observers continued collecting data on the four chimpanzees released and the check sheets were sent to the UK. Overall 240,804 data points were entered onto spreadsheets.

Chapter 4 explains that the chimpanzees were not all released at the same time, and consequently the post-release study periods for each chimpanzee do not necessarily correspond to one another (Table 5.1). Between 1996-1999 (Release 1-4) 20 chimpanzees have been released, but data were only collected on 15. As mentioned previously (see Chapter 4, p.81-84) three chimpanzees disappeared immediately post-release and another disappeared a few days after being released. Data were not collected on Valentine, a baby chimpanzee released with her mother Sophie, as at the age of one and a half months many activities would not yet be routinely performed and additionally her activity profile would be very closely linked to that of Sophie.

The data were collected by myself, a number of long-term staff (n=22) and short-term volunteers (n=17). Over 80% of data were collected by long-term staff. All new and short-term staff were trained by experienced members of staff and the inter-observer reliability (IOR) scores were high (see section 5.9, p.120).

5.2 Study animals

Study animals were 15 chimpanzees (*Pan troglodytes troglodytes*), 11 females, four males aged between six to ten years at release. All chimpanzees were wild-born and had spent varying periods of time in captivity prior to arriving at the HELP project and at the sanctuary prior to release (see Table 4.1, p.70-73).

Table 5.1 Date of release and period of data collection for each chimpanzee released

Chimpanzee	Date of release	Release	Study period
Bougnoule	24.11.96	1	24.11.96 – 23.01.98
Yvette	24.11.96	1	24.11.96 – 23.01.98
Mekoutou	24.11.96	1	24.11.96 – 23.01.98
Jeanette	24.11.96	1	24.11.96 – 23.01.98
Choupette	26.11.96	1	26.11.96 – 25.01.98
Rosette	25.01.97	2	25.01.97 - 24.03.98
Fanny	25.01.97	2	No data collected due to immediate disappearance
Nyasha	20.11.97	3	No data collected due to immediate disappearance
Kakamoeka	20.11.97	3	No data collected due to immediate disappearance
Massabi	28.11.97	3	28.11.97 – 27.01.99
Cabinda	28.11.97	3	28.11.97 – 27.01.99
Mossendjo	28.11.97	3	28.11.97 – 27.01.99
Hinda	28.11.97	3	28.11.97 – 27.01.99
Caline	28.11.97	3	28.11.97 – 27.01.99
Dolisie	28.11.97	3	Only present for 4 days - data not included in study
David	01.02.99	4	01.02.99 – 21.05.99 Last seen 21.05.99
Agathe	01.02.99	4	01.02.99 – 31.03.00
Sophie	01.02.99	4	01.02.99 – 31.03.00
Valentine	01.02.99	4	Released with mother (Sophie) but no data collected
Koutou	01.02.99	4	01.02.99 – 31.03.00

5.3 Pre-release period

I was in the field from October 1998-September 1999. Release 4 took place on 1st February 1999. Part of the pre-release period (October 1998-January 1999) was spent at the sanctuary and part at the release site. The period at the sanctuary was used to become familiar with the chimpanzees to be released and furthermore to accustom the chimpanzees to contact with humans to facilitate post-release monitoring. I worked closely with Emmanuel Dilambaka, a field assistant, who knew the chimpanzees well. During this period we encouraged the chimpanzees to remain at the edge of the island following feeding so that contact could be established (Plate 5.1). Attention was paid to associations with a view to considering who should be released with whom, and to prepare the chimpanzees for the release process by playing with syringes (see Chapter 4, Plate 4.3, p.91).

Several trips were made to the release site where I was introduced to the chimpanzees already released and spent time following them in the various forest types refining data collection procedures. This period was extremely useful in becoming familiar with the forest trails and plant species.

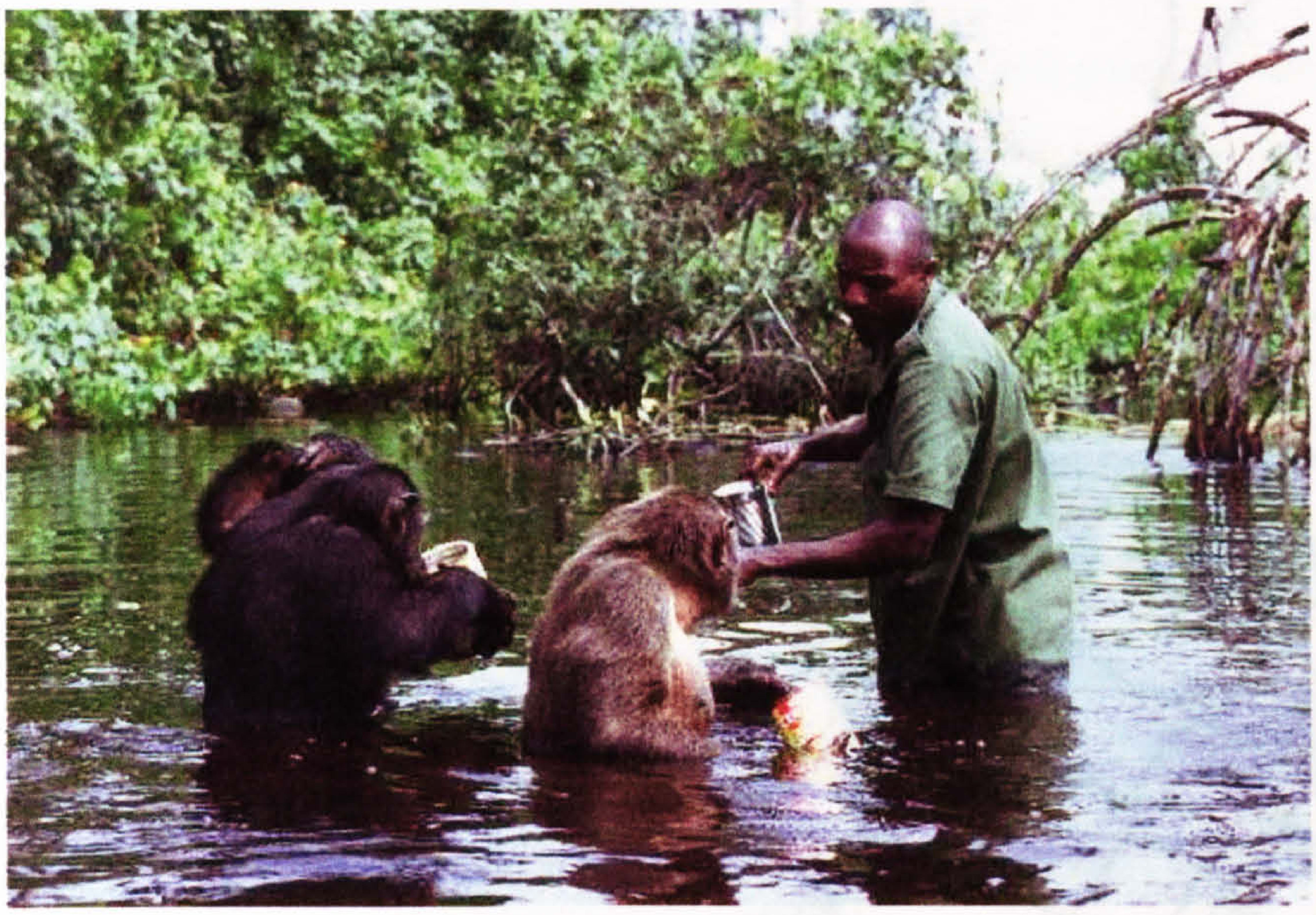


Plate 5.1 Emmanuel feeding Cerelac to the chimpanzees on Yombe Island

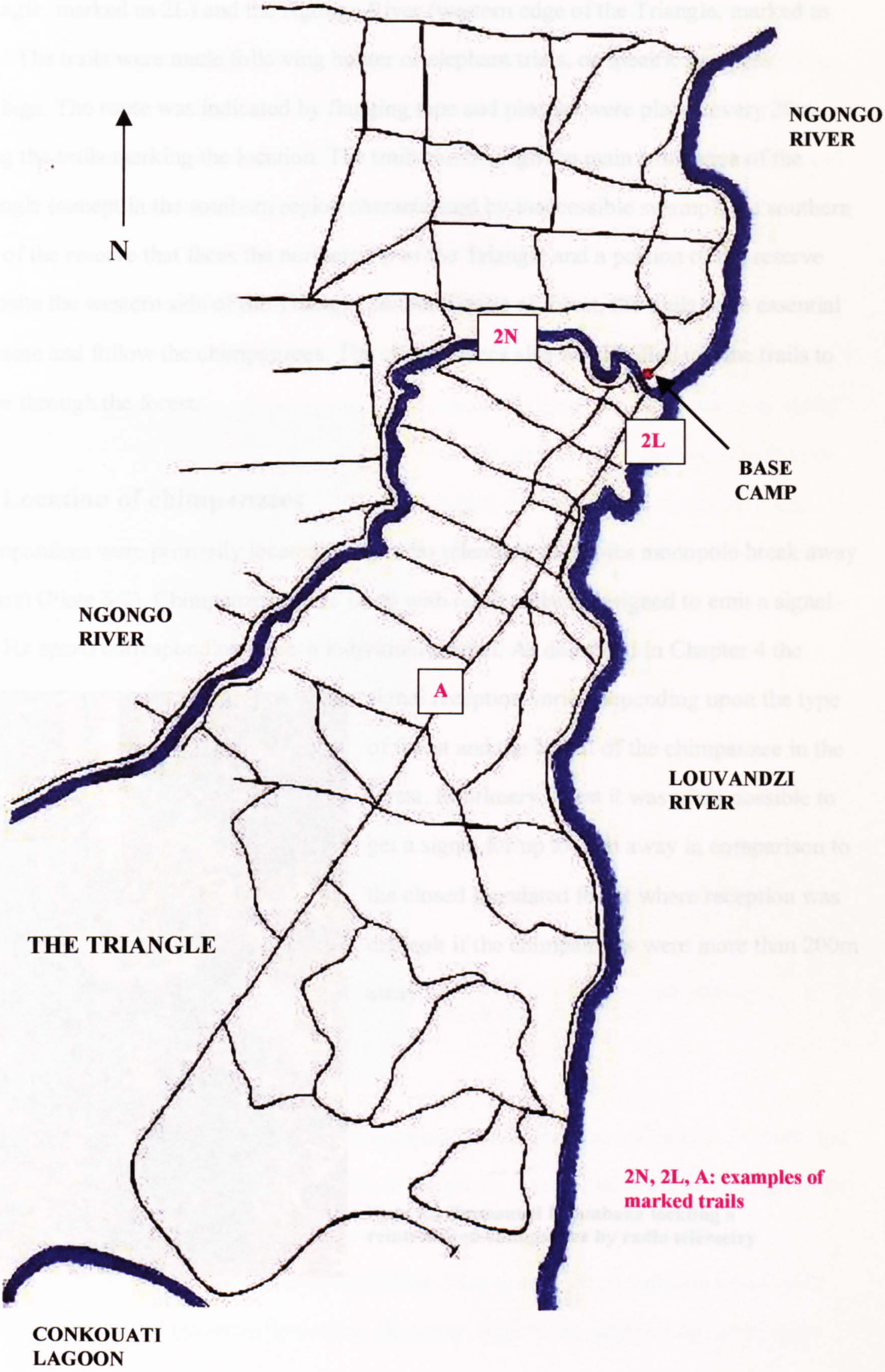
5.4 Temperature and rainfall

Temperature and rainfall data were collected regularly by HELP at the release site base camp. These data were used to assess which month should be categorised as falling into either the dry or rainy season. Rainfall data were collected using a rain gauge in an open area approximately 20m from the edge of the forest. Minimum and maximum temperature data were taken from a thermometer in the base camp office. Although the temperatures gave a relative indication of increase and decrease, as they were not taken in the forest, they do not reflect a 'true' reading of forest temperature. The readings were taken early morning normally between 06h00-07h00. Unfortunately due to a change in project management in August 1999, neither rainfall nor temperature readings were continued.

5.5 The trail system

A trail system was created to facilitate location data on the released chimpanzees, phenology studies and for noting signs of other species (Figure 5.1). Approximately 160-200km of trails were made in the Triangle and reserve (southern and western sectors of reserve only). A central trail (A) ran from north of the Triangle to the south. Subsequent

Figure 5.1 Trail system within and outside of the Triangle for tracking the chimpanzees post-release



trails were located perpendicular to trial A, along the Louvandzi River (eastern edge of the Triangle, marked as 2L) and the Ngongo River (western edge of the Triangle, marked as 2N). The trails were made following hunter or elephant trials, or specific compass bearings. The route was indicated by flagging tape and plaques were placed every 20m along the trails marking the location. The trails ran through the main study area of the Triangle (except in the southern region characterised by inaccessible swamp), the southern part of the reserve that faces the northern tip of the Triangle and a portion of the reserve opposite the western side of the Triangle. In many areas of forest, the trails were essential to locate and follow the chimpanzees. The chimpanzees also would often use the trails to move through the forest.

5.6 Location of chimpanzees

Chimpanzees were primarily located using radio telemetry (Telonics monopole break away collars) (Plate 5.2). Chimpanzees were fitted with radio collars, designed to emit a signal (10kHz apart) corresponding to each individual animal. As described in Chapter 4 the signal reception varied depending upon the type of forest and the height of the chimpanzee in the forest. In primary forest it was often possible to get a signal for up to 1km away in comparison to the closed inundated forest where reception was difficult if the chimpanzees were more than 200m away.

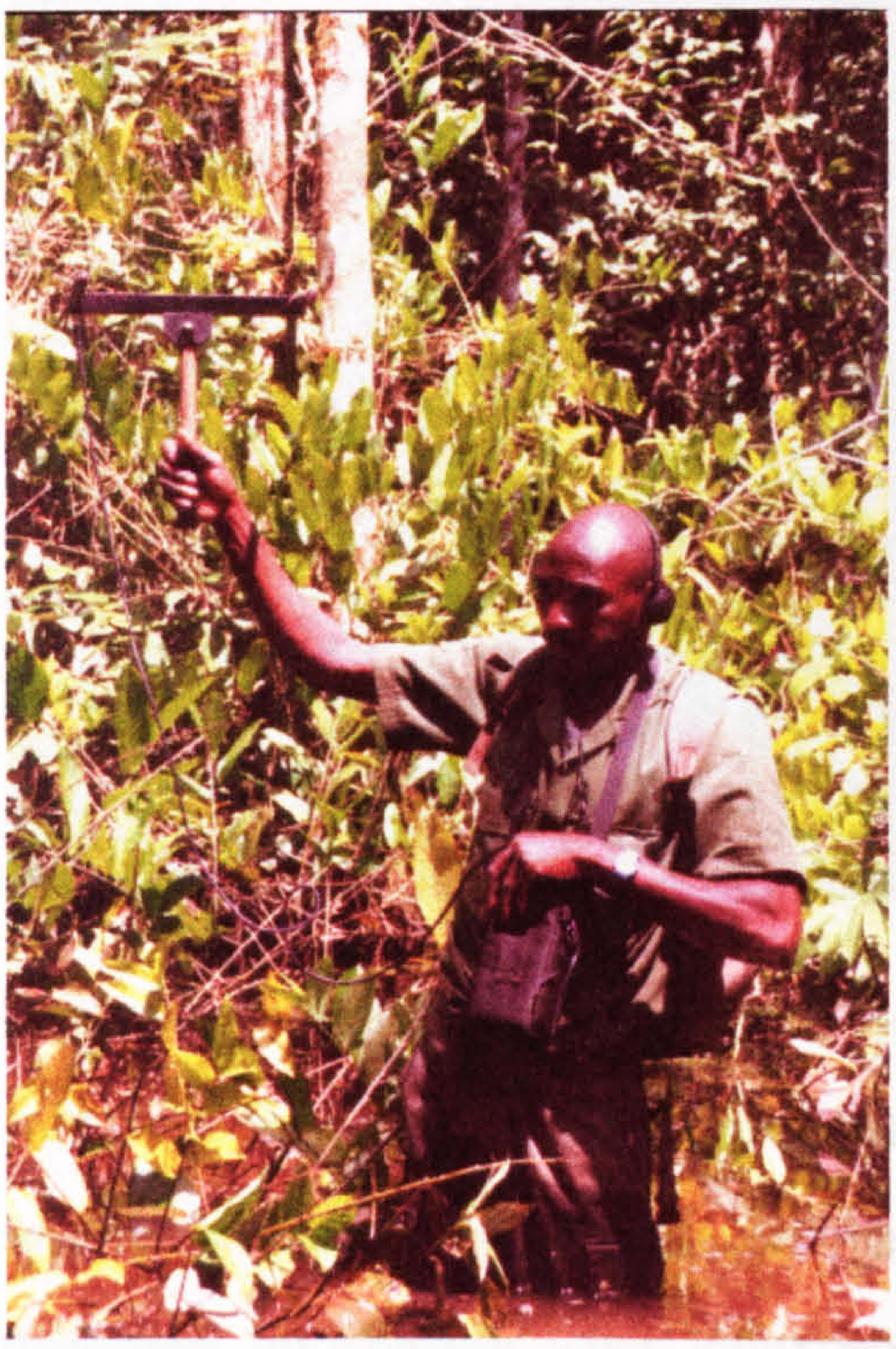


Plate 5.2 Emmanuel Dilambaka locating a reintroduced chimpanzee by radio telemetry

Normally, if the chimpanzees had been seen making a nest the night before, then the location would be noted and the following morning the direction of the nest taken with checks made along the route with the radio to confirm that the chimpanzees were still in that direction. Once within the vicinity of the chimpanzees, exact location relied upon listening to sounds of movement/feeding in the undergrowth or canopy, vocalisations and occasionally the chimpanzees would seek out the observers.

5.7 Following the chimpanzees post-release

The general rule when following the chimpanzees was to follow at a reasonable distance (obviously close enough not to lose them but not too close to influence direction or disturb behaviour) and not to have any physical contact (Plate 5.3). Project policy was that observers should interfere as little as possible in the activities of the chimpanzees.

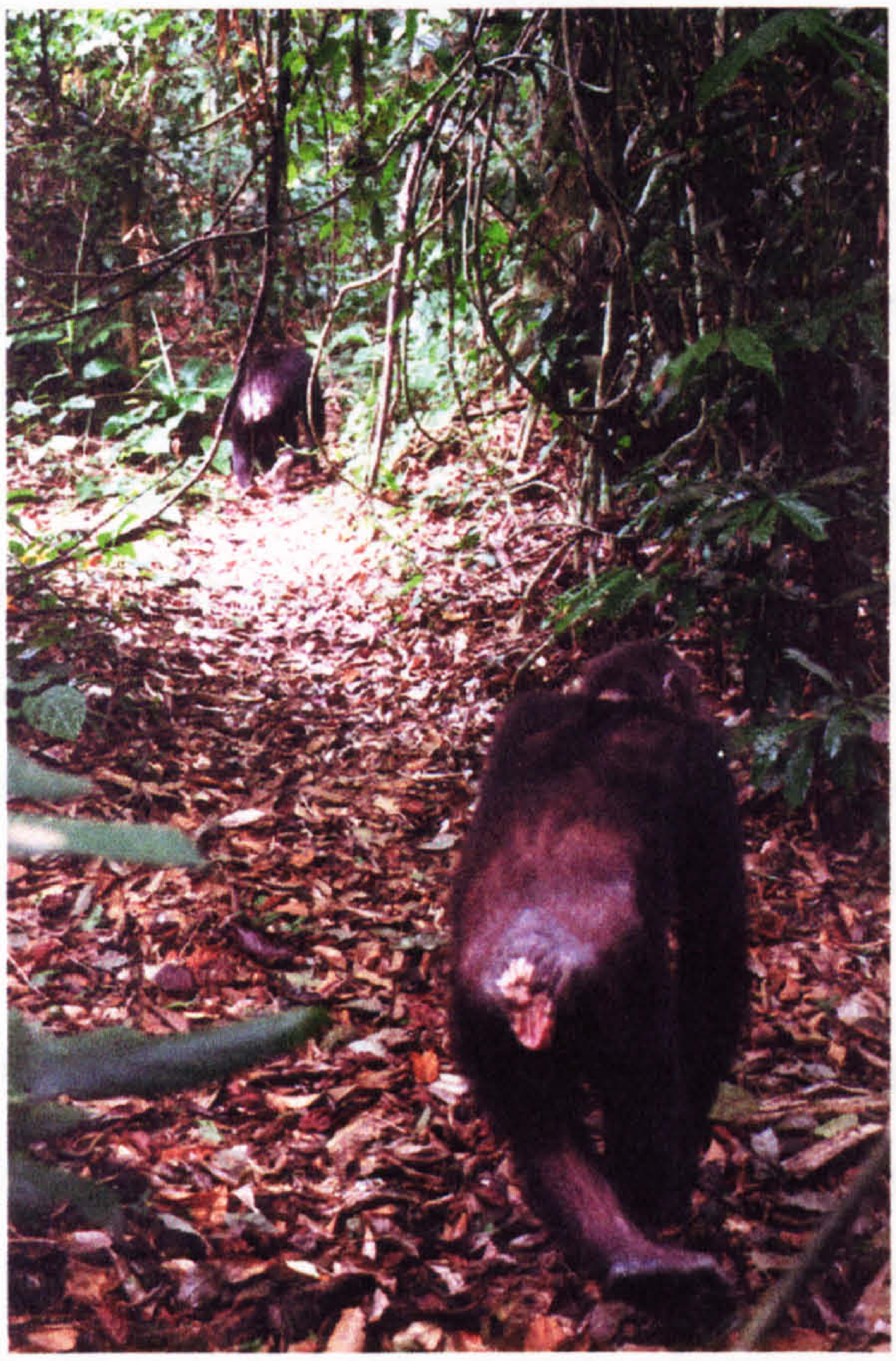


Plate 5.3 Following the reintroduced chimpanzees post-release

This policy was important so that the chimpanzees would become and remain focused and reliant on one another and not on humans, and negate any potential problems of aggression towards humans as the chimpanzees matured. Occasionally physical contact was necessary, for example, when Valentine became weak and required supplementary milk and vitamins, and to change radio collars. However, sometimes, and this occurred more frequently with some individuals than others (e.g., Mekoutou), chimpanzees would move close to the observers, in such cases observers would either move away or simply ignore the animal. Too much attention to an individual such as Mekoutou who was very focused on people can hinder the adaptation process. Mekoutou would readily oblige young volunteers on the project wanting contact with a chimpanzee. He would stop feeding and interacting with other chimpanzees, to sit on the ground and wait to be groomed by a human (personal observation). As already stated this behaviour in both volunteer and chimpanzee was actively discouraged. However, the majority of the chimpanzees simply ignored the observers and continued with what they were doing making them ideal subjects to study (personal observation).

The extent of visibility varied according to forest type. There was better visibility in the primary forest but reduced visibility in the inundated and swamp forest. It was difficult to follow chimpanzees in the swamp forest and also in some areas of seasonally inundated forest as they could easily move from tree to tree in the canopy whilst the observers struggled through areas of chest high water, balancing bags on head whilst removing leeches! However, due the experience of the local staff, who nearly always managed to find a navigable route on which to follow the chimpanzees, and their skill of identifying individual animals even in the tallest tree, facilitated data collection.

5.8 Chimpanzee behavioural sampling

During this study, data were collected using scan and time sampling recording rules. A number of empirical studies have shown that scan sampling can give a good approximation to the proportion of time spent performing an activity (e.g., Dunbar, 1976; Leger, 1977; Simpson and Simpson, 1977; Rhine and Flanigon, 1978).

5.8.1 Overview

This section is applicable to the methodology employed in observing all chimpanzees in both the present and earlier releases. All behavioural data were collected using a check-sheet (Appendix C). Normally a team of two people worked together in the forest. I had one pair of binoculars (Leica 10x40) and the project had another (the same model) that was shared between field assistants. Each observer had a waterproof watch to record the time. In the earlier releases (prior to 1999) observers would frequently work alone. In the present study I always worked with a trained local field assistant to facilitate identification of plant species. Furthermore, a two-person team can aid data collection in conditions of low visibility and with chimpanzees that form groups over areas too great for one observer to watch all individuals simultaneously. Locations off the grid system were recorded using a compass and pacing by foot. On initial contact with the group all chimpanzees were identified, and if any were missing from the group attempts were made to locate them. Once the chimpanzees were identified watches were synchronised and if two observers were present both collected data simultaneously.

5.8 2 Collection of scan data

These were collected every 10 minutes and started once all individuals had been identified and accounted for. Scan sampling means that a whole party of study animals is rapidly scanned or censused at regular intervals, and the behaviour of each individual at that instant is recorded. This technique enabled data to be collected that were evenly representative across all individuals, time of day and season. Table 5.2 describes the information recorded at the top of each check-sheet, Table 5.3 the information that was collected every 10 minutes and Table 5.4 the definition of behaviours.

Water level, weather and forest type, were noted at the top of each check-sheet to determine terrain and meteorological variables at the time of data collection (Table 5.2). If this changed during the course of the check-sheet, it was noted in the comment section on the check-sheet. The project categorised forest according to three types; inundated, primary and swamp, and this methodology was continued in the present study to facilitate data comparison.

Table 5.2 Information recorded at the top of each check-sheet

Category	Category description
Date	e.g., 10.3.1999
Name of observer	e.g., Kay Farmer
Forest type	I = inundated, S = swamp, P = primary
Height of water	0 = no water, 1 = below ankle, 2 = below the knee, 3 = above the knee
Weather	S = sunny, C= cloudy, P = rainy, FP = heavy rain

Table 5.3 Information collected every 10 minutes and entered on the check-sheet

Category	Category description
Time	e.g., 10.40
Chimpanzee	e.g., David
Location	Recorded using compass co-ordinates and pacing from the nearest transect
Activity	The behaviour of all independent individuals (see Table 5.4)
Height of activity	From the first release in 1996 until 10/07/1999 this was categorised as 0 = ground, 1 = <5m, 2 = 5-15, and 3 = >15m. However, due to a change in management from 11/07/1999, the categories changed to 0 = ground, 1= <5m, 2 = 5-20m, 3 = 20-30m, 4 = >30m. The assessment of the height above ground was made by estimation (see section 5.9 for IQR scores)
Food item	Feeding species and part. If species were not known then a sample would be taken and preserved for identification

If an individual was present on scan A but not the next (scan B), the chimpanzee was marked as 'not seen'. The activity of an individual was only recorded if the observer succeeded in having a clear view of the subject and if not the behaviour was marked as 'not known'. An effort was made to record as much detail as possible using the comment section on the check-sheet. For example, when aggression occurred, the initiator, recipient, context and outcome were noted by the author. The direction of the behaviour was indicated with arrows, for example, for grooming D → S indicates that David was grooming Sophie, whereas D ↔ S indicates that they were grooming one another at the same time. Sometimes groups would split and the decision of whom to stay and follow was dependent upon a number of factors but primarily based upon the necessity to gain an equal number of observations on all released individuals, and to ensure that all the chimpanzees were healthy and behaviourally 'normal'.

Table 5.4 Behaviour classifications and description

Category label	Definition of activities included within category
Feed	Remove food item (fruit, leaves, stem pith etc.,) from the substrate, process, put into mouth, bite and chew, wadge and swallow it.
Rest	Remain immobile (sit, lie) both on the ground and in trees. If within nest, then noted in comment section.
Move	Moving (walk, run, jump, somersault, climb and descend) between A and B on the ground and within trees.
Groom	Hair pulled back with the thumb or finger of one hand and holding it back while picking at the exposed skin with the nail or finger of the other hand. Grooming may occur whilst sitting or lying. Indicated whether self or social with 'groomer' and 'recipient' named in comment section.
Aggression	Attack (aggressive physical contact between two or more chimpanzees) or threaten (repertoire of behaviours (e.g., arm wave, hit towards, branch wave, charge, slap etc.,) to elicit submissive behaviour.
Play	Divided into lone and social play. Can involve locomotor (e.g., dangle, leap, swing, somersault, tickle, chase, slap etc.,) and object play (e.g., pick up, throw, drag, drape etc.,).
Other	All other behaviours: (a) Copulation (intromission and pelvic thrusting between a male and estrous female). (b) Drinking (drinking of water or other liquids by directly leaning over source, dripping water from fingers, licking water from substrates etc.,). (c) Coprography (eating of faeces). (d) Urine drinking (drinking of urine from substrate or from own up-jetted stream). (e) Nest building (construction of a bed by bending branches). (f) Urinate. (g) Defecate. All of these behaviours were indicated in the comment section.

(Adapted from Nishida, Kano, Goodall, McGrew and Nakamura, 1999)

New 'releasees' were followed from nest to nest for the first year and this meant that two teams of two people were responsible for data collection. The first team would enter the forest at 06h00 and the second team at 12h00, normally meaning that each team would spend approximately seven to eight hours a day in the forest. Obviously depending upon where the chimpanzees were, time to locate them could take anything from 10 minutes to several hours, affecting the number of observations that could be made. Occasionally a boat was used to deposit observers up or down stream if the chimpanzees were either known or thought to be a long distance from base camp. The protocol for following all chimpanzees from nest to nest for the first year post-release has not always been strictly adhered to due to a variety of reasons ranging from staff shortages to individual chimpanzees disappearing with the resultant search becoming the focus of attention. Consequently data were not collected evenly for each chimpanzee and each month (Table 5.5). At the end of the observation period, any chimpanzees that had either left the group or not been present would be located as and when possible.

Table 5.5 The number of observations (10 minute scans) for each chimpanzee per month post-release

	MONTH														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	TOTAL
CHIMP															
Bougnoule	1276	1349	1994	1742	1956	2113	2318	2100	1980	1968	1850	925	271	701	22543
Yvette	1230	1349	1993	1732	1872	2109	2318	2103	1980	1968	1851	929	271	697	22402
Mekoutou	927	1660	1320	233	1839	2106	1800	2071	1980	1995	1862	760	427	824	19804
Jeanette	1255	1717	1969	1742	1956	2087	2265	2084	2016	1987	1991	1134	324	339	22866
Choupette	1126	1399	1897	1754	1923	2134	2206	2097	2014	1992	1977	1007	324	354	22204
Rosette	1939	1733	1935	2128	2307	2094	1977	2025	1852	865	895	715	1323	985	22773
Massabi	1048	34	889	983	1040	434	770	821	653	596	658	818	735	672	10151
Cabinda	826	699	1003	991	991	738	947	888	856	821	1013	1026	892	995	12686
Mossendjo	1046	34	905	983	1040	434	770	821	653	596	658	818	735	672	10165
Hinda	546	696	1003	987	1030	772	965	903	852	816	1033	1026	892	986	12507
Caline	460	470	962	957	1145	792	1128	929	875	912	839	980	889	810	12148
Dolisie	131	-	-	-	-	-	-	-	-	-	-	-	-	-	131
David	86	1273	1795	1002	-	-	-	-	-	-	-	-	-	-	4156
Agathe	86	1178	1829	1470	1975	1485	1363	728	1383	1133	568	452	989	1312	15951
Sophie	86	1272	1787	1887	1968	1489	1499	735	1379	1290	568	452	989	1299	16700
Koutou	-	1470	1757	1872	1870	1419	1270	557	843	905	440	121	-	1093	13617
TOTAL	12068	16333	23038	20463	22912	20206	21596	18862	19316	17844	16203	11163	9061	11739	240804

5.9 Inter observer reliability

In any study involving two or more observers, it is important to verify that observers are recording the same behaviour in the same way; that the between-observer reliability for each category of behaviour is good. This is particularly important in the present study where a large number of field assistants have been responsible for collecting the data. A common and relatively simply measure, the index of concordance, was used. At the end of an observation session, observers compared the total number of agreements (A) and disagreements (D). The index of concordance is the proportion of all occurrences about which the two observers agree; A/(A+D) (Martin and Bateson, 1998).

It was only possible to compare commonly occurring behaviours such as feed, move and rest due to insufficient observations of other behavioural categories and height categories of ground, less than 5m, 5-15m and above 15m. I compared my data collected to that of five field assistants (Alexis Mayet, Anselme Taty, Emmanuel Dilambaka, Eric Tchimdongo and Nestin Moutogo-Lissassaga) with whom I primarily worked. They had been employed for varying periods at HELP ranging from one to three years. The comparisons were made approximately three months after the chimpanzees had been released. The inter-observer reliability score at its lowest was 86% and highest 100% (Table 5.6) and was taken to indicate an acceptable level of agreement between observers. Long-term experienced field staff trained all new observers (including myself) and therefore the high level of concordance is not surprising.

Table 5.6 Inter-observer reliability scores (%) between the author and five field assistants

		Observers									
		Alexis		**Anselme**		**Emmanuel**		**Eric**		**Nestin**	
		%	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**
Categories											
Behaviour	**Feed**	99.5	206	100	206	97	64	99	89	100	170
	Move	100	42	96	49	100	61	94	36	100	41
	Rest	99.5	196	99	153	97	54	99	100	100	76
Height	**Ground**	99.5	211	100	153	98	266	100	79	100	68
	<5m	95	20	86	6	98	49	97	58	86	7
	5-15m	100	30	100	51	95.5	86	97	32	97	33
	>15m	100	217	99.6	224	100	129	96	76	99	194

5.10 Analyses

The behavioural data were collected simultaneously using the same check-sheet (except in the case of nesting behaviour, see Appendix H) and then later separated for analyses. Due to the uneven number of observations collected for each chimpanzee and month, analyses have been performed on mean percentage scores unless stated. To gain an overview of results from the reintroduction process, means were pooled for each chimpanzee. Although this may result in some loss of accuracy it offers the best solution to answer the questions posed. It was not within the scope of this thesis to also look at individual differences but this would be a suggestion for future research.

To test for normality of the data, a histogram was produced for each data set, followed by p-plots. The data were judged to be normal according to how close the values lay along the line. Mean with standard deviation (SD) and median with inter-quartile range (IQR) descriptive measures are shown. The symbol ± refers to the standard deviation or inter-quartile range where applicable. In some cases due to small sample size the IQR was not computed and SD due to little or no variation. Each chapter specifies normality of data and tests performed. All analyses were performed using SPSS version 9, Minitab version 13 and Microsoft Excel '97. Throughout the thesis exact values of probability are provided up to four decimal places, values lower than this are displayed as $p<0.0001$. Further details of data analysis are presented in each of the following chapters.

Chapter 6

Activity budgets and patterns of behaviour

6.1 Introduction

Primates are continually faced with conflicting pressures on their allocation of time to a variety of activities and hence studies of activity budgets provide useful information about an animal's ecology. For example, primates need to find and gather food, avoid predators, contend with competitors and weather, maintain social relationships, and reproduce.

Since food is such a crucial resource, a fundamental influence central to an animal's ecology is feeding. Whatever an animal does, it must acquire, consume and digest enough food to provide it with sufficient energy to carry out any other activities. Indeed a number of activities such as moving and resting can be accounted for either directly or indirectly, by feeding (Teleki, 1977). This has resulted in some cases with the inclusion of movement within feeding activity budgets (Hladik, 1973). However, travel, a relatively energetically expensive activity may serve a number of functions.

Plate 6.1 Sophie and Agathe feeding

Travel may be required when harvesting a food resource, when defending a resource, gaining access to a mate, and seeking protection from the elements. Measures of inactivity can be as informative as measures of activity because the relative amount of time spent resting reveals much about levels of energy expenditure which in turn can reveal something about the pressures to which individuals are subjected.

A number of factors are known to influence activity budgets. The effect of sex, life history, group size, the environment and time of day are described in the following sections. These factors are subsequently investigated with regards to the budgets shown by the reintroduced chimpanzees.

Sex, life history and social influences

Some studies have described differences in activity levels between males and females, for example, at Gombe, male chimpanzees were found to spend more time interacting and resting, whereas females spent more time feeding and travelling. In contrast, Fawcett (2000) found that males spent more time moving than females. However, some studies do not support the existence of differences between the sexes in activity patterns (Wrangham and Smuts, 1980; Doran, 1997).

Age and stage of sexual receptivity are influencing factors on the different proportions of time allotted to various activities, and this is particularly apparent when the two sexes are compared. For example, Gombe males become more social and more mobile as they grow older whereas females (to a lesser extent) are inclined to become less social and less mobile with increasing age (Teleki, 1977). Adolescent females have been found to spend more time resting than adult females (Fawcett, 2000) and cycling females travel further than non-cycling females (Wrangham, 1979; Hasegawa, 1990). Allo-grooming budgets have been found to increase with age for both sexes and Teleki (1977) suggests that this supports the premise that grooming activities are one of the major social underpinnings of chimpanzee society.

Plate 6.2 Sophie grooms her infant whilst Agathe rests

Social factors may complement or counteract environmental factors in the regulation of routine activities. The activity budgets of male chimpanzees at Gombe have been found to differ as much as 50% in solitary versus group situations. A male chimpanzee may spend only 28% of the day feeding when accompanied by companions, versus 78% when alone (Bygott, 1974, cited in Teleki, 1977). However, group size and party composition are inextricably inter-linked with environmental variables, with communities dispersing and spending more time as solitary chimpanzees in response to scarce resources during the dry season (Doran, 1997).

Environmental influences

The effect of seasonal environments and scarce resources on primates has been well studied. If there is a necessity to allot a large amount of time to feeding during periods of food scarcity in the dry season, then the opportunity to perform other activities will be correspondingly influenced. For example, Doran (1997) found that the amount of time chimpanzees spent travelling, decreased as the chimpanzees fed on figs and on leaves during the food scarce dry season. Fawcett (2000) found that time spent grooming and resting at Budongo were inversely correlated to food availability, indicating that the chimpanzees responded to limited food availability by decreasing time spent foraging and increasing time spent resting and grooming, thus conserving energy. Conversely, feeding budgets at Gombe were found to vary little across the seasons even though radical changes occurred in the vegetation cover (Teleki, 1977).

Diurnal temporal variation

Activity budgets also show diurnal temporal patterns. Wrangham (1977) found three feeding peaks between which grooming tended to occur, whilst Goodall (1968) and Nishida (1974) found two feeding peaks occurring late morning and early evening. In contrast, Teleki (1977) found a relatively steady rate of feeding from sunrise to sunset. The charting of chimpanzee feeding activity across hours of the day may also highlight trends in food intake (see Chapter 8, p.255-258). Peaks of frequency have also been found in grooming, sexual and aggressive behaviours (Nishida, 1974; Teleki, 1977).

Influence of the captive environment on behaviour

Animals in the wild have evolved to live in an environment of great physical (e.g., soil, rock and water) and temporal complexity (e.g., light, temperature, humidity, food availability and seasonal changes in vegetation). Animals also have to interact with other animals in the environment, whether they are predators, prey or conspecifics. In contrast the captive environment is considerably less complex; we protect animals from predators, shelter them from extreme weather conditions, and meet their nutritional needs. In captivity, the occurrence and frequency of behaviours are influenced and constrained by the provision of food, the size and type of captive environment, and the number and range of social companions. During the past three decades, the significant role that captive environments play in the development of primate behaviour has been recognised. Research has shown that animals kept in socially and physically impoverished environments may develop inflexible behaviour patterns and that early experience may have long-term effects on emotional reactivity and cognitive performance (Pfeiffer and Koebner, 1978; Bard and Gardner, 1996). Studies on a number of species have shown that manipulation of the captive environment and provision of environmental enrichment can dramatically alter behaviour (Chamove, Anderson, Morgan-Jones and Jones, 1982; Bloomstrand, Riddle and Maple, 1986; Markowitz and Spinelli, 1986; Jerome and Szostak, 1987; Bryant, Rupniak and Iversen, 1988; Brent, Lea and Eichberg, 1989; Shepherdson, Carman and Bremment, 1989; Bloomsmith, Finlay, Mershalski and Maple, 1990; Gilloux, Gurnell and Shepherdson, 1992). Environmental enrichment aims to restore the contingency between the performance of behaviour and appropriate consequences, for example foraging and finding food (Shepherdson, 1988). Furthermore, Box (1991b) highlighted the influence of interrelated factors such as cognitive capacity, temperament, physiology, social context and individual differences on behaviours in response to environmental change.

The influence of the captive environment on behaviour has clear implications for reintroduction projects that are attempting to move animals that have in some cases spent considerable amounts of time if not their whole lives in captivity, to live and survive in a natural environment. In contrast translocation projects normally involve moving animals that have spent very little time if any in captivity. Strum (2002) argues that captivity robs primates of the skills and knowledge that they need to survive in the wild, and that translocation projects, are more likely to succeed. Animals born and reared in the wild overall have superior survival skills to those reared in captivity (Beck, Kleiman and Dietz, 1991; Miller, Biggins, Hanebury and Vargas, 1994) as do their offspring (Beck et al.,1991) although some behaviours, for example, anti-predator behaviour (Castro, 1990) and nest building (see Chapter 8) may contain both innate and learned components. Chapter 4 described pre- and post-release training protocols and environments that have been used to facilitate acquisition and modification of skills and behaviours necessary to survive in the wild.

Only a small number of studies describe long-term post-release behavioural change. Stoinski (2000) found that by six months post-release, adult captive-born golden lion tamarins fell less, relied more on natural substrates, spent more time foraging and in social behaviour. However, it was not until approximately 18 months post-release that the amount of time spent foraging decreased and foraging efficiency increased. The number of behavioural changes observed during the first year post-release in young captive-born tamarins were higher in comparison to adult captive-born tamarins (Stoinski, 2000) and is consistent with an increased survival rate in animals reintroduced at a young age (Beck et al., 1991). Most studies on behavioural change report rapid change in some behaviours but long periods of adaptation for other behaviours. For example, studies of reintroduced Arabian oryx found that changes in foraging, social organisation and dominance patterns took up to five years (Tear, Mosley and Ables, 1997). Similar changes in the post-release behaviour of ringtailed lemurs (*Lemur catta*) took between 1-22 months to occur (Keith-Lucas, White, Keith-Lucas and Vick, 1999). Yeager (1997) found that while wild-born ex-captive released orang-utans had higher reproductive success than wild conspecifics they remained dependent upon provisioned food for several years and that this transferred to their offspring. Provisioning, however, may delay adaptation and foraging efficiency. With provisioned food there would be less pressure on the animals to develop efficient foraging skills immediately (Stoinski, 2000). Tear et al. (1997) explained the long period of adaptation seen in the oryx as a consequence of their reliance on supplementary food. Similarly, the lemurs were sufficiently provisioned that supplementary foraging was not necessary for survival; the frequency of foraging did not increase over the seven years of the study (Keith-Lucas et al., 1999). Provisioning therefore should be minimal but sufficient to support short-term survival (Tear and Ables, 1999). Conclusions in Chapter 4 concur with this finding.

The habitat in which an animal lives has clear implications for its ecology and behaviour. Different habitats will have different resources, different physical features and constraints. In long established environments, behavioural patterns expressed are likely to produce increased fitness and represent the position and adaptation of an organism in relation to its ecological niche. This niche depends not only on where the organism lives but also on what it does. The fit of a society, in this case, chimpanzee society to its environmental setting can be evaluated in terms of the differential budgeting of various routine activities that are vital to individual and group survival. Quantification of behaviour patterns in the form of activity budgets have been offered as a means of expressing the adaptation of an organism to environmental conditions; its habitat type, distribution and type of food resources, conspecific densities, predation levels, etc. Therefore, the examination of activity budgets exhibited by the reintroduced chimpanzees and direct comparison to those of their wild conspecifics may provide a measure of their behavioural and social flexibility, reflect the quality of the pre-release environment, and ultimately their adaptive potential.

6.2 Aims

- To describe the activity budgets of the reintroduced chimpanzees.
- To investigate the influence of sex, life history and ecological variables on activity budgets of the reintroduced chimpanzees to understand behaviour patterns.
- To describe the temporal pattern of activity across the day.
- To examine any changes in activity budgets across the course of the study to assess the extent of change in post-release behaviour.
- To compare the activity budgets of the reintroduced chimpanzees with published data on various wild chimpanzee populations.

6.3 Method

Each individual's (n=15) activity post-release was recorded every 10 minutes using scan sampling with instantaneous recording (see Chapter 5, p.115). This technique was employed as it provided the opportunity to potentially collect data evenly across all individuals, time of day, season, month post-release etc., facilitating comparisons between behavioural and ecological indices.

In the present study the relative proportions of time engaged in various activities have been calculated from the number of scans in each category, for example, a chimpanzee has 100% of possible time and the number of counts for each activity represent a percentage of total time. The total number of data points used to assess activity budgets was 240,673. The number of data points collected per individual varied (Table 6.1). The mean number of observations made for each chimpanzee in Table 6.1 were calculated from the total number of observations divided by the number of months during which observations were made. Activity budget behavioural data were analysed for the first 14 months post-release for each chimpanzee.

Table 6.1 Number and mean number (±SD) of observations taken for each chimpanzee

Chimpanzee	Number of observations	Mean number of observations per month	±SD
Bougnoule	22543	1610	612.04
Yvette	22402	1600	610.68
Mekoutou	19804	1415	653.39
Jeanette	22866	1633	633.98
Choupette	22204	1586	643.16
Rosette	22773	1627	549.07
Massabi	10151	725	264.33
Cabinda	12686	906	106.35
Mossendjo	10165	726	264.94
Hinda	12507	893	144.75
Caline	12148	868	198.96
David	4156	1039	715.51
Agathe	15951	1139	529.42
Sophie	16700	1193	561.21
Koutou	13617	1135	577.35

6.3.1 Activity Budgets

The chimpanzee behavioural regime can be segmented into four basic core categories: feed, rest, travel and interaction with conspecifics (Teleki, 1977; Dunbar, 1988). Core activities can be defined as those actions and interactions that any primate must repeatedly perform in the course of subsisting and socialising over some natural span of time. This elementary yet comprehensive means of collapsing activity categories was also employed in the present study with changes made to two category labels and behaviours included in two activity categories (Table 6.2). Travel implies prolonged locomotion relocating from one place to another, such as moving from one feeding patch to another rather than within. All 'move' behaviours may be associated with the search for food, but they may also be combined with other activities such as patrolling and searching for mates. In practise it is difficult to differentiate these activities and therefore the more general category label of 'move' has replaced 'travel' and employed to include all locomotive movements from A to B regardless of distance. Within 'interact' Teleki (1977) included all instances of groom and play despite some groom being self and some play being solitary in nature. The present study has been rigorous in its allocation of activities to categories. The label of 'interact' has been replaced with 'social' to indicate that only activities judged to involve interaction were included; social groom, social play, copulation and aggression. The implication of refining behavioural categories is discussed later (see p.162 and p.165). Refer back to Table 5.4 (p.118) for detailed definition of behaviours.

Table 6.2 Behaviour categories and definition

Category label	Definition of activities included within category
Feed	Includes all behaviour involved in the direct processing and ingestion of food
Rest	All periods of immobility, both on the ground and in trees
Move	All locomotion both on the ground and within trees
Social	All incidences of social groom (one way and mutual), social play, aggression and copulation

These four categories are so general that they include all or most activities performed by chimpanzees (accounts for approximately a mean 95% of behaviour observed for the reintroduced chimpanzees, see Figure 6.3, p.140). Behaviours that do not readily fit into these four basic categories are likely to be so rare that the budgets comprising the complete regime will remain unaffected (Dunbar, 1988). By compartmentalising the behaviour in this way, the categories can be combined or refined (e.g., by sub-dividing social into groom, play, copulate and aggression), accordingly to specific questions and level of detail required.

6.3.1.1 Overall and daily activity budgets

One aim of this chapter is to compare the activity budgets of the reintroduced chimpanzees with published data collected from various wild chimpanzee populations. This form of meta-analysis has inherent complications, as there is no standardised form of data collection, analysis, and presentation adopted by field workers. Frequently insufficient raw data are presented, preventing readers from manipulating the statistics required for comparative purposes. Therefore the activity budgets in the present study have been calculated and presented in both overall and daily form to facilitate direct comparisons to studies of wild chimpanzee populations (see section 6.4.5, p.160).

For overall activity budgets, the monthly mean percentage for each chimpanzee and activity were calculated and then averaged across the months to get a mean score for each chimpanzee and activity performed. The means were then averaged across chimpanzees to get the overall mean budget for each activity. The same calculation process was used for daily activity budget except months were replaced with mean scores averaged across hours.

Overall and daily mean activity budgets for the four main categories are displayed in Figures 6.3 and 6.5 (p.140 and p.142). The behaviours and their percentages that comprise these categories are shown in Table 6.5 and 6.6 (p.140 and p.142). This is to present the reader with sufficient detail to examine the remaining 5% of activity not accounted for by the four behavioural categories, and to facilitate comparisons between the reintroduced group and wild chimpanzee populations. Behavioural sub-divisions that occur infrequently have been compiled within the category of 'Other'. A further sub-division within 'Other' of 'General other' refers to those activities that fall beyond the limits of general recognisable divisions. They range from stealing equipment from observers, having wounds cleaned by humans and being anaesthetised in order to change radio collars. The percentages of collapsed and sub-divided activities do not always add up to exactly 100% due to rounding.

Throughout this chapter the primary analysis has concentrated on the four main behavioural categories of feed, rest, move and social activities. Social activity includes all instances of social groom, social play, aggression and copulation. Within the category of groom, 97% represents social grooming and therefore only the category of social activity has been included in analyses and not groom as they would not be mutually exclusive. However, for comparative purposes with wild chimpanzee populations the mean percentage time spent grooming has been presented in both overall (Figure 6.4 and Table 6.6, p.141) and daily (Figure 6.6 and Table 6.8, p.143) formats. Furthermore, a t-test was performed to examine potential differences between males and females in time spent grooming. This was necessary to be able to make comparisons to studies on wild chimpanzee populations that have varied in their classifications of behaviours within categories.

Overall activity budgets (not daily) were used to investigate the influence of sex, age, pre-release island and environmental variables (seasonal variation and forest type). For descriptions of forest type refer to Chapter 3 (p.62-63) and season p.134-135 of this chapter.

Age

To investigate the possible effect of age on activity, the age in years/months that the released chimpanzees would have been exactly mid study (i.e., age at release plus seven months) were calculated and used in analyses. Rather than use actual age at release this method was employed to provide a more representative age of the chimpanzees during the post-release study period. However, actual age at release was used for analyses comparing the overall age of chimpanzees released from the two islands.

6.3.2 Temporal dimensions of activity

Hourly variation in activity schedules

To investigate temporal variation in levels of activity across the day, the proportion of time spent in the four main behavioural categories were examined on an hourly basis. The time that observations were recorded during the day ranged from 05h00 until 19h20. Consequently the day was divided into 15 hourly segments ranging from 05h00 to 20h00 spanning the full diurnal day. However, when considering the first (05h00-05h55) and last (19h00-19h55) hours it must be noted that the number of scans for these times were considerably lower than for all other hours (Figure 6.1, Table 6.3). On the majority of days the chimpanzees had not yet left (am) or had already entered (pm) the sleeping site during hours one and fifteen. In Conkouati hours of sunrise range from 05h50-06h22 and sunset 18h05-18h36 (US Naval observatory web site: http//mach. usno.navy.mil/data//docs/RS_OneYear.html). Data collection normally started when the emerging daylight facilitated safe navigation of the forest and accurate observations, normally from approximately 6h00 onwards. This can be clearly seen in Figure 6.1. The majority of observations were collected during the period of mid morning to mid afternoon. Consequently, observations taken during the first and last hour of the day have not been included in analyses.

Figure 6.1 Mean number of observations made in each hour (±SD)

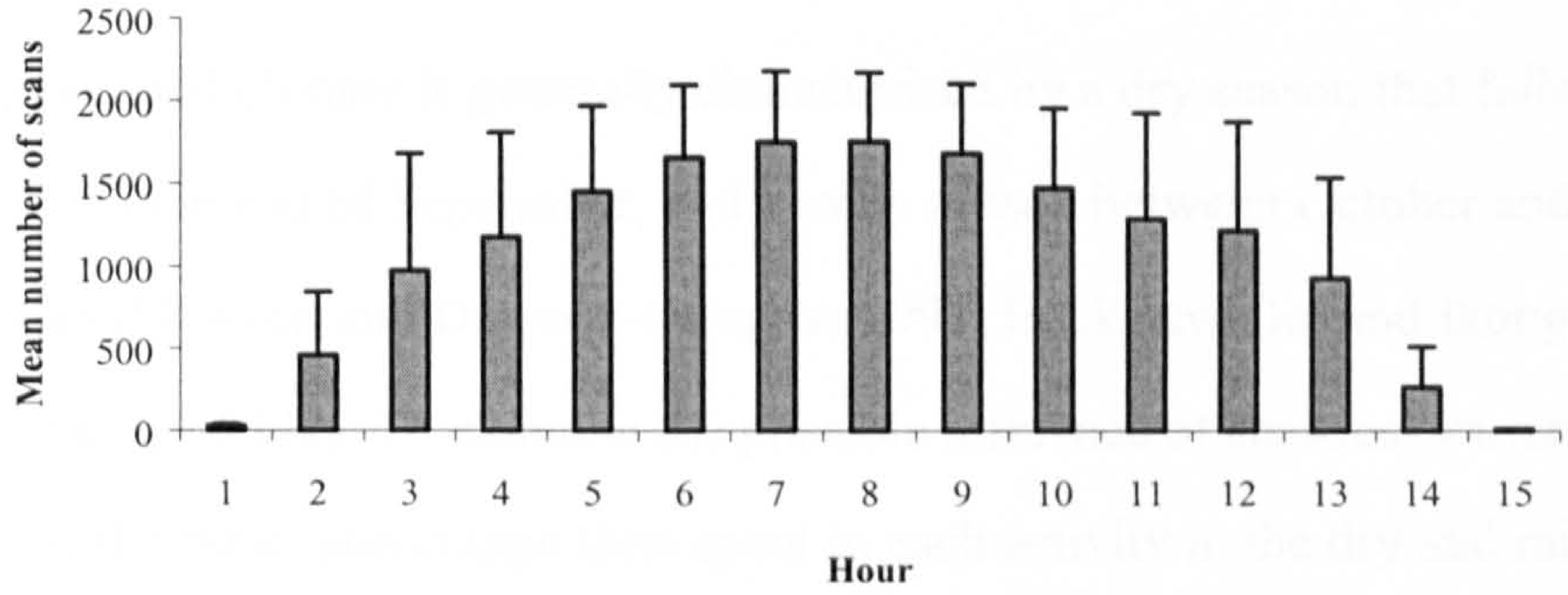


Table 6.3 Number and percentage of observations for each hour of the diurnal day

Hour	Time	n of scans	%
1	05h00-05h55	209	0.09
2	06h00-06h55	6906	2.87
3	07h00-07h55	14576	6.06
4	08h00-08h55	17585	7.30
5	09h00-09h55	21702	9.00
6	10h00-10h55	24731	10.28
7	11h00-11h55	26105	10.85
8	12h00-12h55	26164	10.88
9	13h00-13h55	25150	10.45
10	14h00-14h55	22059	9.17
11	15h00-15h55	19282	8.00
12	16h00-16h55	18182	7.56
13	17h00-17h55	13906	5.78
14	18h00-18h55	4040	1.68
15	19h00-19h55	76	0.03
Total	05h00-19h55	240673	100%

99.88% between hours 2-14

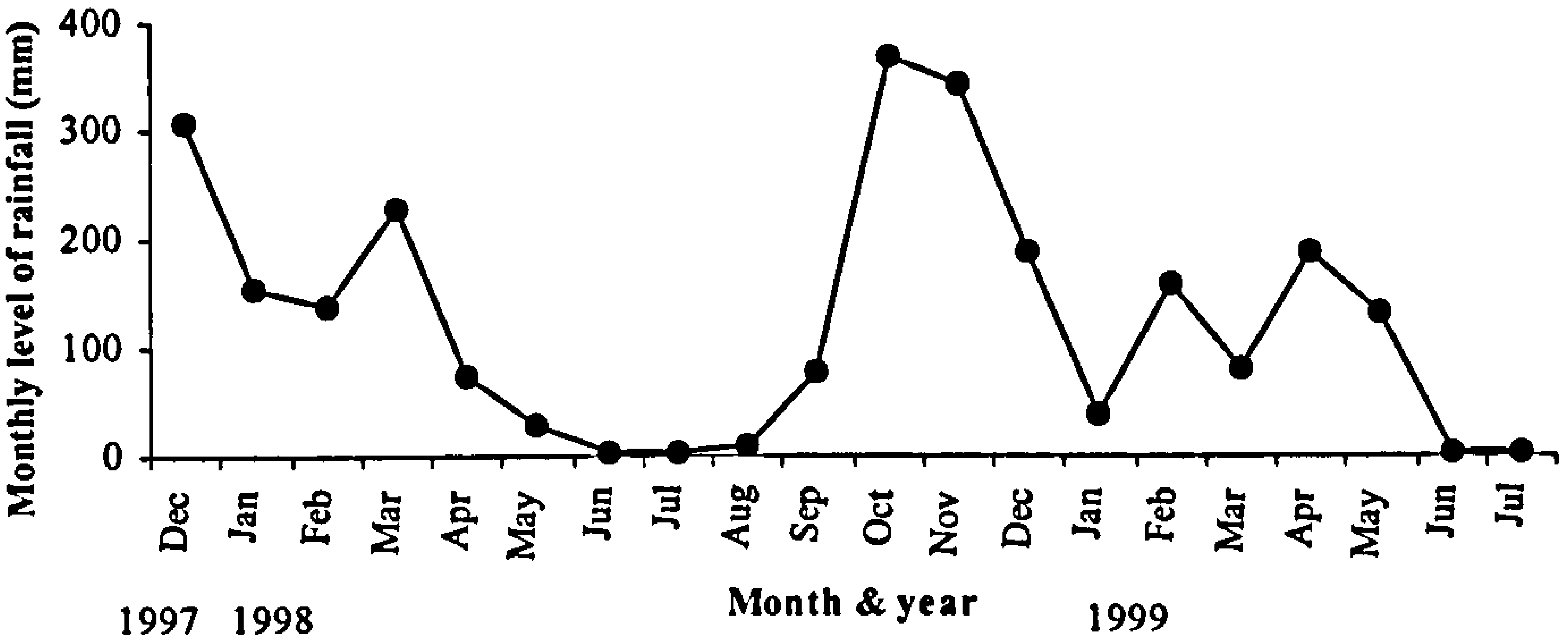
Monthly variation in activity schedules

The mean proportion of time observed in the four main behavioural categories were examined monthly to assess whether, and if so by how much, the activity budgets changed across the course of the 14 month study period. As with time of day, the number of observations made did not remain constant across the months (see Chapter 5, Table 5.5, p.119). David (4156 data points) was excluded from all analyses in this section due to his disappearance four months post-release. Likewise, Koutou (13617 data points) was excluded from all monthly analyses due to two disappearances during month one and thirteen when no observations were made.

6.3.3 Seasonal classification

The regional climate is generally characterised by a dry season that falls between mid May and the end of September, and a rainy season between October and the beginning of May (Dowsett and Dowsett-Lemaire, 1991; Hecketsweiler and Ikonga, 1991; Doumenge, 1992). To examine the possible influence of seasonal variation on activity levels, the mean percentage time spent in each activity in the dry and rainy season, were compared (see section 3.2, p.61-62 for a full description of climatic variables). Climatic data were collected at the release site consistently during 1998 and the earlier half of 1999 (Figure 6.2).

Figure 6.2 Level of monthly rainfall (mm) at the base camp release site in the Conkouati-Douli National Park



A distinct pattern emerged with virtually no rain in months June, July and August in 1998 and for June and July in 1999, with varying levels of rain throughout the rest of the year peaking in October and November. This mean level of rainfall was used as a guide to determine which months fell into the two seasons as they are site specific and more recent than other climatic data (Dowsett and Dowsett-Lemaire, 1991; Hecketsweiler and Ikonga, 1991; Doumenge, 1992). Only the three months of June, July and August were categorised as comprising the dry season. In contrast to Doumenge (1992) the months of May and September were excluded from the category of dry season as a similar mean level of rainfall found in these two months were also found in January and March. Therefore the remaining nine months of the year were classified as the rainy season. Furthermore, initial analyses were run with both the present seasonal categories and that of Doumenge (1992). The results were the same but only those of the present classification are presented.

6.3.4 Activity budgets of wild chimpanzee populations

A thorough literature review on wild chimpanzee activity budgets revealed ten frequently quoted studies conducted at five different field sites. There was only one other study that has collected data on a group of reintroduced chimpanzees to include as a comparison. The activity budgets and information thought to be possible influencing factors such as habitat type, season during which study was conducted, age and sex of chimpanzee, and type of budget measurement were all included on a table to facilitate comparison and discussion (see Table 6.19, p.161). Overall, 13 descriptions of forest type, nine age categories, and three main types of analyses for budget presentation are presented. Five of these studies presented data 'overall', three 'daily' and two 'hours per day'. In only two cases where studies presented data 'overall' did the authors specify how the data had been manipulated to produce the budget. Wrangham (1977) calculated the overall budget from monthly figures as in the present study, and Fawcett (2000) pooled scores into time blocks corresponding to two week phenology periods, and calculated proportions from total number of scores for each period. It has only been possible to include the size of study population in five out of 11 studies. Frequently figures were provided of approximate group numbers and composition, but not corresponding numbers for analyses. Without knowing the criteria for inclusion and exclusion of age and sex class, approximations of group size cannot be estimated. For example, sub-adults still dependent on their mothers have activity profiles closely linked to the schedules of their adult companions. Furthermore, many activities may not yet be routinely performed at certain points along the life cycle, and therefore some authors such as Teleki (1981) chose to exclude them from analyses. There has only been one other study that has collected data on a reintroduced chimpanzee group and this was limited (Hladik, 1973). Only levels of feeding activity were collected and presented in an 'hours per day' format.

6.3.5 Statistical analyses

All analyses in this chapter have been performed on mean percentage scores. Although these may result in losing some degree of detail, within the present data set where data were not collected evenly for each chimpanzee, the use of percentages not only offers the best solution but also allows the data to answer fully the questions posed. Data were tested for normality as outlined in Chapter 5 (p.121). Where possible, error bars representing standard deviations have been presented on figures. However, where a large number of multi-comparison tests have been run, it has not always been possible to include all.

Variables were analysed using ANOVA's, Bonferroni post-hoc tests, t-tests (2-tailed) and Pearsons correlation (2-tailed) where applicable. Table 6.4 details the analyses; the number of chimpanzees included in each analysis, months and hours included, data type, activity included and tests performed for each analysis. Due to the large number of post-hoc tests generated by the multivariate analyses, only significant and non-significant results illustrating a pattern of activity are presented.

Table 6.4 Details of statistical analyses performed on activity budgets and patterns of behaviour

Analysis	Chimpanzees	Months/hours	Data	Behaviour	Test
Overall activity budgets	n=15	Months 1-14 Hours 2-14	Overall mean (chimp/month)	All	Pie charts
Daily activity budgets	n=15	Months 1-14 Hours 2-14	Overall mean (chimp/hour)	All	Pie charts
Sex	♀ = 11 ♂ = 4	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor sex, within factor activity) and Bonferroni post-hoc tests
Pre-release island	Yvette = 9 Yombe = 6	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor island, within factor activity) and Bonferroni post-hoc tests
Age on islands	n = 14 (no David)	N/A	Age per chimp per pre-release island	N/A	Independent t-test (2-tailed)
Age vs activity	n = 14 (no David) ♀ = 11 ♂ = 3	Months 1-14 Hours 2-14	Overall mean (chimp/month) Age at release + 7 months	Feed, move, rest, social	Pearsons product moment correlation (2-tailed)
Seasonal variation	n = 14 (no David as only present in rainy season)	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor season, within factor activity) and Bonferroni post-hoc tests
Forest type	n = 11 (no David, Agathe, Sophie, Koutou)	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor forest, within factor activity) and Bonferroni post-hoc tests
Temporal patterns					
Hourly	n = 15	Months 1-14 Hours 1-15	Mean of hour per chimp	Feed, move, rest, social	Graphical display
Hourly	n = 15	Months 1-15 Hours 2-14	Mean of hour per chimp	Feed, move, rest, social	Repeated measures ANOVA (between factor hour, within factor activity) and Bonferroni post-hoc tests
Monthly	n = 13 (no David or Koutou)	Months 1-14 Hours 2-14	Mean of month per chimp	Feed, move, rest, social	Graphical display
Monthly	n = 13 (no David or Koutou)	Months 1-14 Hours 2-14	Mean of month per chimp	Feed, move, rest, social	Repeated measures ANOVA (between factor month, within factor activity) and Bonferroni post-hoc tests

6.4 Results

6.4.1 Overall and daily activity budgets

Analyses showed that the majority of time was spent feeding and in other activities associated with the indirect ingestion of food; moving and resting. This accounted for approximately 92% of all activity performed (Figure 6.3). Nearly twice as much time was spent feeding in comparison to resting, and resting in comparison to moving. Very little time was devoted to social activities (2.87%), and approximately the same amount of time was devoted to grooming (2.57%) (Figure 6.4). The majority of both groom and play were social in form (Table 6.6) and of the total time engaged in social activity, groom predominated (Table 6.5). Table 6.5 (corresponds to Figure 6.3) and Table 6.6 (corresponds to Figure 6.4) details behavioural subdivisions.

Analyses of daily activity budgets showed the same pattern as overall activity budget. The majority of time was spent feeding and in other related activities such as moving and resting (Figure 6.5 and Table 6.7). As with overall activity budgets the majority of daily groom and play were social in form (Table 6.7). Table 6.7 (corresponds to Figure 6.5) and Table 6.8 (corresponds to Figure 6.6) details daily behavioural subdivisions.

Figure 6.3 Overall mean time engaged in core activities (number of scans in brackets)

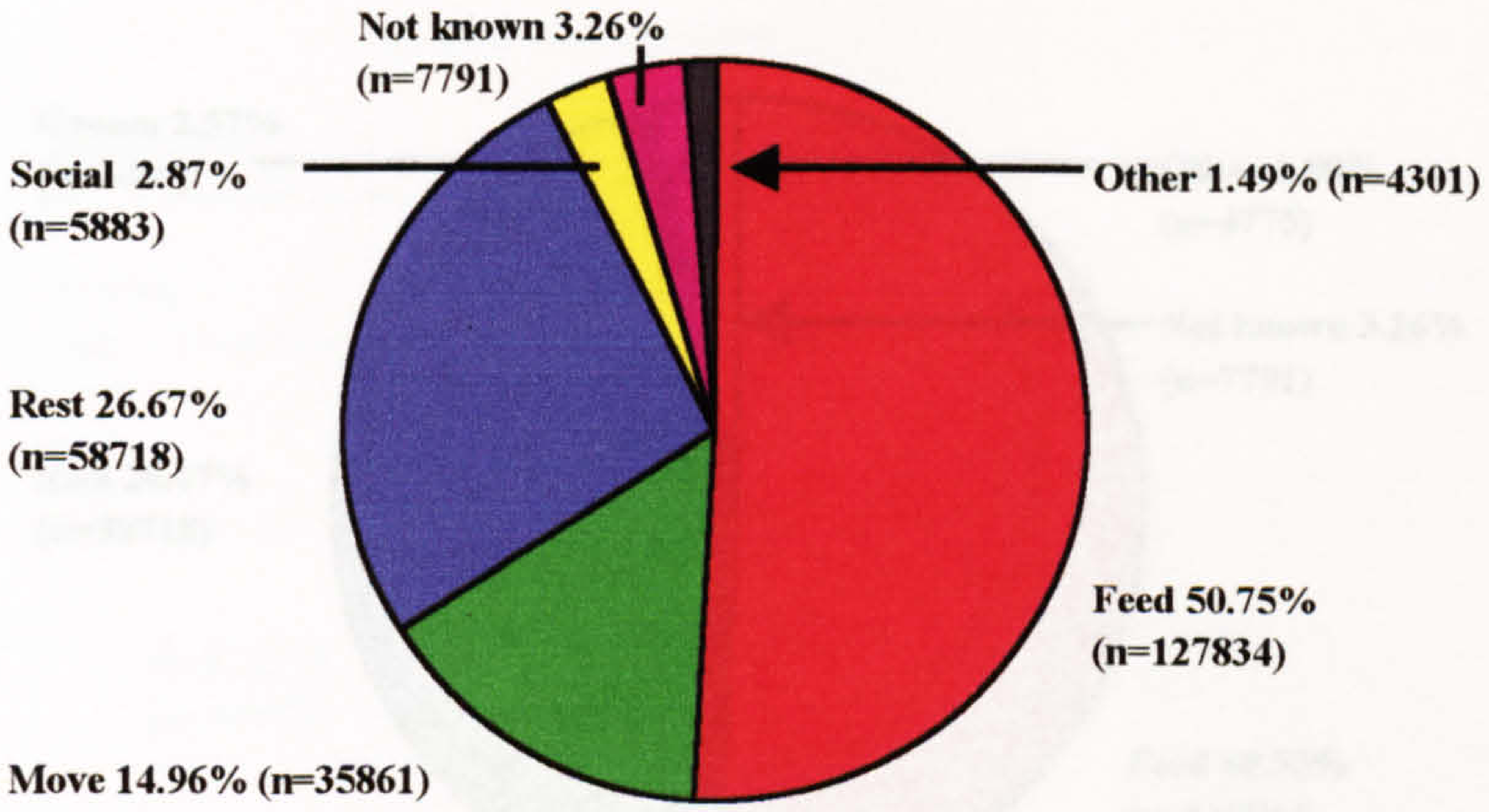


Table 6.5 Overall mean time engaged in core and non-core activities

Behavioural categories	Subdivisions	Mean %	n	% within category
Social	Groom	2.50	5237	(85 %)
	Play	0.24	436	(8.68%)
	Copulate	0.07	86	(2.43%)
	Aggression	0.06	124	(2.08%)
	Sub-total	2.87	5883	(100%)
Rest	General rest	25.05	53684	
	In day nest	0.11	265	
	In night nest (evening)	1.18	3631	
	In night nest (early morning)	0.35	1138	
	Sub-total	26.69	58718	
Other	Self-groom	0.06	160	
	Non-identified groom	0.01	12	
	Solitary Play	0.03	84	
	Non-identified play	0.04	85	
	Drinking	0.07	188	
	Drinking urine	0.03	39	
	Coprophagy	0.89	2773	
	Nest making (day & night nests)	0.27	786	
	Urinate/defecate	0.03	42	
	General other	0.07	132	
	Sub-total	1.49	4301	

Figure 6.4 Overall mean time engaged in core and groom activities (number of scans in brackets)

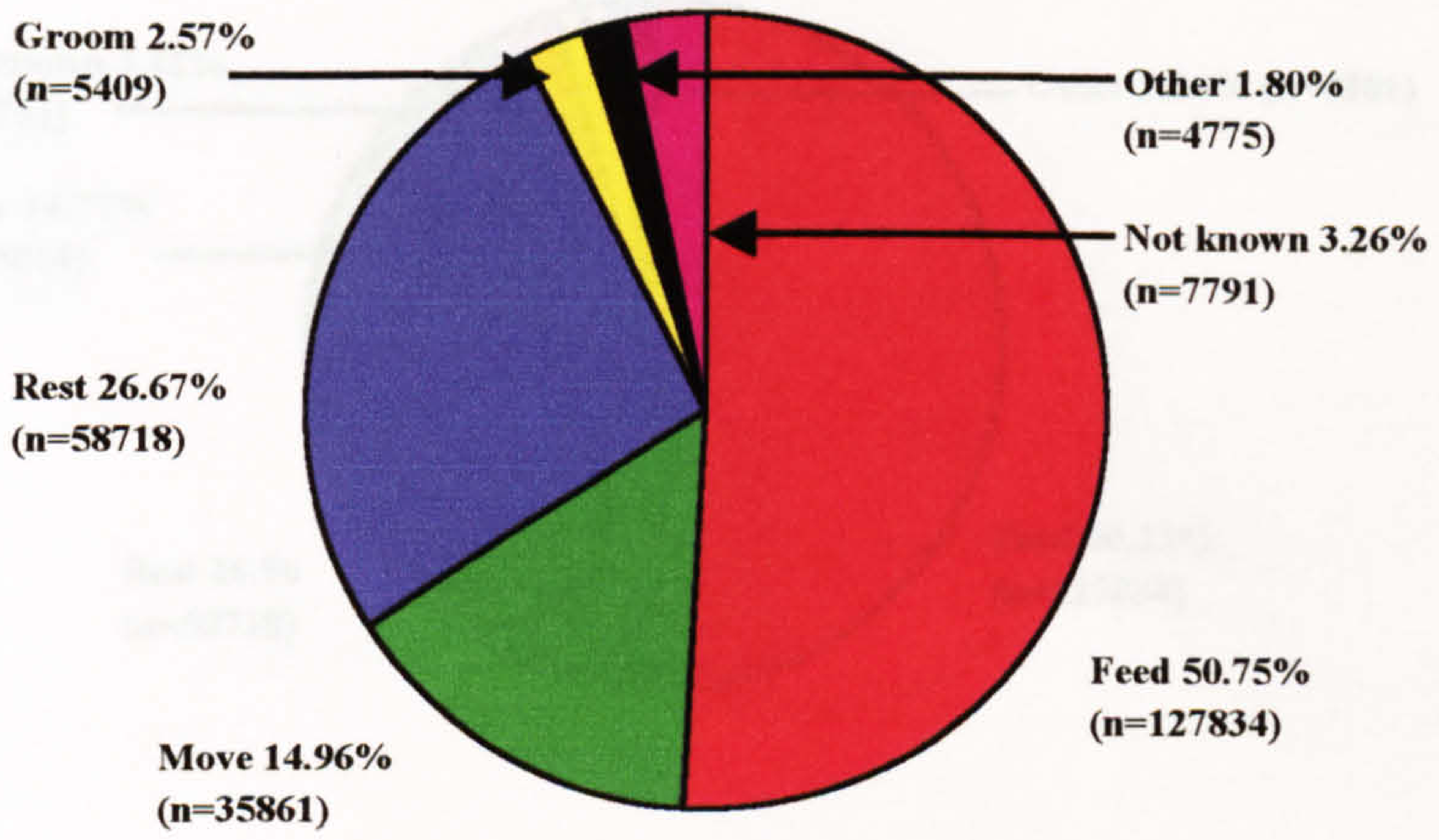


Table 6.6 Overall mean time engaged in core activities with groom, play and non-core sub divisions

Behavioural categories	**Subdivisions**	**Mean %**	**n**	**% within category**
Groom	Social	2.50	5237	(97.28%)
	Self	0.06	160	(2.33%)
	Non-identified	0.01	12	(0.39%)
	Sub-total	2.57	5409	
Rest	General rest	25.05	53684	
	In day nest	0.11	265	
	In night nest (evening)	1.18	3631	
	In night nest (early morning)	0.35	1138	
	Sub-total	26.69	58718	
Other	Social play	0.24	436	(77.42%)
	Solitary play	0.03	84	(9.68%)
	Non-identified play	0.04	85	(12.90%)
	(Play ***Sub-total***	**0.31**	**605)**	(100%)
	Aggression	0.06	124	
	Copulate	0.07	86	
	Drinking	0.07	188	
	Drinking urine	0.03	39	
	Coprophagy	0.89	2773	
	Nest making (day & night nests)	0.27	786	
	Urinate/defecate	0.03	42	
	General other; falling outside of recognisable categories	0.07	132	
	Sub-total	1.80	4775	

Figure 6.5 Daily mean time engaged in core activities (number of scans in brackets)

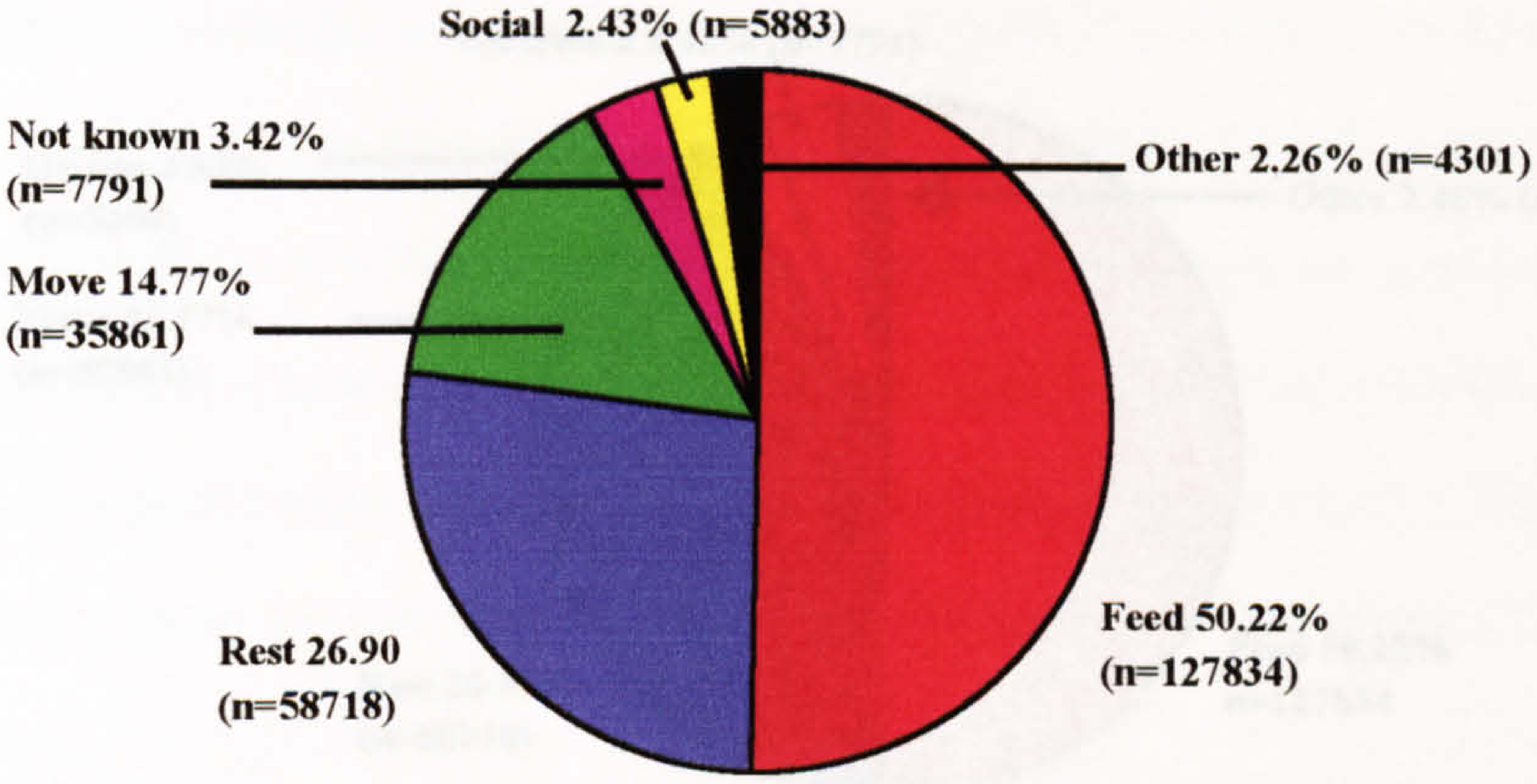


Table 6.7 Daily mean time engaged in core and non-core activities

Behavioural categories	Subdivisions	Mean %	n	% within category
Social	Groom	2.15	5237	(89.02%)
	Play	0.15	436	(7.41%)
	Copulate	0.07	86	(1.46%)
	Aggression	0.06	124	(2.11%)
	Sub-total	2.43	5883	(100%)
Rest	General rest	21.70	53684	
	In day nest	0.09	265	
	In night nest (evening)	3.81	3631	
	In night nest (early morning)	1.30	1138	
	Sub-total	26.90	58718	
Other	Self groom	0.07	160	
	Non-identified groom	0.01	160	
	Solitary play	0.03	84	
	Non-identified play	0.05	85	
	Drinking	0.07	188	
	Drinking urine	0.04	39	
	Coprophagy	0.93	2773	
	Nest making (day & night nests)	0.91	786	
	Urinate/defecate	0.09	42	
	General other	0.06	132	
	Sub-total	2.26	4301	

Figure 6.6 Daily mean time engaged in core and groom activities (number of scans in brackets)

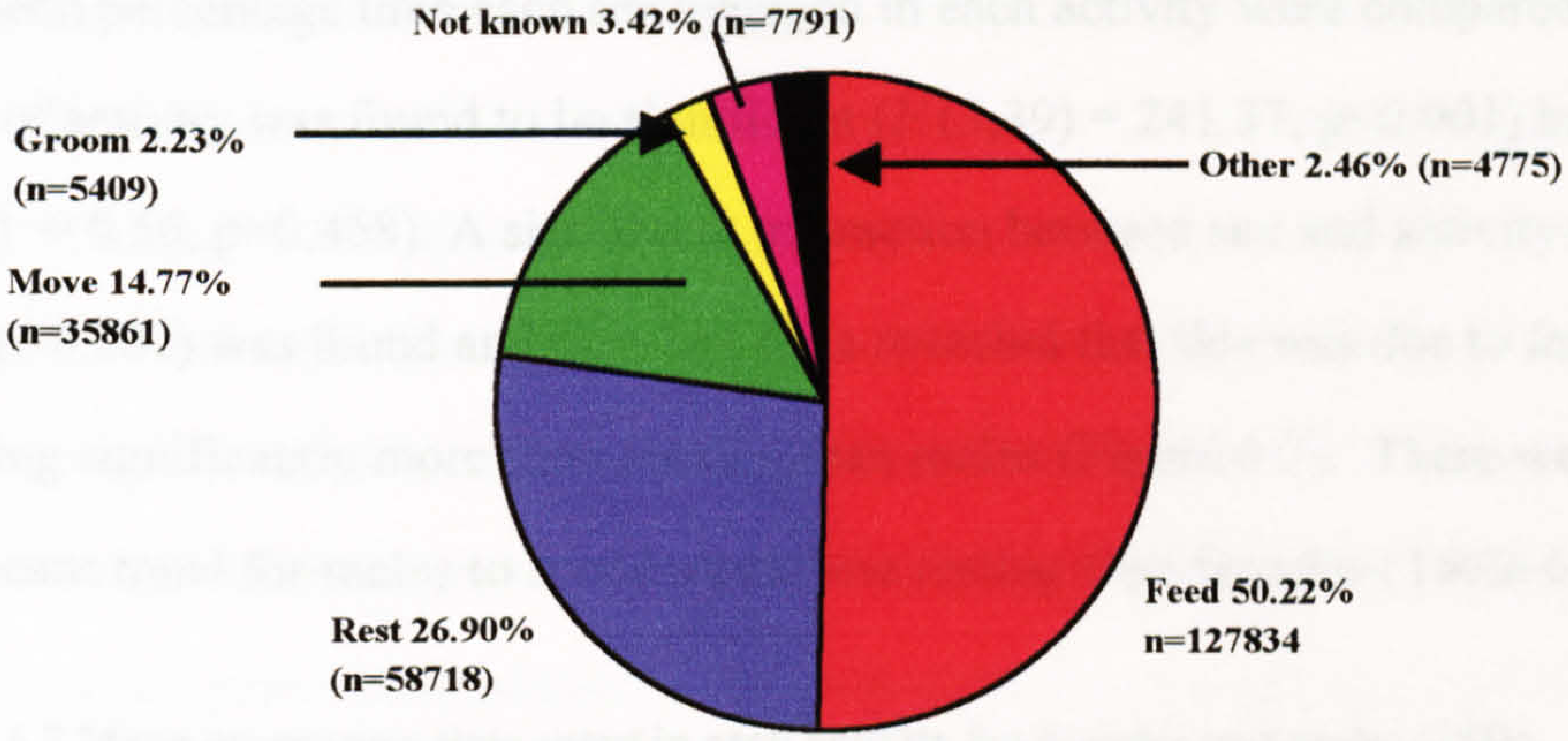


Table 6.8 Daily mean time engaged in core activities with groom, play and non-core sub- divisions

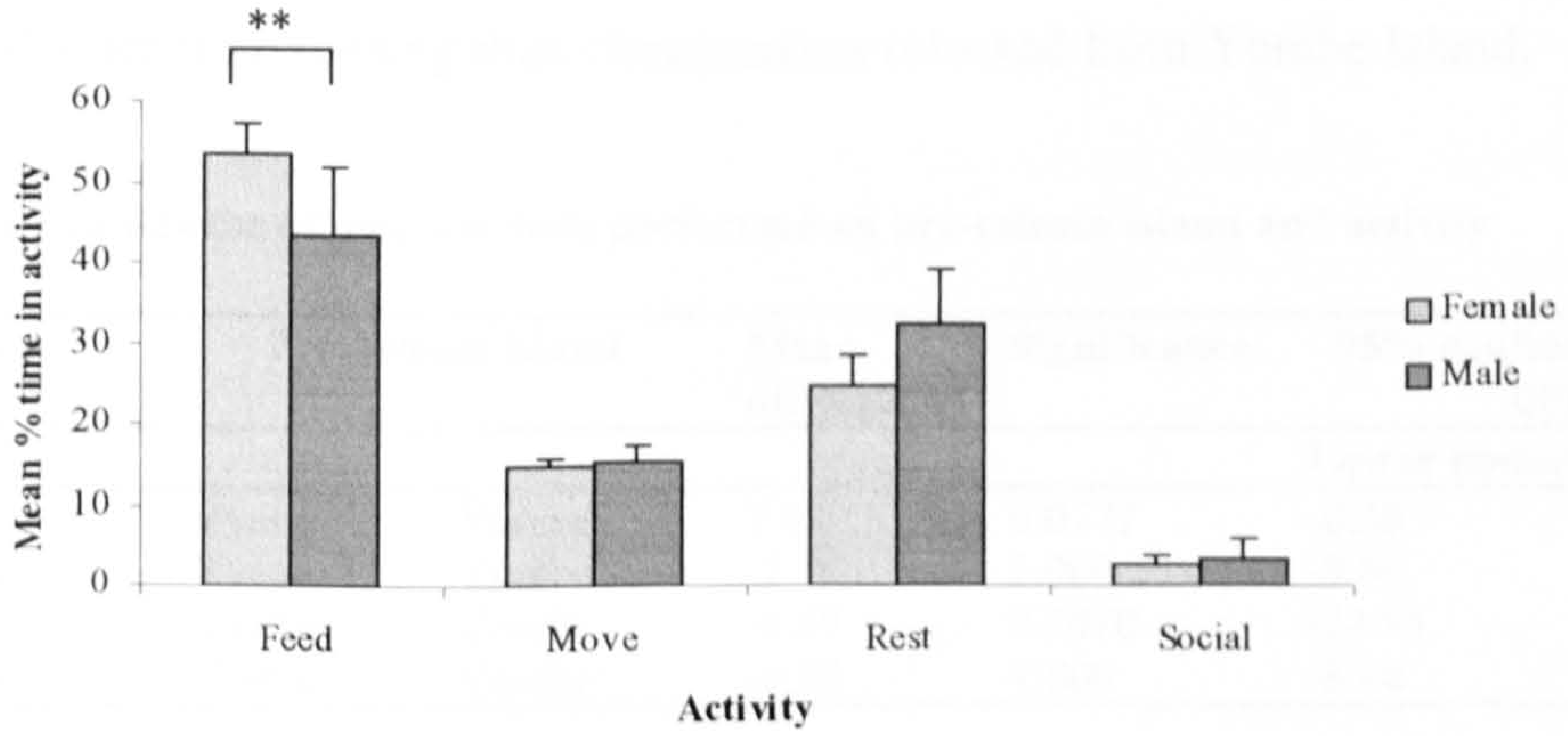
Behavioural categories	Subdivisions	Mean %	n	% within category
Rest	General rest	21.70	53684	
	In day nest	0.09	265	
	In night nest (evening)	3.81	3631	
	In night nest (early morning)	1.30	1138	
	Sub-total	26.90	58718	
Groom	Social	2.15	5237	(96.41%)
	Self	0.07	160	(3.14%)
	Non-identified	0.01	12	(0.45%)
	Sub-total	2.23	58718	(100%)
Other	Social play	0.15	436	(65.22%)
	Solitary play	0.03	84	(13.04%)
	Non-identified play	0.05	85	(21.74%)
	(Play *Sub-total*	**0.23**	**605)**	(100%)
	Aggression	0.06	124	
	Copulate	0.07	86	
	Drinking	0.07	188	
	Drinking urine	0.04	39	
	Coprophagy	0.93	2773	
	Nest making (day & night nests)	0.91	786	
	Urinate/defecate	0.09	42	
	General other	0.06	132	
	Sub-total	2.46	4301	

6.4.2 Sex, pre-release island, and age differences

6.4.2.1 Sex

The mean percentage time each sex engaged in each activity were compared. The main effect of activity was found to be significant (F (3,39) = 241.37, $p<0.001$) but not sex (F (1, 13) = 0.56, $p=0.468$). A significant interaction between sex and activity (F (3,39) = 8.85, $p<0.001$) was found and post-hoc tests revealed that this was due to females spending significantly more time feeding than males (Figure 6.7). There was a non-significant trend for males to spend more time resting than females (Table 6.9).

Figure 6.7 Mean percentage time spent in each activity for females and males (±SD)



**p<0.01

Table 6.9 Results of post-hoc tests performed on sex and activity

Activity	Sex		Mean difference	Significance	95% confidence interval for difference	
					Lower bound	Upper bound
Feed	♂	♀	-10.17	0.0064**	-18.56	-1.77
Move	♂	♀	0.76	1.0000	-7.63	9.16
Rest	♂	♀	7.90	0.0860	-0.49	16.30
Social	♂	♀	0.52	1.0000	-7.88	8.92

**p<0.01

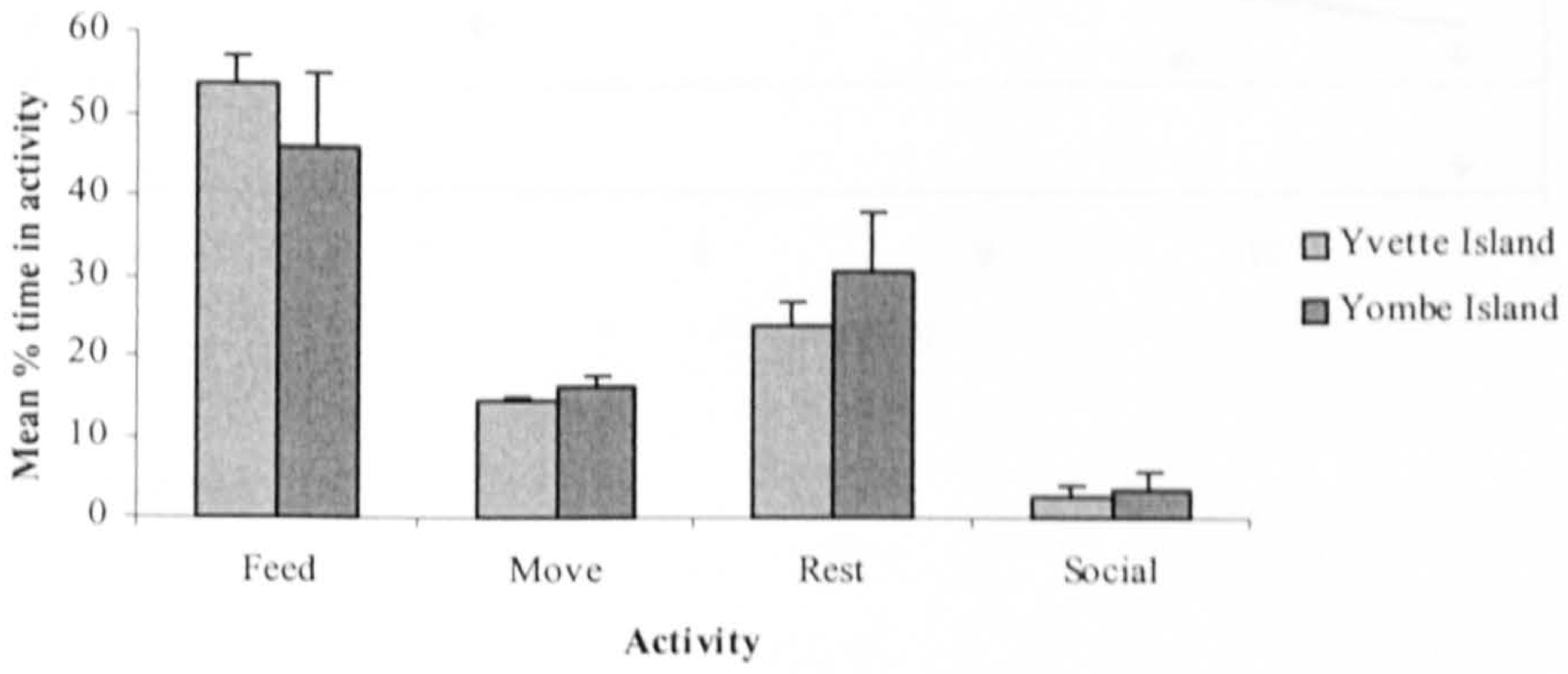
6.4.2.2 Pre-release island

To examine the possible influence that a pre-release island may have had on post-release behaviour, the mean percentage time engaged in each activity for chimpanzees released from Yombe and Yvette Island were compared. A significant main effect of activity (*F* (3,39) = 278.76, $p<0.001$) but not pre-release island (*F* (1,13) = 0.15, $p=0.70$) were found, and a significant interaction of island and activity (*F* (3,39) = 131.40, $p=0.001$). However, post-hoc tests revealed that there were no significant differences in the mean percentage time that chimpanzees spent in each of the four activities when pre-release islands were compared for each activity (Table 6.10, Figure 6.8). There was a non-significant trend for chimpanzees released from Yvette Island to spend more time feeding than chimpanzees released from Yombe Island.

Table 6.10 Results of post-hoc tests performed on pre-release island and activity

Activity	Pre-release island		Mean difference	Significance	95% confidence interval for difference	
					Lower bound	Upper bound
Feed	Yvette	Yombe	7.68	0.0772	-0.38	15.75
Move	Yvette	Yombe	-1.74	1.000	-9.80	6.32
Rest	Yvette	Yombe	-6.89	0.1870	-14.95	1.17
Social	Yvette	Yombe	-0.92	1.000	-8.98	7.14

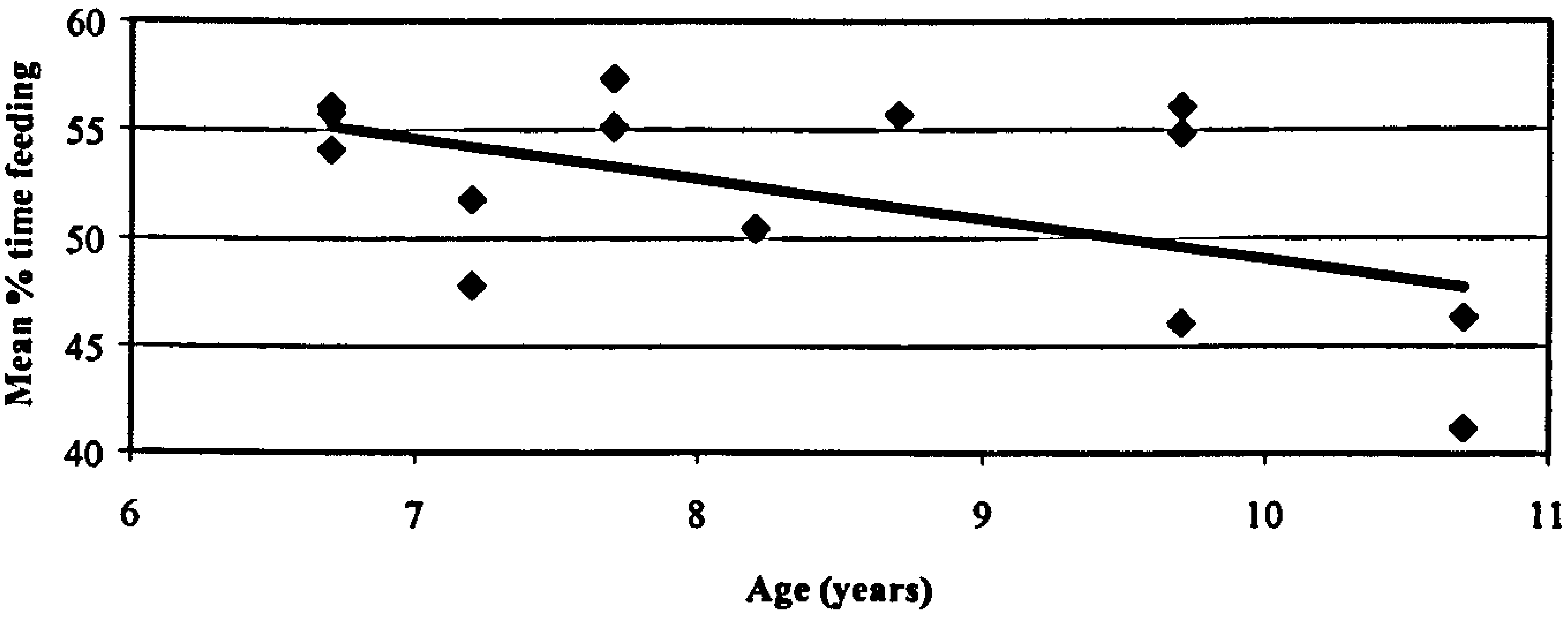
Figure 6.8 Mean percentage time spent in each activity for each pre-release island (±SD)



6.4.2.3 Age

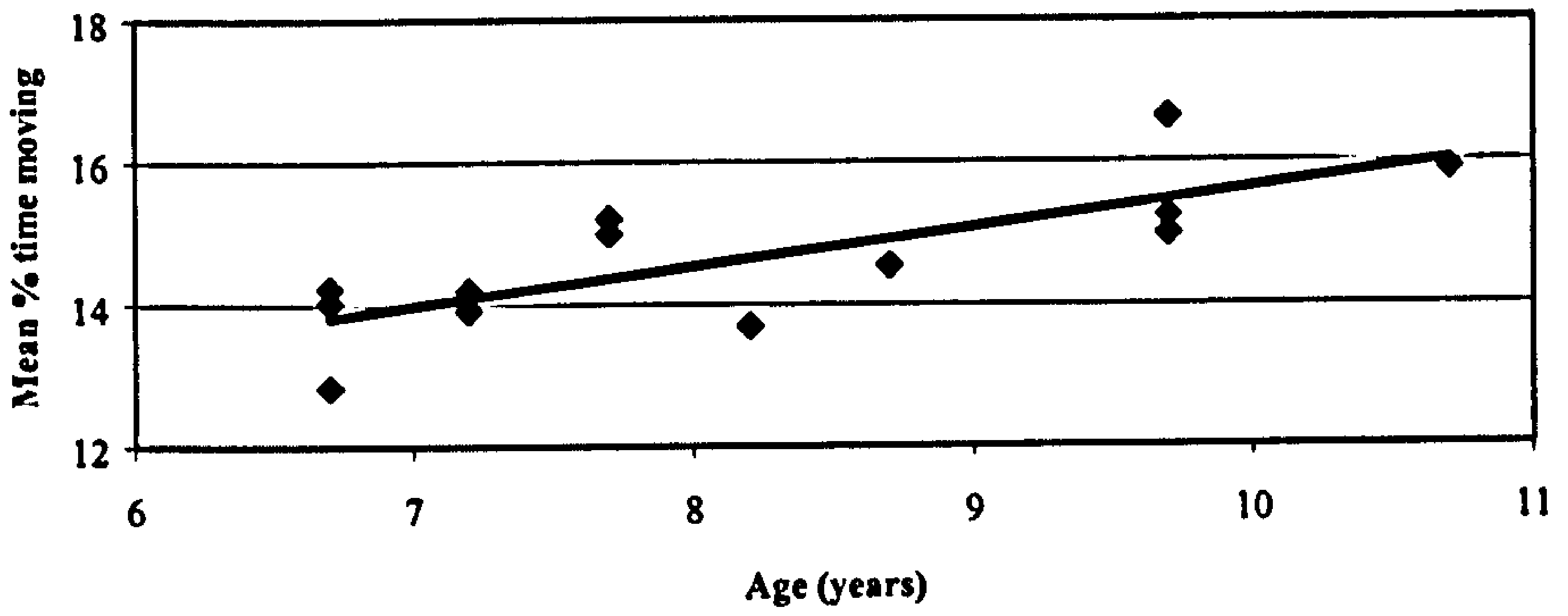
The mean age of chimpanzees released from Yombe Island was nine years (±1.30) in comparison to seven years (±1.21) for Yvette Island. This mean difference reached statistical significance, and the chimpanzees from Yombe Island were significantly older upon release than those from Yvette island (t (12) = 2.52, p=0.027). To examine the possible effect that age may have had on time engaged in the activities, a series of correlation's were run. Chimpanzees were found to engage in less feeding activity (r = -0.56, n=14, p=0.039) but more movement (r = 0.79, n=14, p=0.001) as age increased. No significant correlation's were found between age and rest (r = 0.45, n=14, p=0.11) or social activities (r = 0.01, n=14, p=0.96). Figures 6.9-6.12 illustrate the relationship, or lack of relationship, between age and the four variables. Correlation's performed on age and activity for each sex separately revealed that only moving was significant; the older the female chimpanzee, the more mean time was spent moving (r =0.74, n =11, p=0.009).

Figure 6.9 Relationship between age and time spent feeding



*p<0.05

Figure 6.10 Relationship between age and time spent moving



**p<0.01

Figure 6.11 Relationship between age and time spent resting

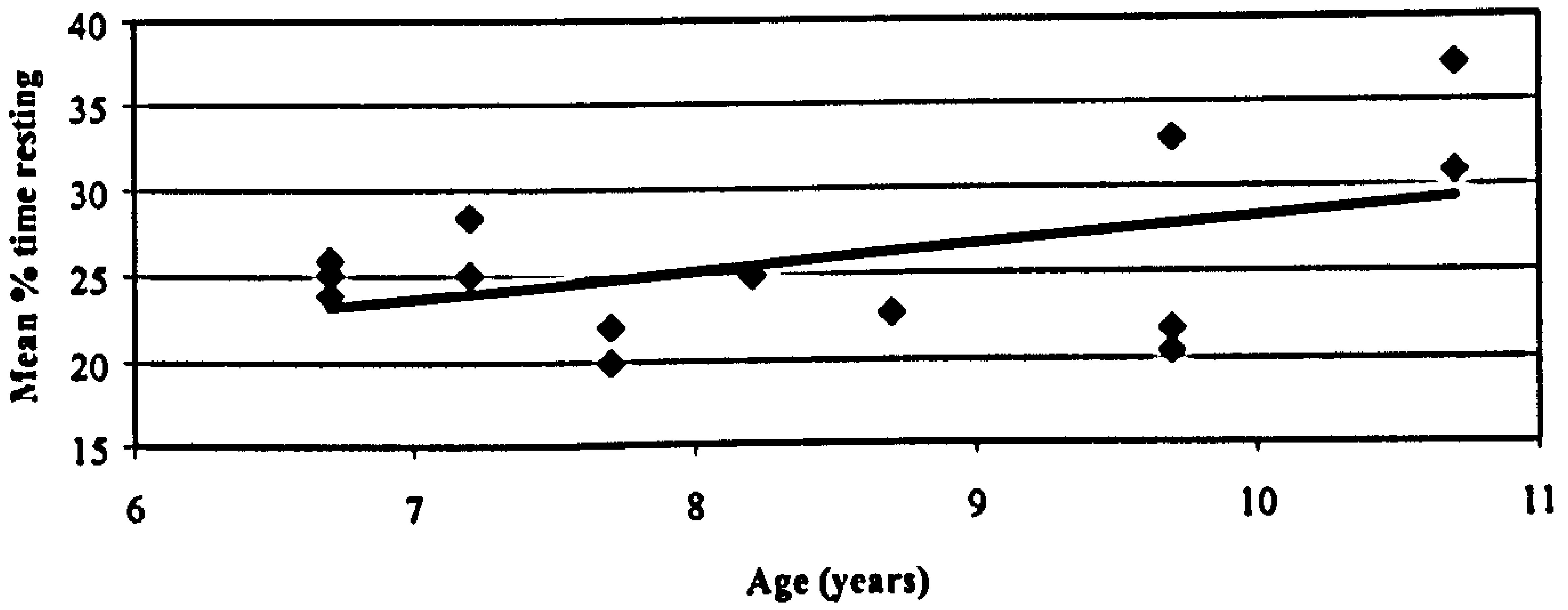
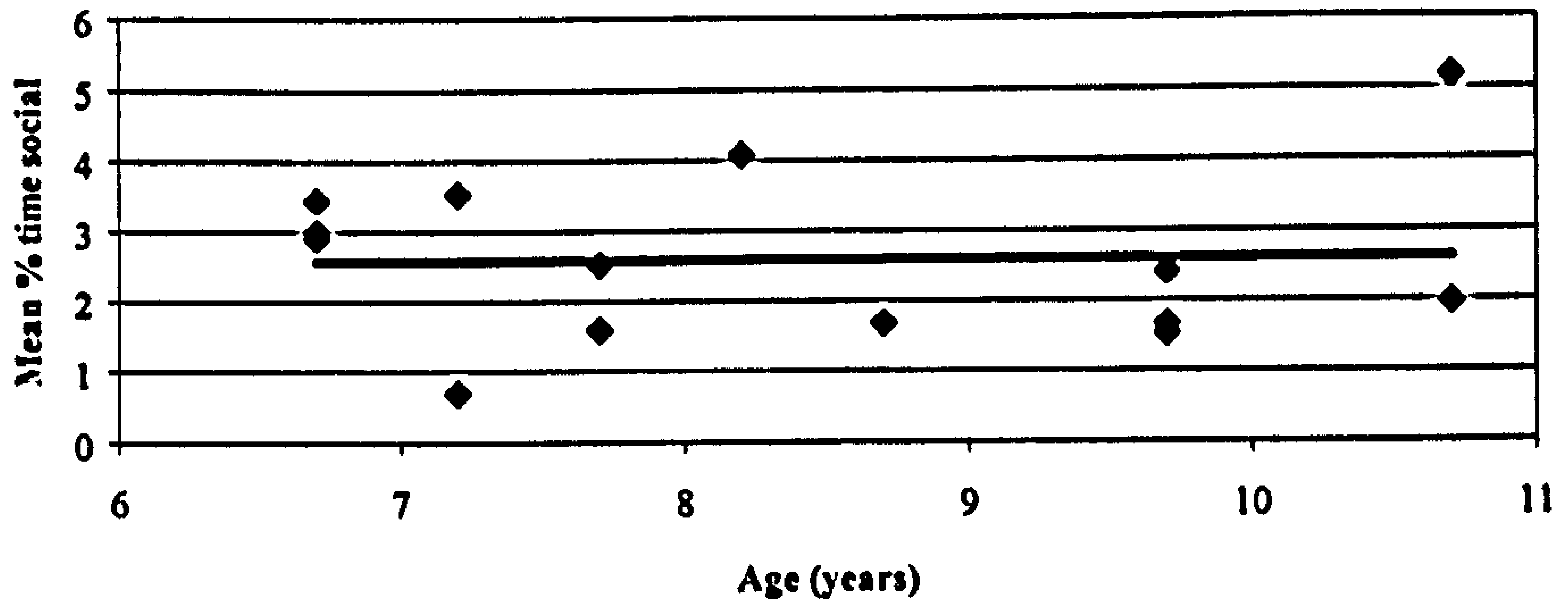


Figure 6.12 Relationship between age time spent in social activities



6.4.3 Environmental differences in activity budgets

6.4.3.1 Season

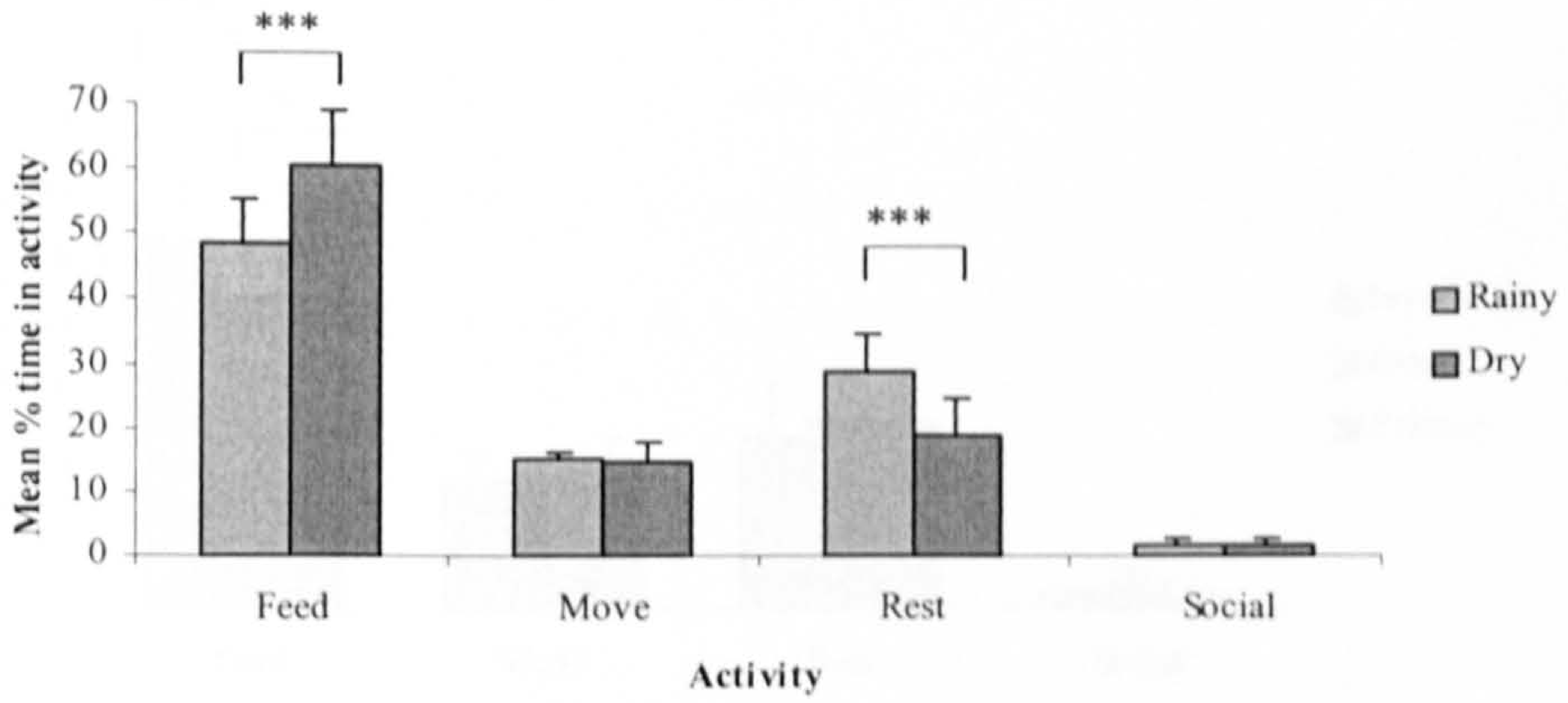
Effects of seasonal influence on activity budgets were examined. Significant main effects of activity (*F* (3.39) = 365.94, $p<0.001$) and season (*F* (1,13) = 7.47, $p=0.017$) were found. Post-hoc tests revealed that a significant interaction between season and activity (*F* (3, 39) = 37.04, $p<0.001$) was due to the chimpanzees spending more time feeding but less time resting in the dry season than the rainy season (Table 6.11). There were no significant differences in time spent moving or within social activities in the dry and wet season (Figure 6.13).

Table 6.11 Results of post-hoc tests performed on season and activity

Activity	Season		Mean difference	Significance	95% confidence interval for difference	
					Lower bound	Upper bound
Feed	Dry	Rainy	35.21	<0.001***	6.49	15.44
Move	Dry	Rainy	-0.08	1.000	-4.39	4.56
Rest	Dry	Rainy	8.91	<0.001***	-13.39	-4.43
Social	Dry	Rainy	-0.29	1.000	-4.19	4.77

***p<0.001

Figure 6.13 Mean percentage time spent in each activity and season (±SD)

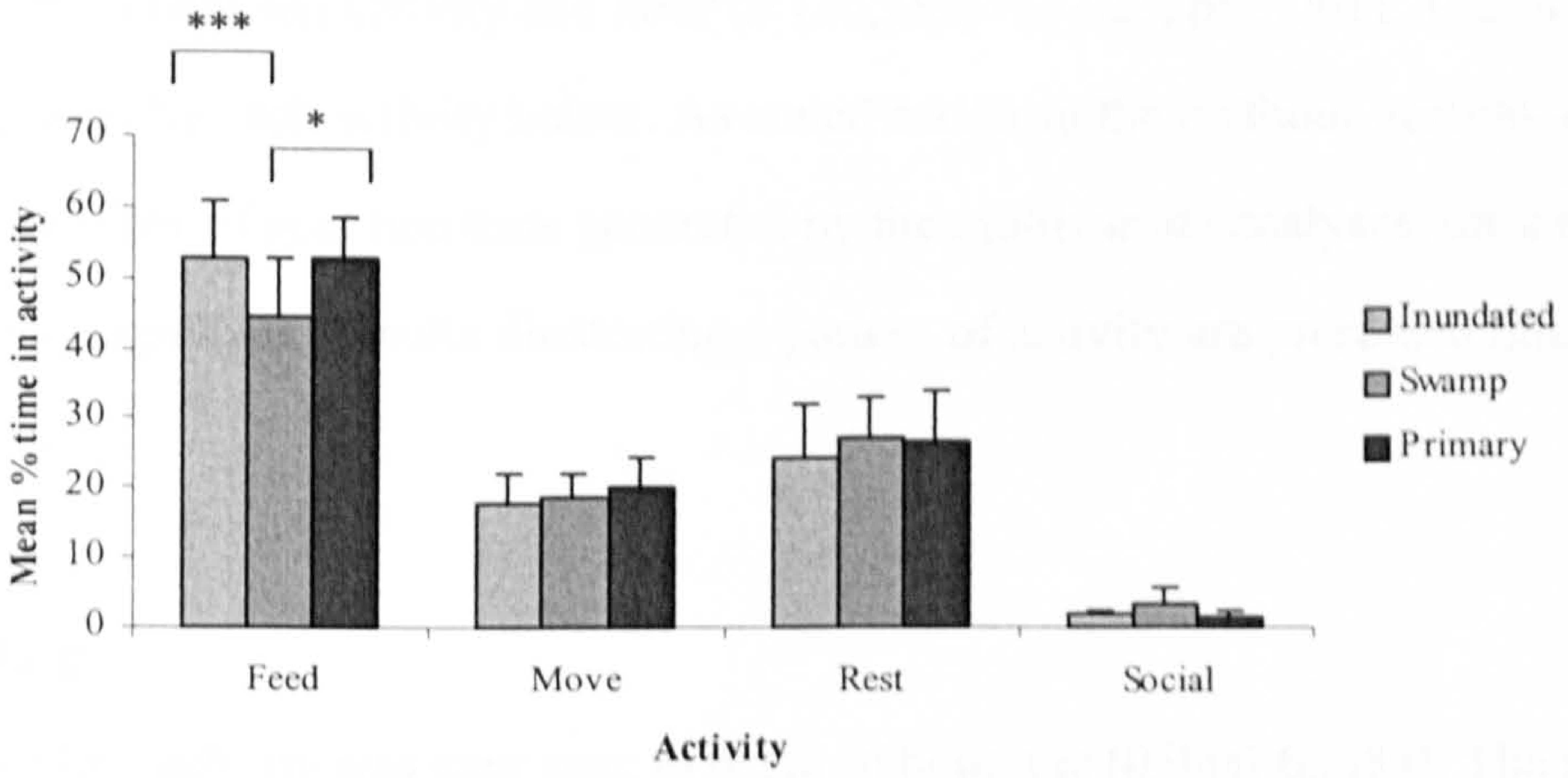


***p<0.001

6.4.3.2 Forest

The mean percentage time spent in each activity across the three forest types; inundated, swamp, and primary were examined. A significant main effect of activity (*F* (3,30) = 307.10, p<0.001) and forest (*F* (2,20) = 4.66, p=0.022) were found. A significant interaction of activity and forest (*F* (6,60) = 5.84, p<0.001) was a result of chimpanzees spending more mean time engaged in feeding activity when in inundated and primary forests compared to swamp forest (Figure 6.14). There were no significant differences in the mean percentage time spent moving, resting and within social activities in the different forest types (Table 6.12). Due to missing values in primary forest for four of the chimpanzees, the sample size was reduced to 11 for these analyses. However, to examine the possible effect that the reduced sample size may have had on the results, the same analyses were performed for all subjects comparing inundated and swamp forest only. The same results were found. Interactions between forest type and season were not examined due to missing values within and across the levels demanded by the factorial design.

Figure 6.14 Mean percentage time spent in each activity and forest type (±SD)



***p<0.001, *p<0.05

Table 6.12 Results of post-hoc tests performed on forest type and activity

Activity	Forest	Forest	Mean difference	Significance	95% confidence interval for difference	
					Lower bound	Upper bound
Feed	Inundated	Swamp	10.40	<0.0001***	-16.97	-3.83
	Inundated	Primary	3.63	1.0000	-10.20	2.94
	Swamp	Primary	-6.77	0.0358*	0.20	13.34
Move	Inundated	Swamp	-0.95	1.0000	-5.62	7.52
	Inundated	Primary	-1.89	1.0000	-4.68	8.46
	Swamp	Primary	-0.93	1.0000	-5.64	7.50
Rest	Inundated	Swamp	-3.44	1.0000	-3.13	10.01
	Inundated	Primary	-3.99	1.0000	-2.58	10.56
	Swamp	Primary	-0.55	1.0000	-6.02	7.12
Social	Inundated	Swamp	-0.74	1.0000	-5.84	7.30
	Inundated	Primary	0.15	1.0000	-6.72	6.42
	Swamp	Primary	0.88	1.0000	-7.45	5.69

*p<0.05, ***p<0.001

6.4.4 Temporal variation in activity budgets

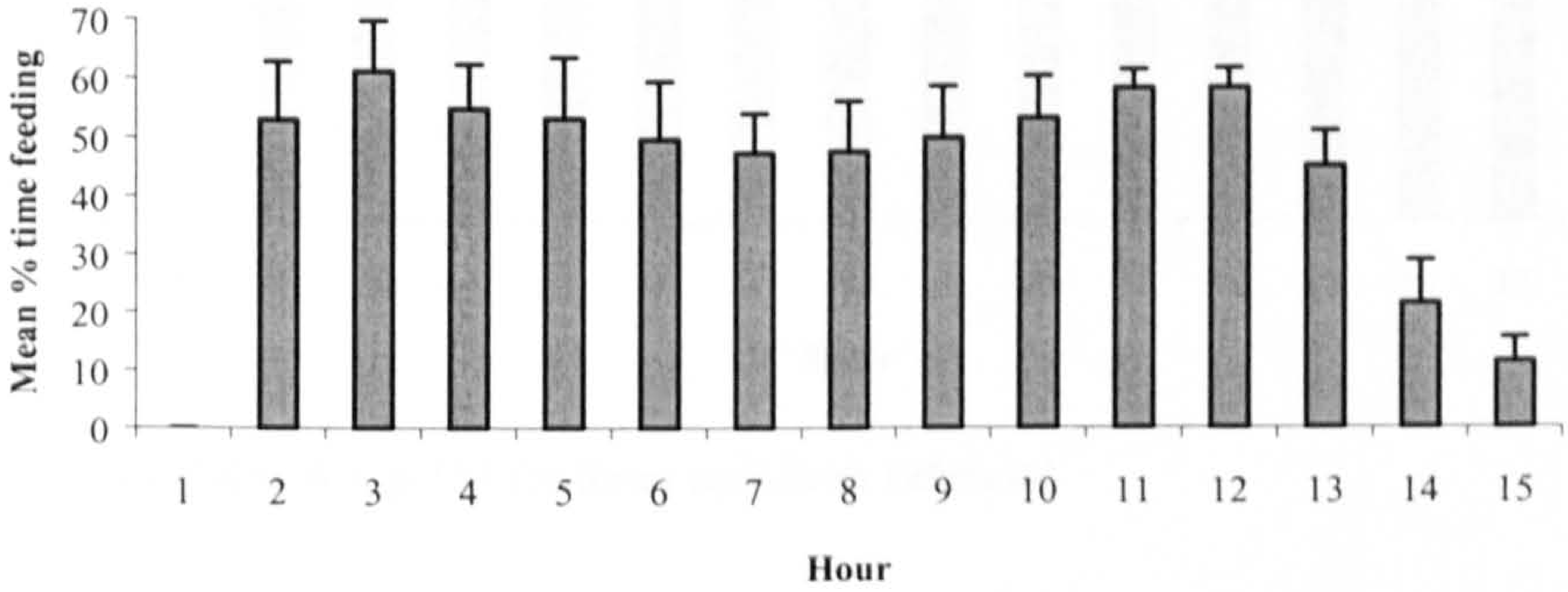
6.4.4.1 Hourly variation in activity schedule

To examine any possible temporal variation in levels of activity across the day, the time that observations were made during the day were subdivided into hours and compared. Graphical displays include all hours but due to missing values analyses have not included hours 1 and 15. Significant main effects of activity (F (3,42) = 270.82, p<0.001) and hour (F (12,168) = 15.87, p<0.001) were found and a significant interaction between activity and hour (F (36,382) = 37.23, p<0.001). The interaction is interpreted by each activity below. As stated earlier in the methods section, due to the large number of post-hoc tests generated by the multivariate analyses, only significant and non-significant results illustrating a pattern of activity are presented throughout the chapter.

Feeding

No feeding activity was ever seen to occur in hour one (05h00-05h55). The first feeding bout observed occurred at 06h00 and the last at 19h10. Two small feeding peaks could clearly be seen, relating to early morning (hour three) and early afternoon (hours 11 and 12) (Figure 6.15). Post-hoc tests revealed that the level of feeding activity was significantly lower in hour two in comparison to hour three, reflecting the first feeding peak of the day. Additionally the mean percentage time spent feeding in hour three was significantly higher than hours five through to ten, where the level of feeding activity decreased and dipped in between the two feeding peaks. Hour three did not differ significantly to hours 11 and 12, the second feeding peak of the day, but was found to be significantly higher than hours 13 and 14, reflecting the decline in feeding activity seen following hour 12 (Table 6.13).

Figure 6.15 Mean percentage time per hour spent feeding (±SD)



(see Table 6.3, p.134 for times each hour refers to)

Table 6.13 Results of post-hoc tests performed on hour and feeding

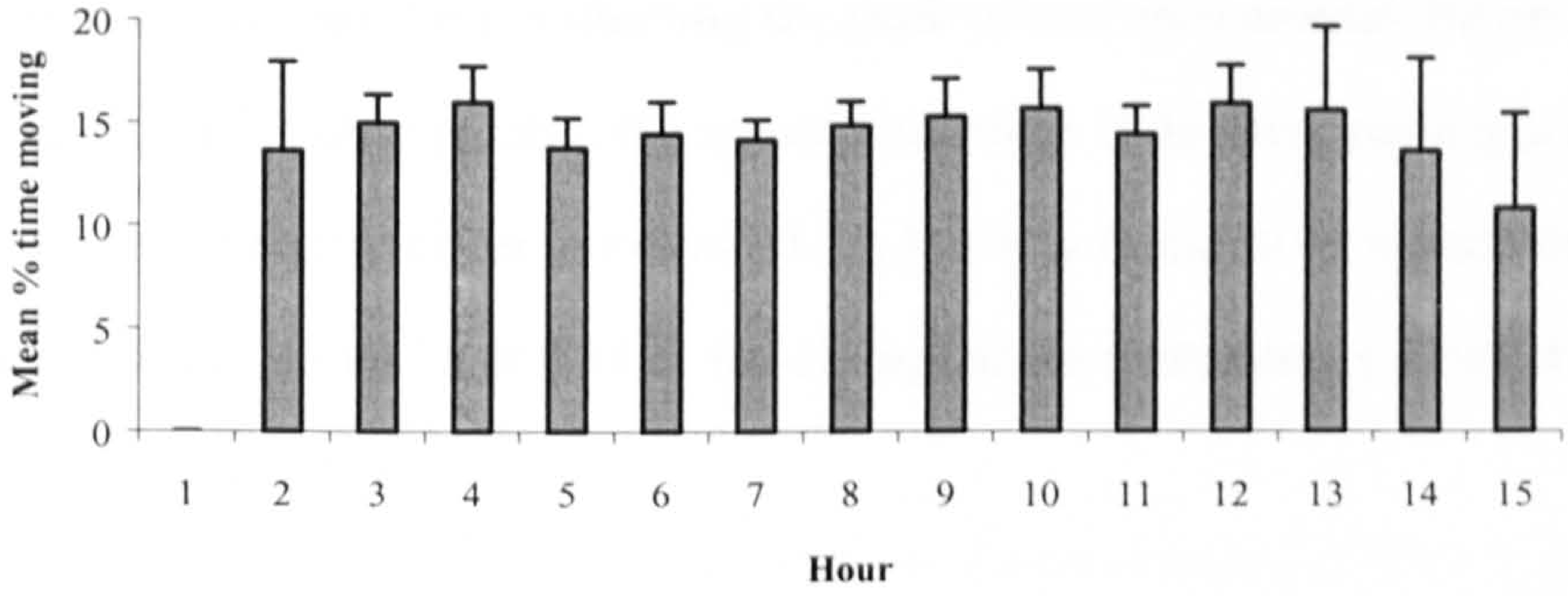
Hour	Hour	Mean difference	Significance	95% confidence interval for difference	
				Lower bound	Upper bound
2	3	-8.16	0.0028**	1.09	15.23
3	5	8.02	0.0041**	-15.08	-0.95
3	6	11.52	<0.0001***	-18.59	-4.46
3	7	13.92	<0.0001***	-20.99	-6.85
3	8	13.70	<0.0001***	-20.77	-6.64
3	9	11.25	<0.0001***	-18.31	-4.18
3	10	8.01	0.0042**	-15.08	-0.94
3	11	2.95	1.0000	-10.02	4.11
3	12	3.03	1.0000	-10.10	4.04
3	13	16.13	<0.0001***	-23.20	-9.07
3	14	39.58	<0.0001***	-46.65	-35.25

**p<0.01, ***p<0.001

Moving

As with feeding activity no movement was observed to occur in the first hour that observations took place. The time when the first and last bout of movement occurred was exactly the same found for feeding. The mean percentage of time spent moving overall appeared consistent across the day (Figure 6.16).

Figure 6.16 Mean percentage time per hour spent moving (±SD)



(see Table 6.3, p.134 for times each hour refers to)

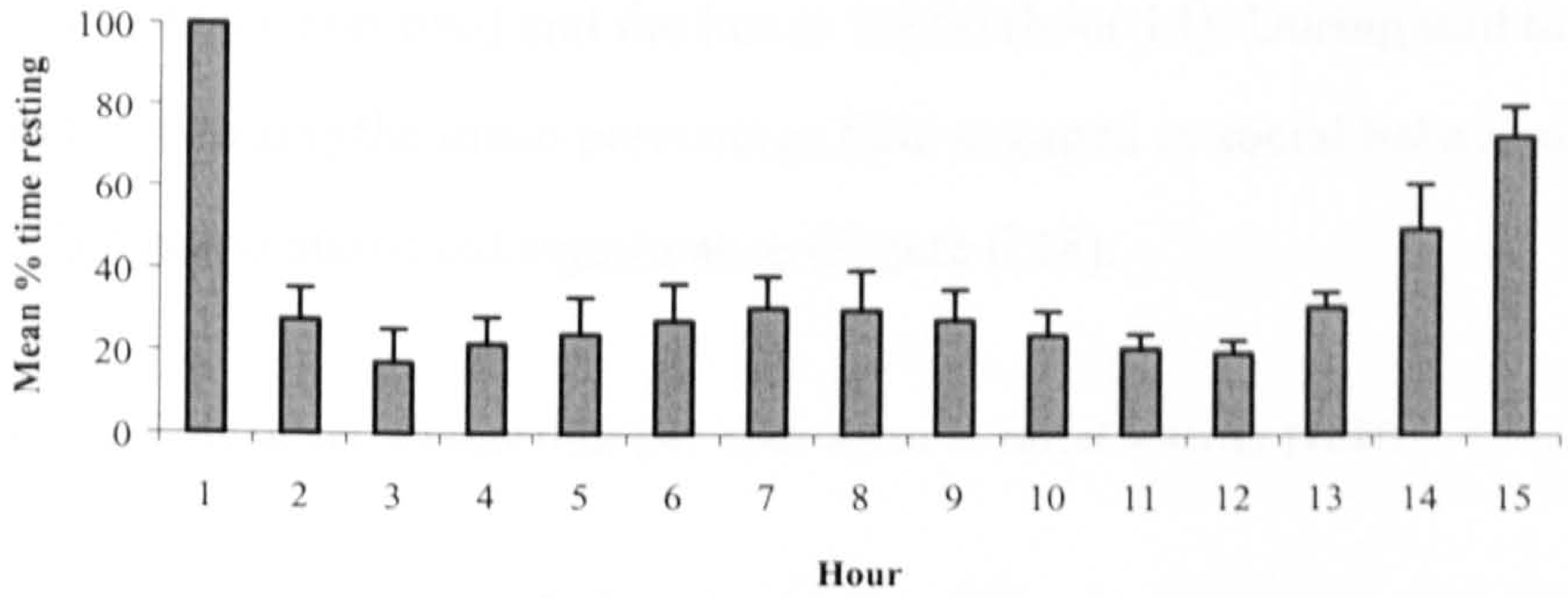
Resting

Seven out of the 15 chimpanzees were observed during the first hour of the day, in comparison to all the chimpanzees during hour two. During the first hour all of the chimpanzees spent 100% of their time resting in the nests that they had built the previous night to sleep in. This resting peak can be clearly seen in Figure 6.17. By hour two, the mean percentage time spent resting had dropped to 27.76%; 15.18% of this was within the night nest.

During the latter part of the day, only six chimpanzees were observed during hour 15, in comparison to all the chimpanzees being observed at some point during hour 14. By hour 14, 36.08% of rest could be accounted for within the night nest (13.51% outside of the nest), and this increased to 56.44% in hour 15 (15.97% outside of the nest). Again this resting peak within the night nest can be clearly seen in Figure 6.17. However, a third yet smaller resting peak, can be observed occurring approximately from late morning to early/mid afternoon time; hours seven and eight.

Post-hoc tests revealed that significantly more rest occurred in hour two in comparison to hour three, as the chimpanzees increasingly became active in the early morning (Table 6.14). No significant differences were found between hour three in comparison to four or five, however, significantly more rest occurred in hours six through to nine in comparison to hour three, reflecting the peak of rest seen around the middle of the day in Figure 6.17. Subsequently, the mean percentage time spent resting seen in hour three did not significantly differ to hours 10-12, but was found to be significantly lower in comparison to hours 13 and 14 as the chimpanzees increasingly entered their night nests at the end of the day.

Figure 6.17 Mean percentage time per hour spent resting (±SD)



(see Table 6.3, p.134 for times each hour refers to)

Table 6.14 Results of post-hoc tests performed on hour and rest

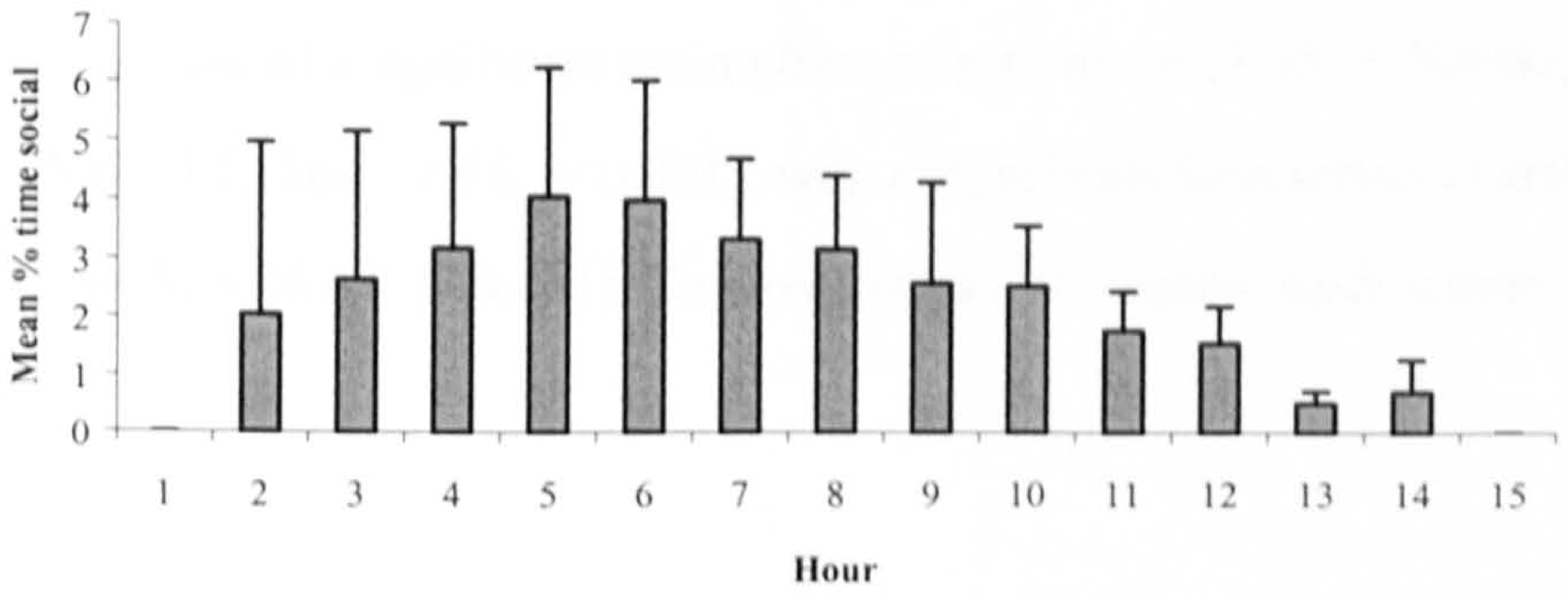
Hour	Hour	Mean difference	Significance	95% confidence interval for difference	
				Lower bound	Upper bound
2	3	10.48	<0.0001***	-17.55	-3.41
3	4	-4.44	1.0000	-2.63	11.51
3	5	-6.96	0.0650	-0.11	14.03
3	6	-10.22	<0.0001***	3.15	17.29
3	7	-13.33	<0.0001***	6.26	20.39
3	8	-12.81	<0.0001***	5.75	19.88
3	9	-10.32	<0.0001***	3.25	17.39
3	10	-6.60	0.1553	-0.47	13.67
3	11	-34.9	1.0000	-3.58	10.56
3	12	-2.32	1.0000	-4.74	9.39
3	13	-13.49	<0.0001***	6.42	20.56
3	14	-32.31	<0.0001***	25.24	39.38

***p<0.001

Social activity

Social activities (groom, play, copulation, and aggression) were not seen during the first and the last hour of observation periods. The first observed bout of social behaviour was seen at 06h00 (hour two) and the last at 18h00 (hour 14). During mid to late morning (hours five to six) the mean percentage time engaged in social behaviour appeared to peak but not to statistical significance (Figure 6.18).

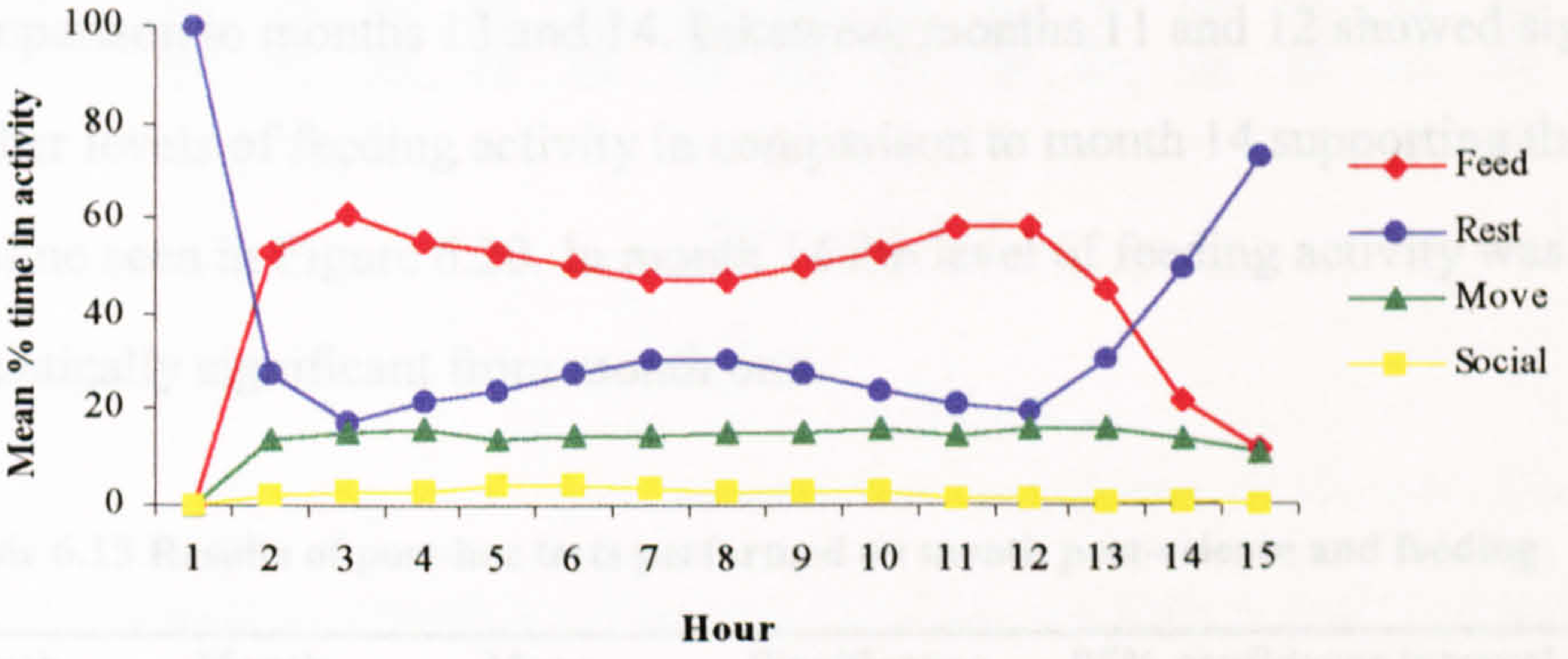
Figure 6.18 Mean percentage time per hour spent in social activity (±SD)



(see Table 6.3. p.134 for times each hour refers to)

By merging the temporal patterns seen for feeding, resting, movement and social activities onto one figure it is possible to view all the routine activities and their interaction as they occurred over the day. It can be seen clearly in Figure 6.19 that feeding and resting showed an inverse relationship, as feeding increased, resting decreased and vice versa.

Figure 6.19 Mean percentage time per hour engaged in each activity



(see Table 6.3, p.134 for times each hour refers to)

6.4.4.2 Monthly variation in activity schedule

To examine any possible temporal variation in levels of activity across the post-release study period, monthly schedules were compared for all activities. Only incidences of day rest (i.e., rest not within a night nest whether early morning or evening) were included in figures and analyses. Analyses performed on activity and month post-release produced a significant main effect of activity (F (3,36) = 506.60, $p<0.001$) and month (F (13,156) = 4.74, $p<0.001$), with a significant interaction of activity and month (F (39,463) = 16.43, $p<0.001$). To interpret the interaction, each activity is described below.

Feeding

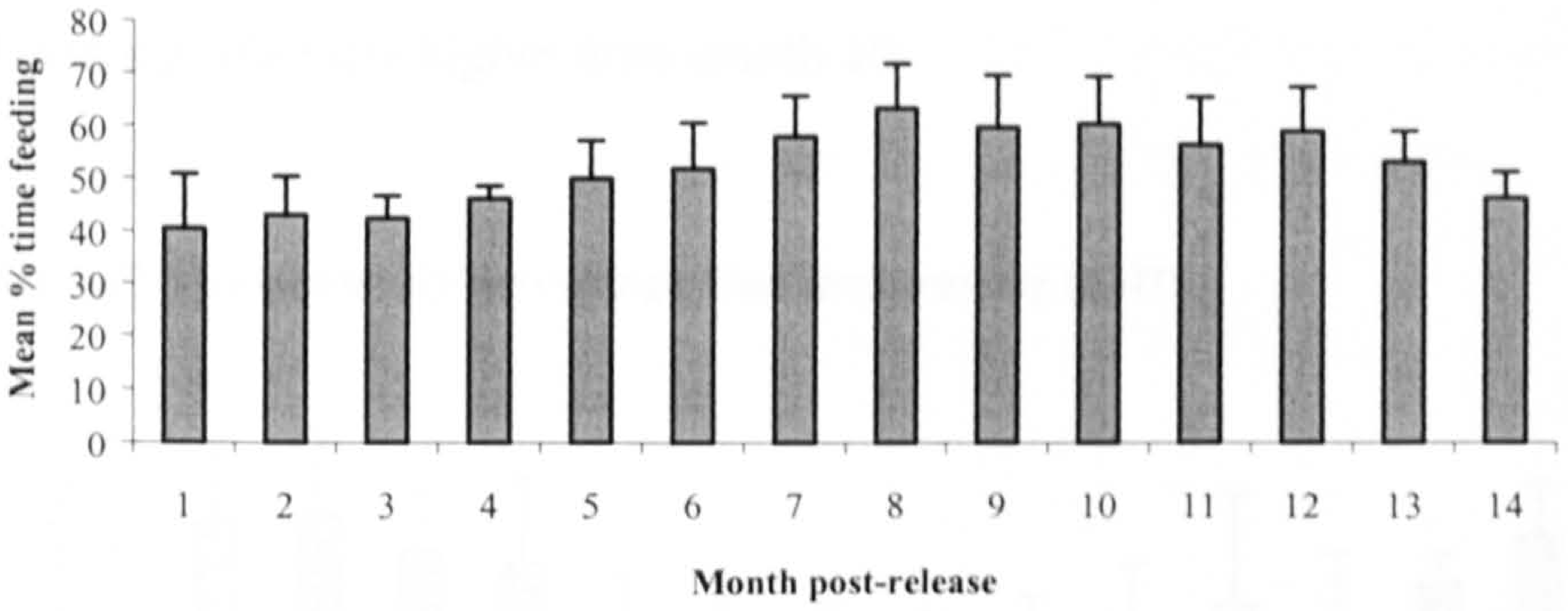
For the first four months post-release, the level of feeding activity appeared consistent with months one, two, three and four not significantly differing from one another (Table 6.15). However, following this, a gradual increase in feeding activity could be clearly seen, peaking at month eight, after which the mean percentage remained fairly steady until a small gradual decline started to occur around month 13 (Figure 6.20). Post-hoc tests revealed that the mean percentage time spent feeding in month seven through to ten was significantly higher than months one to five. In month eight, the mean level of feeding activity did not significantly differ from months nine through to twelve. However, in month ten, the mean activity level was significantly higher than in comparison to months 13 and 14. Likewise, months 11 and 12 showed significantly higher levels of feeding activity in comparison to month 14 supporting the gradual decline seen in Figure 6.20. In month 14 the level of feeding activity was not statistically significant from month one.

Table 6.15 Results of post-hoc tests performed on month post-release and feeding

Month	Month	Mean difference	Significance	95% confidence interval for difference	
				Lower bound	Upper bound
1	2	-3.33	1.0000	-5.02	11.68
1	3	-2.35	1.0000	-6.00	10.70
1	4	-6.58	1.0000	-1.77	14.93
2	3	0.98	1.0000	-9.33	7.37
3	4	-4.23	1.0000	-4.12	12.58
5	7	-8.93	0.0139*	0.58	17.28
5	8	-14.37	<0.0001***	6.02	22.72
5	9	-10.97	0.0001**	2.62	19.32
5	10	-12.07	<0.0001***	3.72	20.42
8	9	3.40	1.0000	-11.75	4.95
8	10	2.30	1.0000	-10.65	6.05
8	11	6.52	1.0000	-14.87	1.83
8	12	3.87	1.0000	-12.22	4.48
10	13	8.89	0.0154*	-17.24	-0.54
10	14	15.21	<0.0001***	-23.56	-6.86
11	14	10.99	0.0001**	-19.34	-2.64
12	14	13.63	<0.0001***	-21.98	-5.28
1	14	-6.36	1.0000	-1.99	14.71

*p<0.05, **p<0.01, ***p<0.001

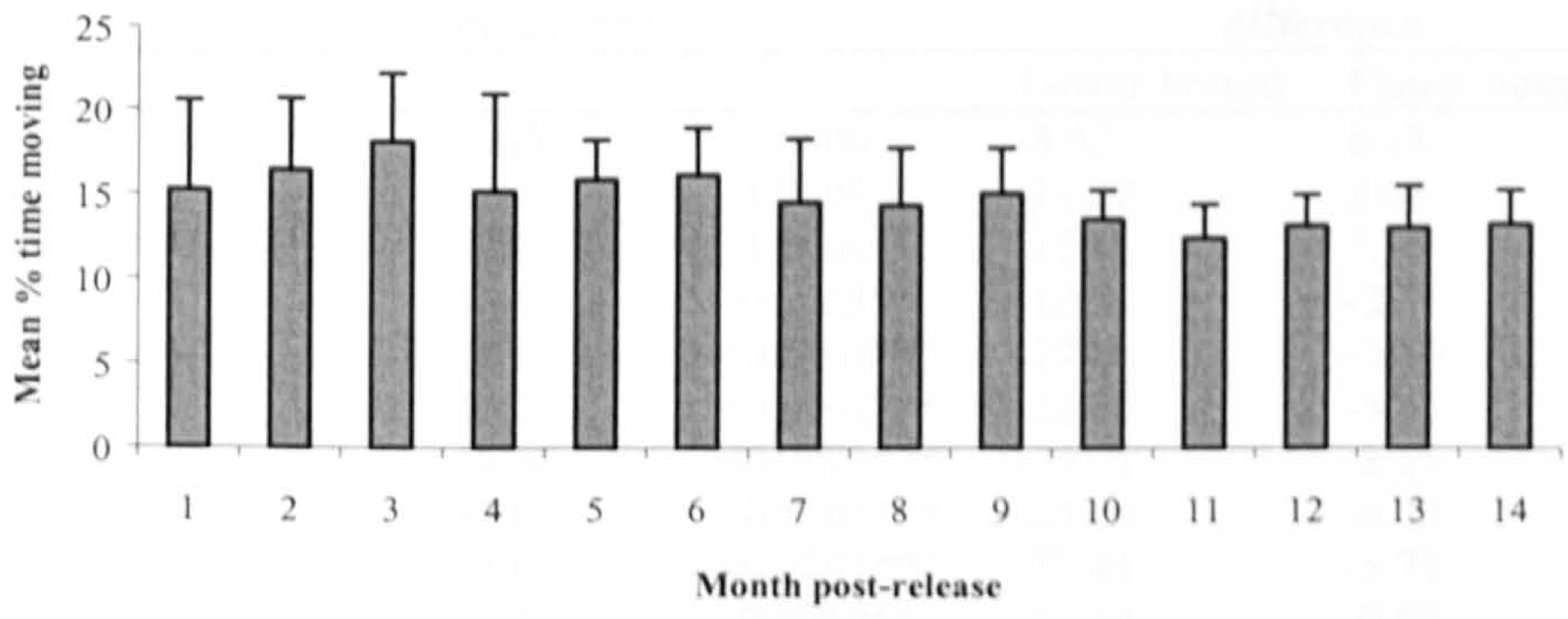
6.20 Mean monthly percentage time spent feeding (±SD)



Moving

The mean percentage time spent moving from month one to 14 post-release, showed no distinct pattern or variability (Figure 6.21). Post-hoc tests revealed no significant differences between all comparisons of month post-release.

6.21 Mean monthly percentage time spent moving (±SD)



Resting

A distinct pattern of mean time engaged in rest is clearly seen in Figure 6.22. The mean percentage time spent resting showed the opposite pattern as seen for feeding. Levels of rest were initially fairly consistent and no significant differences were found between month one and two, three and four (Table 6.16). However, the amount of time spent resting was significantly lower in months five through to 12 in comparison to month one, representing the dip seen in Figure 6.22 during which levels of rest remained fairly consistent and no significant differences were found between months six through to 10. However, by month 13 and 14, the mean percentage time spent resting had increased and was significantly higher than month 10.

Figure 6.22 Mean monthly percentage time spent resting (±SD)

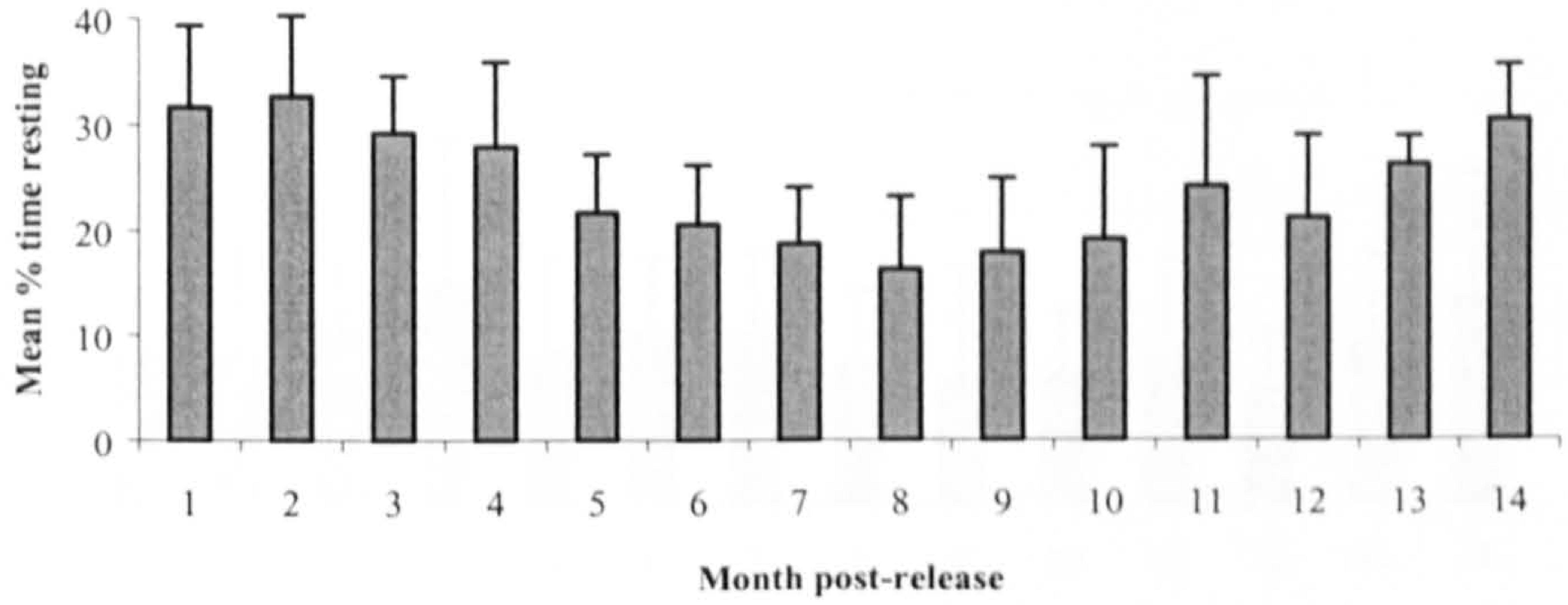


Table 6.16 Results of post-hoc tests performed on month post-release and rest

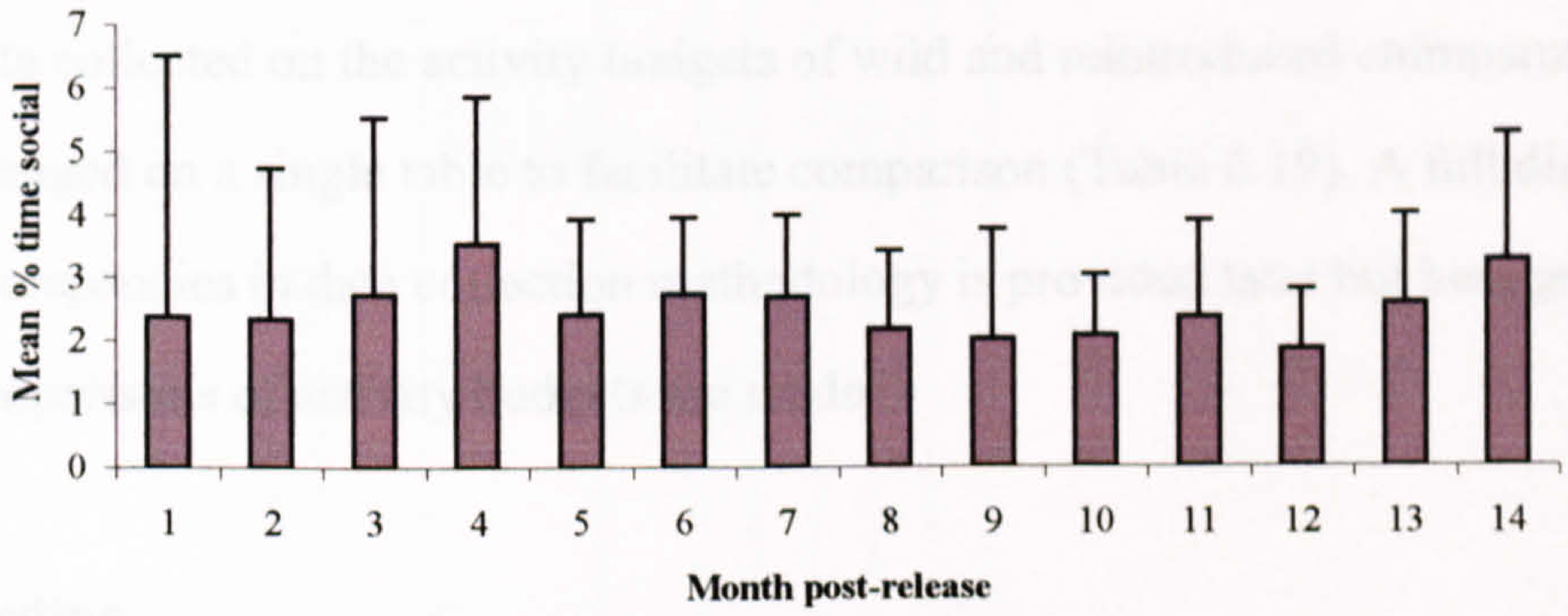
Month	Month	Mean difference	Significance	95% confidence interval for difference	
				Lower bound	Upper bound
1	2	-0.17	1.0000	-8.52	8.18
1	3	3.27	1.0000	-11.62	5.08
1	4	4.80	1.0000	-13.15	3.55
1	5	10.51	0.0003**	-18.86	-2.16
1	6	11.51	<0.0001***	-19.86	-3.16
1	7	14.01	<0.0001***	-22.36	-5.66
1	8	16.66	<0.0001***	-25.01	-8.31
1	9	15.05	<0.0001***	-23.40	-6.70
1	10	14.09	<0.0001***	-22.44	-5.74
1	11	9.24	0.0069**	-17.59	-0.89
1	12	11.50	<0.0001***	-19.85	-3.15
1	13	5.57	1.0000	-13.92	2.78
1	14	2.09	1.0000	-10.44	6.26
4	7	9.21	0.0073**	-17.56	-0.86
4	8	11.87	<0.0001***	-20.22	-3.52
4	9	10.25	0.0006**	-18.60	-1.90
4	10	9.30	0.0006**	-17.65	-0.95
6	7	2.50	1.0000	-10.85	5.85
7	8	2.65	1.0000	-11.00	5.70
8	9	-1.62	1.0000	-6.73	9.97
9	10	-0.96	1.0000	-7.39	9.31
10	13	-8.52	0.0344*	0.17	16.87
10	14	-12.00	<0.0001***	3.65	20.35

*p<0.05, **p<0.01, ***p<0.001

Social activity

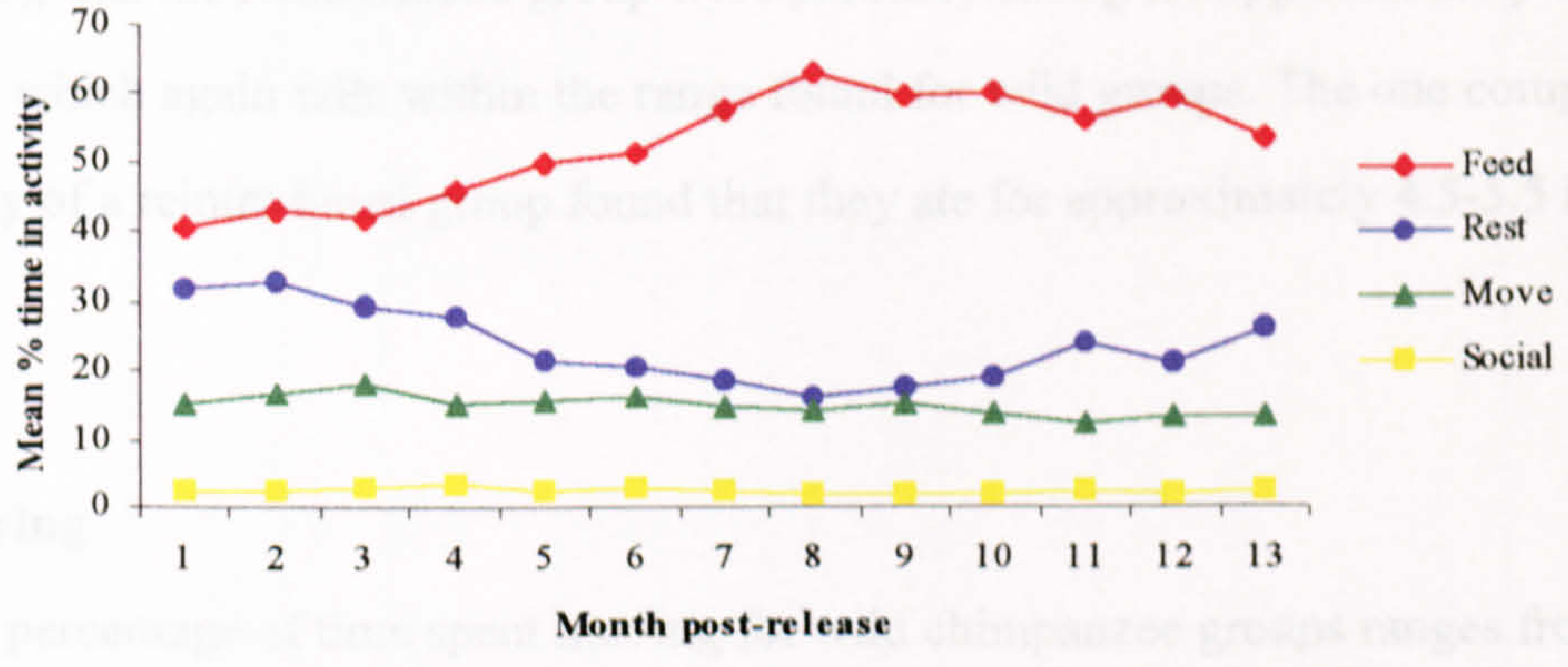
The percentage of mean time engaged in social activities showed no distinct pattern across the study period (Figure 6.23). Post-hoc tests revealed no significant differences between all combinations of comparisons made on month post-release.

Figure 6.23 Mean monthly percentage time spent in social activity (±SD)



The interaction between activity and month post-release can be clearly viewed by merging all the activities onto one figure (Figure 6.24). As the mean proportion of time spent feeding increased, resting decreased.

Figure 6.24 Mean monthly percentage time engaged in all routine activities



Analyses were also conducted comparing the amount of time that females and males, and chimpanzees released from Yombe and Yvette Island engaged in each activity across the study period. No significant difference or pattern was found other than what has already been shown. Chapters 4 and 5 highlighted that the chimpanzees were not all released at exactly the same time and data were plotted for each individual release (Release 1-4). Although some variation may have been expected, overall approximately the same patterns emerged as shown in Figure 6.24. These data and figures have not been included due to space restrictions within the thesis

6.4.5 Activity budgets of reintroduced and wild chimpanzees

Data collected on the activity budgets of wild and reintroduced chimpanzees were all arranged on a single table to facilitate comparison (Table 6.19). A full discussion of discrepancies in data collection methodology is provided later but here gross comparisons of activity budgets are made.

Feeding

The level of feeding activity for wild chimpanzee groups ranges from 45-56% (overall), 41-62% (daily), and 6-8 hours per day. Analyses from the present data set found that the reintroduced chimpanzees spent 51% of their time eating overall and 50% daily; falling within the range found for wild chimpanzee populations. With a daily feeding rate of 50%, it was calculated working on the principle of a 15 hour diurnal day (*after* Teleki, 1981), that the reintroduced group were probably eating for approximately 7.5 hours per day, which again falls within the range found for wild groups. The one comparative study of a reintroduced group found that they ate for approximately 4.5-5.5 hours per day.

Moving

The percentage of time spent moving for wild chimpanzee groups ranges from 8-22% (overall), and 12-28% (daily). Analyses from the present data set found that for both overall and daily rates the reintroduced chimpanzees were moving 15% of the time, again within the range found for wild chimpanzee populations.

Table 6.19 Activity budgets with details of study and study site of wild and reintroduced chimpanzee populations

	Wild chimpanzee populations										Reintroduced chimpanzee populations		
Country	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Uganda	Eq. Guinea	Ivory Coast	Ivory Coast	Gabon	Republic of Congo	
Study site	Gombe	Gombe	Gombe	Budongo	Budongo (Sonso)	Budongo (Sonso)	Kibale	Rio Muni	Tai Forest	Tai forest	Ipassa	Conkouati	
Reference	Goodall 1965	Wrangham 1975	Teleki 1981	Reynolds & Reynolds 1965	Newton-Fisher 1999	Fawcett 2000	Ghiglieri 1984	Sabater-Pi 1979	Doran 1997	Boesch & Boesch-Achermann 2000	Hladik 1973	Current data	
Habitat	E/SD/G /BW	E/SD/G /BW	E/SD/G /BW	CL/MF/ CF/S	CL/MF/ CF/SF	CL/MF/ CF/SF	PF/G/ SF/SC	PF/RF/ SF/MF	LRF	LRF	SF	IF/PF/SF	IF/PF/SF
Season	D/R	D/R	D/R	R	D/R	D/R	D/R	D/R	D/R	D/R	D/R	D/R	D/R
n	?	14	31	?	?	36	?	?	30	?	8	15	15
Age	M/IM/I	P/PP	8-35yrs	ALL	NS	A/AD	A/SA/J/I	ALL	ALL	ALL	4-8yrs	6-10yrs	6-10yrs
Sex	M/F	M	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F
Measurement	HD	O	D (15hr)	HD	O	O	D	D	D	O	HD	O	D
ACTIVITY:													
Feeding	6-7	55.7%	42.8%	6-8	48.8%	52.8%	62.1% (♂) 52.5% (♀)	40.8%	43%	45%	[f]4.5-5.5	50.75%	50.22%
Moving	-	13.8%	13.5%	-	-	7.5%	12.1% (♂) 10% (♀)	27.5%	12%	22%	-	14.96%	14.77%
Resting	-	[a]24.1%	18.9%	-	-	25.0%	[e]25.8% (♂) [e]37.6% (♀)	-	39%	[e]22%	-	26.67%	26.90%
Grooming	-	[b]6.2%	-	-	-	14.3%	-	-	-	-	-	2.57%	2.20%
Social	-	-	[c]24.9%	-	-	[d]0.04%	-	-	-	-	-	[g]2.88%	[g]2.45%

Key:- Habitat: E = Evergreen forest, SD = Semi-deciduous forest, G = grassland, BW = *Brachystegia* woodland, CF = colonising forest, MF = mixed forest, CF = *Cynometra* forest, SF = swamp forest, PF = primary forest, SC = scrub, RF = regenerating forest, MF = montane forest, LRF = lowland rain forest, IF = inundated forest; Season: D = dry, R = rainy; n: ? = insufficient detail to estimate; Age: NS = not specified, ALL = all ages, M = mature, IM = immature, I = infant, P = prime, PP = past prime, A = adult, AD = adolescent, SF= sub-adult, J = juvenile; Sex: M = male, F =female; Measurement: O = overall, D = daily, HD = Hours per day.

[a] sit/stand inactive 17.8% and lie (not in night nest) 6.3% = total 24.1%; [b] allogroom only; [c] includes all instances of self-groom and solitary play in addition to social instances

[d] includes all instances of social behaviours except groom such as copulation, dominance and vocalisation; [e] includes social time

[f] Chimpanzees were provisioned in this study accounting for approximately 30% of their diet. Hladik argues that if movements necessary to locate food are included then the time involved in feeding would rise to 6.5-7.5 hours. However, he does not describe how he distinguishes feeding from non-feeding movements; [g] includes social grooming, social play, aggression and copulation

Resting

The percentage of time spent resting for wild chimpanzee groups ranges from 22-25% (overall), and 19-39% (daily). As with moving, the reintroduced spent approximately the same amount of time resting for both overall and daily rates; 27%. This is a slightly higher percentage than the overall rate found for wild populations (although minimally) but falls within the range found for daily rates.

Grooming

There are only two studies of wild populations offering comparative grooming data, their overall rates are 6% (allo-groom only) and 14% (includes all instances of groom). In the present study the overall mean percentage of 3% (includes all instances of groom) was considerably smaller than that found in either of the two wild populations.

Social activity

As with groom only two studies of wild populations offer comparative social activity data, one expressed as a daily rate of 25% and the other as an overall rate of 0.04%. The discrepancy between these data and the reintroduced group are readily apparent and are likely at least in part due to differences in social activity categorisation, i.e., 25% includes all instances of self-groom and solitary play in addition to social instances. In the present study the overall rate of social activity was found to be 3% and the daily rate 2%.

Sex differences in wild and reintroduced chimpanzee activity budgets

Three of the ten wild chimpanzee studies listed on Table 6.20 have data available on sex differences in activity budgets. Doran (1997) examined sex differences but found approximately the same levels of activity for feeding, locomotion and rest for females and males (reference presented rounded figures only). Fawcett (2000) found that female chimpanzees engaged in more feeding and social activities, but moved, rested and groomed less than male chimpanzees. However, Ghiglieri (1984) found that males fed and moved more, but rested less than females. In the present study (section 6.4.2, p.144 in only one activity was a significant difference found between the sexes; the reintroduced females spent significantly more time feeding than the males, although a non-significant trend was found for males to spend more time resting than females (Table 6.20).

Table 6.20 Activity budgets and results of comparisons made between female and male wild and reintroduced chimpanzees groups

Activity	Chimpanzee group	Reference	n		Activity budget %		Significant
					Females	Males	
Feed	Wild	Fawcett, 2000	19	17	54.73	50.60	NS trend
		Ghiglieri, 1984	?	?	52.50	62.10	*p<0.05
		Doran, 1997	23	7	43	43	NS
		Teleki, 1981	13	18	51.80	40.10	NT
	Reintroduced	Current data	11	4	53.45	43.32	**p<0.01
Move	Wild	Fawcett, 2000	19	17	6.33	8.83	**p<0.01
		Ghiglieri, 1984	?	?	10	12.10	*p<0.05
		Doran, 1997	23	7	12	12	NS
		Teleki, 1981	13	18	14.60	13	NT
	Reintroduced	Current data	11	4	14.76	15.52	NS
Rest	Wild	Fawcett, 2000	19	17	24.58	25.49	NS
		Ghiglieri, 1984	?	?	37.6	25.8	*p<0.05
		Doran, 1997	23	7	39	39	NS
		Teleki, 1981	13	18	15.50	20.10	NT
	Reintroduced	Current data	11	4	24.56	32.48	NS trend
Groom	Wild	Fawcett, 2000	19	17	13.90	14.76	NS
		Ghiglieri, 1984	-	-	-	-	-
		Doran, 1997	-	-	-	-	-
		Teleki, 1981	-	-	-	-	-
	Reintroduced	Current data	11	4	2.23	2.81	NS
Social	Wild	Fawcett, 2000	19	17	0.04	0.03	NS
		Ghiglieri, 1984	-	-	-	-	-
		Doran, 1997	-	-	-	-	-
		Teleki, 1981	13	18	18.10	26.80	NT
	Reintroduced	Current data	11	4	2.98	3.27	NS

NS = non-significant, NT = not tested, ? = not known, - not collected

6.5 Discussion

This section discusses the activity budgets of the reintroduced chimpanzees in relation to sex, pre-release island, and environmental variables. Each sub-section compares the activity budgets and patterns of behaviour of the reintroduced chimpanzees to that observed in wild chimpanzee populations where data are available and applicable.

6.5.1 Overall and daily activity budgets

Analyses of activity budgets show that both overall and daily patterns are dominated by the proportion of time spent feeding (51%) and in other activities associated with the indirect ingestion of food, that of rest (27%) and move (15%). The high percentage of time engaged in these core activities reflects the overall patterns observed in wild chimpanzee populations (Wrangham, 1975; Teleki, 1981; Doran, 1997; Boesch and Boesch-Achermann, 2000; Fawcett, 2000). This implies that the reintroduced chimpanzees, like their wild counterparts, have shown successful (defined here as surviving and in good health 14 months post-release) differential budgeting of activities in response to the environmental conditions surrounding them. There is some degree of variance in core activity budgets between the reintroduced and wild chimpanzee groups, although the mean scores for the reintroduced group do fall within the ranges found for all wild populations. However, variation can also be seen across wild populations (Table 6.19), and no chimpanzee communities are likely to have exactly the same diets even those that are neighbours. Habitat type is clearly one factor that influences activity budgets. The studies of wild populations as shown in Table 6.19 have used a total of 13 labels to describe habitat type of the study site. This may reflect personal choice in terminology and categorisation, and/or distinct habitat types, although it is likely that there will be some degree of overlap of habitat type. However, each population in response to environmental conditions and pressures will have to respond by budgeting activities in order to survive. Consequently one should not expect budgets to be directly comparable as they reflect adaptation to a particular ecological niche. The only comparative study of reintroduced chimpanzees to the present data simply gives a figure of hours per day spent feeding (Table 6.19). The low number of daily feeding hours (4.5-5.5) can be explained by the group receiving approximately 30% of their diet through provisioning of bananas at an artificial feeding site. Hladik (1977) argues that if movements necessary to locate food were included then the time involved in feeding would rise to 6.5-7.5 hours. However, he does not describe how he distinguishes feeding from non-feeding movements and as no other study appears to have made this distinction, it would not be comparable.

Teleki (1981) argues that social activities are crucial for group survival, but despite this only three out of the ten studies in Table 6.19 collected data on levels of social and groom activity. Within these three studies there is great variation in behaviours included in the social or interacting category. For example, Teleki (1981) included all instances of groom (allo and self) and play (solitary and social) in budgets he labelled 'interact'. In contrast, Fawcett (2000) included copulation, dominance and vocalisation in her 'social' category but not groom. Consequently it is extremely difficult to make a direct comparison as the variation in behavioural categories across studies necessarily distorts the mean range of activity budgets. However, although there are obvious problems about using data collected by investigators and their varying definitions, biases are unlikely to be in any consistent direction and will in fact reduce not inflate any significant differences (Dunbar, 1988). The social activity budget reported by Fawcett (2000) was extremely low (0.04%), but if the category of groom is included (14.34%), this totally transforms the budget (assuming that the majority of groom is social in nature as found in the present study and by Teleki (1981). Likewise, the interact budget described by Teleki (1981) was extremely high (24.9%) but if the instances of solitary play and self-groom were removed (which are not strictly social in nature) then this figure would be likewise transformed. However, in both cases, the social budgets expressed (including groom) would remain substantially higher than that observed in the present study. This discrepancy can be clearly seen in the category of groom; the reintroduced group engaged in substantially less grooming than reported by the two studies on wild populations. From the studies that have reported social and groom budgets in addition to core activities, comparatively the reintroduced group engaged in a similar level of feeding activity but slightly elevated levels of rest and move, explaining the lower levels of mean time engaged within social activities. The low levels of social interaction (2.88%), primarily made up of social groom, could be explained as an adaptation to the environmental conditions in which the chimpanzees found themselves. Prior to release the chimpanzees received supplementary feeding on the islands in addition to any natural edible vegetation that could be found. Post-release the chimpanzees were immediately confronted with the task of having to forage (locate, process and ingest food items) for all their dietary requirements, a task that would undoubtedly dominate their day. Reduced levels of social activity in the face of demands made on time by ecological factors, indicates that primates are willing to withdraw from grooming when extra feeding time is required (Dunbar and Sharman, 1984; Lee, 1984). However, with no comparative pre-release data it is impossible to make such a claim. In situations of extreme food shortages, chimpanzees at Budongo increased the time they spent moving to extend their range and locate food resources but decreased the time that they spent grooming (Fawcett, 2000).

Several features of grooming (i.e., that grooming often occurs following agonistic interactions and copulation, and that time spent grooming is correlated to group size) suggests that social complexity and the servicing of relationships may have a great deal to do with the amount of time spent grooming (Dunbar, 1988). The mean group size of a wild chimpanzee party ranges from 4 at Bossou (Sakura, 1994), 3.45 at Tai (Doran, 1997), 4.66-11.20 at Rio Muni (Jones and Sabater-Pi, 1979) to 6.36 at Budongo (Fawcett, 2000). However, a great deal of variation of group size exists as a consequence of composition, seasonal influence, and food availability (Boesch and Boesch-Achermann, 2000; Fawcett, 2000). In the present study, the overall mean group size is 4.17 (±1.16) with a minimum-maximum group size of 1-11. With only one study to compare to that has data on both the mean time spent grooming (14.30) and mean group size (6.36), it is difficult to make any firm conclusions (Fawcett, 2000). A relatively lower mean group size found in the present study may be a factor in partially explaining the low levels of groom. However, the large discrepancy between the comparative levels of time spent grooming between the two studies but not in mean group size suggests that other factors such as subject age and sex might be involved.

Studies suggest that male chimpanzees are more gregarious than females, that cycling females engage in more social activities than non-cycling females and that grooming tends to increase with age for both sexes. The present study group consists primarily of females (2.75 ratio of females to males) with an age range of 6-10 years at release (encompassing childhood and early adolescent as defined by Goodall, 1986). The sex bias and relatively young age of the chimpanzees reintroduced may also help to explain the low levels of social activity observed.

Teleki (1981) suggested that grooming is one of the major underpinnings of chimpanzee society. However, when the present study group arrived at the sanctuary, they had been taken from the wild, orphaned, and on average, arrived less than two years of age. Chimpanzees were placed within similar age class groups and substitute mothers were human in form. Young animals have to learn many types of behaviour and if they are deprived of contact with certain categories of individuals, their social development may be impeded (Spijkerman, Dienske, Van Hooff and Jens, 1995). Chimpanzees reared in large social groups showed higher levels of dominance and activity behaviours than chimpanzees reared in peer groups (Bloomsmith, Alford and Pazol, 1991) and this suggests that a greater variety of social partners, the more social skills can be developed facilitating group living. Furthermore, the work of Bard and Gardner (1996) suggests that early rearing and stress can have long-lasting effects on emotional responses and cognitive performance. We might expect that cumulatively the deprivation of adult chimpanzee role models and wild chimpanzee society substituted with human influence and individuals of the same age group may influence behaviours thought to facilitate social bonding. It seems likely that a combination of all the factors mentioned; the need to locate and process food in a novel environment, chimpanzee age, sex, mean group size, restricted social partners and human contact may have influenced the low level of social activity seen in the reintroduced chimpanzees.

6.5.2 Sex, pre-release island, and age differences

Sex

Female chimpanzees were found to feed significantly more but rest less (latter a non-significant trend) than male chimpanzees. No significant differences were found between the sexes for move or social activity. Studies from wild populations have shown varying results. Some have found no significant differences between the sexes in feeding (Wrangham and Smuts, 1980; Doran, 1997), resting (Doran, 1997) and moving (Hunt, 1989; Doran, 1997). However, studies that have found significant differences, both support and contradict the results of the present study. Ghiglieri (1984) found that male chimpanzees spent more time feeding and moving than females, but less time resting. Fawcett (2000) found that females spent more time feeding but less time moving and resting. Although Wrangham and Smuts (1980) found no significant difference in the proportion of time spent feeding, the medians indicated that the females fed slightly more than the males. When no sex differences in feeding activity are found, or cases when females spend more time feeding than males, may be surprising in view of the substantial differences in body weight. The mean weight of a male chimpanzee is 39.5kg, 33% more than the mean weight of females (29.8kg) (Wrangham and Smuts, 1980). In a number of primate species, females have been found to spend more time feeding in relation to their body weight than males (Clutton-Brock, 1977; Dunbar, 1977; Fossey and Harcourt, 1977). A higher rate of feeding activity by female primates may reflect the nutritional demands of reproductive parameters and motherhood; the need to gestate, lactate and carry infants (Harrison, 1983; Wallis, Mbago, Mpongo, and Chepstow-Lusty, 1995; O'Brien and Kinnaird, 1997; Herrera and Heymann, 2000). In the present study only one female had dependent offspring (carried only for three months) and no other female was known to be pregnant during the post-release period. However, as mentioned in the introduction to this chapter (see p.123) activity budgets have been found to vary between cycling and non-cycling females but these data were not collected in the present study. The significance of time spent feeding is uncertain because little is known about the feeding rates and food selection of females. Differences have not yet been found in the selection of plant foods, but females have been found to spend more time eating insects (obtained by prolonged, systematic, and repetitive sequences) and less time eating meat than males (obtained by a group stalking, pursuing, capturing, killing, and dividing of prey) (McGrew, 1979; Uehara, 1986). Although male chimpanzees forage under the same relatively rigorous regime as female chimpanzee, they are faced with the additional problem of finding females and the problems of competition with other males for access to females. Males need to find females and exert territorial behaviour. This may help to explain the greater time spent moving observed in two out of the three studies on wild populations and in the present study (differences reflected in means only), and the lower levels of proportional feeding activity. The lower rate of feeding activity by male chimpanzees may also be related to the well recognised pattern of social organisation characterised by the gregarious male chimpanzee in comparison to the less sociable female (Goodall, 1986; Nishida, 1979; Wrangham, Clark and Isabirye-Basuta, 1992; Sugiyama, 1968). In the present study, males did spend more mean time in social activity (although not to statistical significance). As mentioned in the introduction of this chapter, males tend to spend less time feeding when in the company of other males (Bygott, 1974, cited in Teleki, 1977), suggesting that feeding activity is sacrificed to engage in social behaviour. This implies that within the reduced period of time available that the male chimpanzee has to feed, he must be doing so efficiently. One tactic observed has been the displacement of one individual by another in a preferred feeding site by means of dominance (Wrangham, 1975).

Pre-release island

Chimpanzees released from Yombe and Yvette Island were not found to significantly differ in the amount of mean time spent in any activity. This is perhaps surprising considering the differing size of the two islands (50 versus 30 hectares). The chimpanzees released from the larger Yombe Island were provided with the opportunity to move, explore, and orient in a comparatively much larger pre-release environment than those released from Yvette Island. Recommendations following the release of chimpanzees onto an island in Liberia suggested that release animals should be kept in a complex pre-release environment to facilitate, for example, skills necessary to negotiate an arboreal environment. Furthermore, subjects should be provided with wild foods that are known to occur at the release site, and with initial provisioning gradually decreased (Hannah, 1989). In the present study both pre-release islands met the criteria and provided opportunities for the chimpanzees to develop climbing skills, social relationships, and knowledge of wild foods in what was very much a micro-habitat representative of the release site. However, no provisioning took place post-release (unless specified in Chapter 4) and the chimpanzees were expected to locate and process food by themselves from day one. That they were all able to do so with activity budgets akin to their wild conspecifics with no differences between pre-release island confirms that the vegetation available on both islands was sufficient to provide them with a basic knowledge and incentive to forage. Residency on Yombe versus Yvette Island conferred no advantage on post-release survival. Prior to release human caretakers observed the chimpanzees on the islands, and a degree of contact was established and maintained for feeding and welfare purposes. However, the policy of the HELP project was one of non-interference, and they were not actively shown how to climb and what to eat. Therefore, regardless of size, both islands seemed to offer suitable 'training' grounds for the chimpanzees to learn how to successfully distribute their available time among categories of activity important for survival.

Age

Despite the age range of reintroduced chimpanzees being relatively narrow (6.7-10.7 years) significantly less time was spent feeding, but more time was spent moving as age increased. Experience and levels of confidence may be a consequence of age; perhaps older animals are more likely to explore and range further rather than remaining close to known smaller feeding patches. The reduced levels of feeding activity may simply be a result of more time being devoted to moving and the possibility of feeding more efficiently due to more experience as a consequence of age. Studies that have observed sex differences in wild chimpanzee populations may also offer an explanation. Cycling females have been found to spend extra time moving, and compensate for this by spending less time feeding (Fawcett, 2000). There are no reliable data on the cycling of the reintroduced females, but it is possible that this is may have been an influencing factor on the activity budgets of older females. Furthermore, wild male chimpanzees increase mobility as they get older and patrol the home range (Teleki, 1977). Additional correlation's performed on age and activity for each sex only produced a significant positive correlation for females and time spent moving. However, caution must be taken in interpreting these results due to not only the narrow range of ages but also that the correlation comparing the sexes may simply reflect a larger sample size for females.

6.5.3 Environmental variables

Season

The reintroduced chimpanzees spent significantly more time feeding but less time resting in the dry season. In the dry season, a period of potential scarce resources, the reintroduced chimpanzees may need to compensate by feeding more, but on lower quality food items. The Tai chimpanzee community similarly increased their feeding activity in the dry season to feed on lower quality foods. However, they also decreased their daily range, increasing foraging efficiency by more efficient use of core areas (Doran, 1997). In the present study the amount of time spent moving did not increase or decrease across the dry and rainy season. Chimpanzees at Budongo responded to a decrease in food availability by reducing time spent foraging and increasing time spent resting and grooming, thus conserving energy (Fawcett, 2000). In contrast, the reintroduced chimpanzees increased their time spent feeding but decreased time spent resting in the food scarce dry season. The decrease in time spent resting can probably be explained as a result of reallocation of increased time spent feeding.

The seasonal changes in food supply that occur to a greater or lesser extent in all primate environments have major consequences for primate feeding behaviour. They produce changes in what is eaten and changes in the pattern of activities in time and space. Primates that live in seasonal environments often show predictable responses to scarce resources. In order to compensate for a poorer quality habitat during a dry season, primates may switch to alternative, poorer quality food resources (Richard, 1985), and incorporate them into their diet in greater than usual quantities (Hladik, 1977). This results in a greater amount of time spent feeding in order to compensate for the poorer quality food eaten (Dunbar, 1988). Primates may either increase the day range in order to find food, or decrease the amount of daily travel resulting in reduced energy requirements (Dunbar, 1988). The chimpanzees would have previously experienced seasonal availability of a limited number of feeding species on the pre-release island, but due to supplementary feeding, this period would not have impinged negatively on their diet. The overwhelming conclusion from these results are that the reintroduced chimpanzees were able to adapt their behaviour to the environmental conditions in which they found themselves; an environment characterised by temporal variability in resource abundance.

No significant seasonal differences were found in time spent moving or in social activity. In the dry season when feeding activity increased the amount of time spent resting significantly decreased and the amount of time spent moving or in social activity remained unaffected. One possible explanation is that the time engaged in social activity, albeit low, was sufficiently important to be maintained at its current level despite the need to reallocate time as a consequence of increased time spent feeding. The majority of social activity consisted of groom (85%) and it serves three primary functions. At a biological level, grooming helps to keep the coat free of parasites and dirt. However, social grooming serves functions beyond skin care and can be an enjoyable activity for both the groomer and the groomee. It can help to promote and cement relationships between participating individuals. Furthermore, social grooming has also become a conciliatory gesture that reduces tension and aggression between individuals, and can maintain hierarchy within a group. The work of Dunbar (1991) suggests that social grooming goes beyond the need of basic hygiene, and as one of the major social underpinnings of chimpanzee society should not be expected to fluctuate greatly seasonally or annually (Teleki, 1977).

Forest

Chimpanzees were found to significantly feed more within inundated and primary forest in comparison to swamp forest. Detailed surveys of forest type and quantity have been conducted within the Conkouati-Douli National Park but not specifically within the Triangle itself. This hinders discussion as 88% of observations were made within this micro-habitat, diminishing the applicability of the surveys conducted in the wider reserve to events within the Triangle. However, from a basic vegetative sketch map of the Triangle it appears that no forest type pre-dominates (Paredes, 1997). Therefore, the only conclusion that can be speculatively made is that the preferred forest types of the reintroduced chimpanzees for feeding were inundated and primary forest. The explanation for this may derive from feeding efficiency and patterns of phenology.

No significant differences were found between the amount of time spent moving, resting or in social activity between forest types. This suggests that as a relatively equal amount of time was spent in each forest type, for each activity, that the chimpanzees are well adapted to live in an environment in which some forest is either permanently or seasonally water logged. Their prior experience of contact with water pre-release has likely reduced the hydrophobia seen in their wild counterparts (see Chapter 7, p.214).

6.5.4 Hourly variation in activity schedule

Studies on wild populations have shown great variation in hourly activity patterns, some authors have found distinctive feeding peaks (Nishida, 1974) whilst others have observed a steady rate of feeding throughout the day (Teleki, 1981). In the present study although a fairly steady rate of feeding is seen throughout the day, two peaks emerge, one early morning and the second mid-late afternoon. These morning and afternoon feeding peaks reflect observations made in several wild populations (Goodall, 1968; Nishida, 1974; Sabater-Pi, 1979). Less obvious but present are corresponding peaks of movement although no significant difference was found when hourly comparisons were made. From late morning to early afternoon, an obvious peak in resting activity is observed. To summarise, after leaving the nest in the morning, the chimpanzees forage (move and feed) in order to satisfy their early morning hunger. Following this, during the hottest part of the day, the chimpanzees rest (facilitating digestion of food). Then mid-late afternoon the second feeding peak of the day occurs. Wrangham (1977) found three feeding peaks between which grooming occurred. In the present study social activity (consisting primarily of social groom) produced no significant differences when hourly comparisons were made. However, from the graphical representations (Figures 6.18 and 6.19) it can be seen that social activity peaked in between the first feeding and resting peak. This occurred during a period when time spent moving was slowly decreasing, and rest gradually increasing. As with comparisons made between activity budgets there seems to be no right or wrong regime. However, this temporal pattern illustrates that the reintroduced chimpanzees were responding 'appropriately' to both environmental variables (e.g., temperature) and physiological mechanisms (e.g., hunger).

6.5.5 Monthly variation in activity schedule

Monthly comparisons of feeding and resting activity showed a distinct and significant pattern across the post-release study period. A relatively steady rate of feeding activity was seen in months one to four followed by a gradual increase, peaking at around month seven and eight, and then gradually decreasing. It seems likely that had the study period been longer then the levels would have decreased sufficiently near that seen at month one. A similar pattern emerged for the activity of rest but in the opposite direction. Levels of rest gradually decreased and a clear dip can be seen around months seven, eight and nine, followed by gradual increase, again almost returning to levels seen in month one. What is interesting to note is that the increase in feeding and decrease in resting corresponds to the approximate arrival of the dry season when feeding was found to significantly increase and rest significantly decrease. Although the chimpanzees were not all released at the exact same time, they were sufficiently close enough to describe the pattern as a seasonal effect. The releases were scheduled to occur approximately around December/January to coincide with known fruiting periods (see Table 4.3, p.80 for details of release dates). If the post-release study period was extended, it seems likely that this seasonal increase/decrease would be seen on an annual basis. That no obvious pattern was seen for move and social activity is not surprising considering the earlier findings that only time spent feeding and resting significantly differed in the dry and rainy season. To provide a more accurate account of seasonal influence on the diet of the reintroduced chimpanzees, in the future data needs to collected on the availability and quantity of feeding species.

6.6 Conclusions

- The activity budgets of the reintroduced chimpanzees were dominated by feeding, moving and resting, reflecting the overall patterns observed in wild populations. Some differences in budgets between reintroduced and wild populations were found and are to be expected in response to differing environmental conditions.
- Female reintroduced chimpanzees were found to spend significantly more time feeding and less time resting (latter trend only). This may be a consequence of differing nutritional and energetic requirements, the chimpanzee social system, or the bias towards females in study group.
- No differences were found between the islands in terms of time allocation to activity budgets, indicating that whatever differences may exist between the islands, they were not important post-release.

- A correlation was found between age and time spent feeding and moving; less time was spent feeding but more time moving. This may be explained in terms of increasing foraging efficiency and confidence to range further.
- In times of food scarcity, the reintroduced chimpanzees were able to adapt their behaviour to the environmental conditions; they significantly increased the amount of time spent feeding but decreased time spent resting.
- More time was spent feeding in primary and inundated in comparison to swamp forests. This suggests that these forests contained more preferred edible plant species.
- Hourly variation of activity schedules indicates that the reintroduced chimpanzees like their wild counterparts, showed peaks of feeding and rest.
- Changes seen in the frequency of feeding and resting activity over the course of the 14-month study corresponded approximately with the dry season. This further supports the finding that the chimpanzees were able to adapt their behaviour to seasonal changes. Furthermore, that no other distinctive pattern of activity was seen over the post-release period confirms that the chimpanzees were able to immediately adapt.

The following chapter considers a similar set of questions as this chapter but examines the height at which each activity was performed.

Chapter 7

Vertical strata of activity

7.1 Introduction

Chimpanzees are adapted to utilise terrestrial as well as arboreal zones in habitats that include forest, woodland and savanna. However, systematic analysis of the vertical distribution of chimpanzee activity is lacking except for a few anecdotal observations (Kortlandt, 1962; Goodall, 1965, 1968; Reynolds and Reynolds, 1965; Izawa and Itani, 1966; Albrecht and Dunnett, 1971; Jones and Sabater Pi, 1971).

Chimpanzees at Budongo were found to spend an average of 50-75% of daylight hours in trees (Reynolds and Reynolds, 1965) and this is supported by other studies. Only in the rainy season at Gombe did time spent in trees increase to 70-80% during daylight hours (Goodall, 1965).

Plate 7.1 Sophie moving at height category 2 (5-15m)

However, the most systematic study on vertical stratification of activities came from Teleki (1977) who found that overall Gombe chimpanzees only spent 37% of their time above ground versus 63% on the ground. Travelling was found to be mostly terrestrial (99%). This is supported by an earlier study at Gombe that found chimpanzees seldom travel from one place to another through trees, but when they do it is normally for distances less than 200m (Goodall, 1965). Teleki (1977) found that interacting was 84% terrestrial, rest 66% and feeding the least terrestrial at 39%. Teleki (1977) also found that arboreality increased during the rainy season but that it never exceeded 50% in any month of the year. It is likely that the terrestrial/arboreal ratio varies from biome to biome. Populations inhabiting savanna-woodland areas are likely to be less arboreal than chimpanzees inhabiting more homogeneous forest areas (Suzuki, 1969,1975).

Interestingly when it comes to travelling across water, chimpanzees are famous for their hydrophobia. Goodall (1968) found that chimpanzees usually cross streams or gulleys with a quadrupedal or a bipedal leap, via stepping stones, or when the water was too wide (i.e., 11 metres or more), by means of overhanging branches. Only one individual was seen to wade across a shallow stream when he was carrying food in both hands. At Lopé chimpanzees have been found to have such a strong dislike of water, they cross even shallow streams through overhead trees or on bridges (Tutin et al. 1991). Chimpanzees of Kasoje (at the foot of the Mahale Mountains, Tanzania) also avoid contact with water as much as possible when crossing streams, although wading has been seen to occur across distances of 15 metres (of running water) when no arboreal pathway was available for crossing (Nishida, 1980). This is in stark contrast to lowland gorillas at Lopé who will wade across shallow streams even if a bridge is nearby, whereas chimpanzees will in preference cross via the bridge (R. J. Parnell, personal communication, 2001). In the present study, the reintroduced chimpanzees did not display the same hydrophobia as their wild conspecifics and furthermore their adaptation to water guided selection of the reintroduction site (Chapter 4, p.78).

Influence of the captive environment on height of activity

Chapter 4 reported how vertical space is important to apes in captivity (p.98) and Chapter 6 described how chimpanzees kept in socially and physically impoverished environments can hamper and even permanently retard behavioural development (p.125). Although two former laboratory chimpanzees transferred onto an island in Florida did learn to climb, two and a half years later the male had still never been observed climbing to the top of a tree (Pfeiffer and Koebner, 1978).

The height at which an animal feeds, moves and rests has implications for its survival and is of obvious importance for reintroduction. Chapter 1 highlighted that co-ordination and locomotion in space was one skill necessary for survival in the wild (Box, 1991a). An animal must be able to locate and forage for food, move expeditiously, avoid predators and engage in social interaction (if a social species) with conspecifics. Wild orang-utans are the most arboreal of the apes (Rowe, 1996) whereas wild-born orphaned orang-utans may even rest and sleep on the ground (Harrisson, 1969; Borner and Stonehouse, 1979). Grundmann, Lestel, Boestanio and Bomsel (2001) concluded that a lack of arboreality due to fear or lack of competence was a major hindrance to orang-utan reintroduction as it prevented access to the best food sources and nest building. Even after rehabilitation orang-utans tend to be largely or entirely terrestrial although arboreality does gradually increase post-release (Peters, 1995; Zhang, 2001). Infant and juvenile ex-captives froze and ducked when exposed to a frightening stimulus, whereas adolescent and sub-adult rehabilitants generally ascended a nearby tree (Rijksen, 1978 cited in Peters, 1995). At Ketambe (Sumatra) eight juvenile rehabilitant orang-utans died due to predation whilst some adolescents were only wounded (Rijksen and Rijksen-Graatsma, 1975). To encourage arboreality climbing lessons were given (Borner and Stonehouse, 1979) and food exclusively provided in trees (Rijksen, 1978 cited in Peters, 1995). Brewer (1978) and Carter (1981) both described how they had to encourage rehabilitant chimpanzees to climb trees, and Carter (1981) had to develop some ingenious techniques to foster nest building high in trees with two captive-born chimpanzees (see Chapter 9, p.294). Likewise captive-born golden lion tamarins were also hampered in their use of vertical strata; they fell more, relied more on the ground and human-made substrates, and ranged at lower heights in comparison to wild-born tamarins (Stoinski, 2000).

7.2 Aims

- To describe the vertical dimensions of chimpanzee activity and where possible compare to wild chimpanzees.
- To investigate the influence of sex, pre-release island, age, and ecological variables on height at which activity was performed.
- To examine any changes in vertical strata use across the course of the study to assess degree of change post-release.

7.3 Method

7.3.1 Overview

The methodology of this chapter is very similar to Chapter 6. The same rationale and consequent behavioural and seasonal classifications were employed. Each behavioural observation that was made was accompanied by the height at which the activity was being performed. Heights were classified into four categories; ground, less than five metres, 5-15m and heights above 15m. However, from 11.7.99 onwards the management of HELP decided to add an additional height, transforming the classification to five categories; ground, less than five metres, 5-20m, 20-30m and heights above 30m. The present analyses includes data collected during the first 14 months post-release for each chimpanzee and consequently the change in height classification affected only the chimpanzees released in 1999 (Release 1) and not chimpanzees released in 1996 and 1997 (Release 1-3). As a consequence of this change in height classification two types of height analyses were initially conducted; the mean percentage time that was spent in each activity were compared for occurring either on or above the ground (n=15 chimpanzees) and likewise for all four heights (n=11). Overall, similar patterns were observed, but only analyses for the four height categories are presented. The four chimpanzees from Release 4 are excluded from these analyses.

To examine the height at which each activity was performed, and the potential influence of sex, pre-release island, age, and environmental variables, the mean percentage time engaged in each activity at each height was compared. The mean percentages were calculated as before, e.g., each chimpanzee has a total 100% of time, spending varying proportions within each activity at the various heights. Monthly mean percentages were calculated and then averaged across the chimpanzees to get an overall mean level of activity performed at each height. Furthermore, monthly patterns were compared to examine possible changes across the post-release study period.

7.3.2 Statistical analyses

As with Chapter 6 all analyses were performed on mean percentage scores. Data were tested for normality as outlined in Chapter 3. Error bars representing standard deviations have been presented on figures, but when large numbers of multi-comparison tests were run, it was not always possible to include all.

Variables were analysed using ANOVA's, Bonferroni post-hoc tests and Pearson's correlation (2-tailed) where applicable. Table 7.1 details the analyses; the number of chimpanzees included in each analysis (some are excluded due to missing data), months and hours included, data type, activity included and tests performed for each analysis. Due to the large number of post-hoc tests generated by the multivariate analyses, only significant and non-significant results illustrating a pattern of activity are presented.

Table 7.1 Details of statistical analyses performed on vertical strata of activity

Analysis	Chimpanzees	Months/hours	Data	Behaviour	Test
Overall activity budgets	n = 11	Months 1-14 Hours 1-15	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor sex, within factor activity and height) and Bonferroni post-hoc tests
Sex	♀ = 9 ♂ = 2	Months 1-14 Hours 1-15	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor sex, within factor activity and height) and Bonferroni post-hoc tests
Pre-release island	Yvette = 9, Yombe = 2	Months 1-15 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor island, within factor activity and height) and Bonferroni post-hoc tests
Age	n = 11	Months 1-14 Hours 2-14	Overall mean (chimp/month) Age at release + 7 months	Feed, move, rest, social	Pearsons product moment correlation (2-tailed)
Seasonal variation	n = 10 (no Mekoutou)	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest, social	Repeated measures ANOVA (between factor season, within factor activity and height) and Bonferroni post-hoc tests
Forest type	n = 9 (no Cabinda and Hinda)	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest (no social activity due to missing values)	Repeated measures ANOVA (between factor forest, within factor activity and height)and Bonferroni post-hoc tests
Monthly variation	n = 11	Months 1-14 Hours 2-14	Overall mean (chimp/month)	Feed, move, rest (no social activity due to missing values)	Repeated measures ANOVA (between factor month, within factor activity and height) and Bonferroni post-hoc tests

7.4 Results

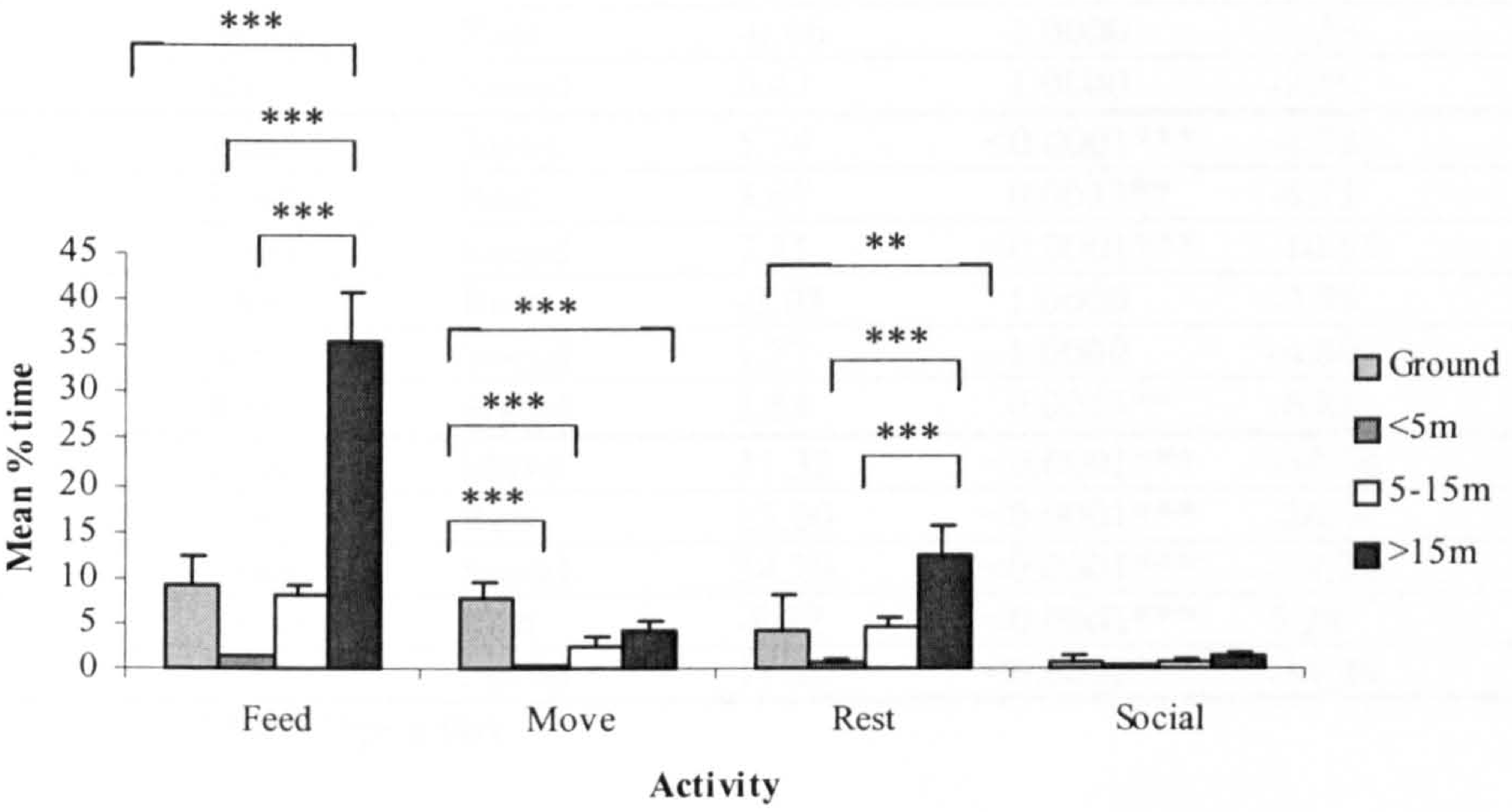
7.4.1 Overview

Post-release the reintroduced chimpanzees (n=11) spent 73% (n=139854) of their time in activities off the ground, and 23% on the ground (n=42652). The remaining 4% (n=7455) consisted of non-identified height use. Within the 73% of time spent off the ground, 56% (n=107235) was accounted for at heights above 15m, 15% at heights between 5-15m (n=28051) and the remaining 2% (n=4568) at heights less than five metres. These percentages include all observed activities and not just those included in the major analyses that follow.

Significant main effects were found for height (*F* (3,30) = 122.72, $p<0.001$) and activity (*F* (3,30) = 956.95, $p<0.001$) and a significant interaction of height and activity (*F* (9,89) = 139.57, $p<0.001$). Post-hoc tests revealed that the significant differences were a result of significantly more mean time spent feeding and resting above 15m in comparison to all the other heights. Approximately four times as much feeding was observed above 15m than was seen either on the ground or between 5-15m (Figure 7.1). Significantly less time was spent feeding and resting at heights less than <5m than at any other height. Furthermore, significantly more mean percentage time was spent moving on the ground than at any of the other height categories. No significant difference was found in the percentage of time engaged in social activities at any height (Table 7.1).

Comparisons of activity within each height category revealed that significantly more feeding occurred on the ground in comparison to rest and social activity (Table 7.2). Although there were no significant differences between the mean time spent feeding and moving on the ground, significantly more moving occurred on the ground in comparison to rest and social activity. At heights of <5m, no significant differences were found between activities. The mean time spent feeding was also found to be significantly greater at heights of 5-15m in comparison to move, rest and social activity. The amount of mean time spent moving at height 5-15m did not differ significantly from rest or social activity but significantly more mean time was spent resting at this height in comparison to social activity. At heights above 15m, significantly more time was spent feeding in comparison to all other activities. Furthermore, significantly less moving occurred than resting, but more resting occurred than social activity at heights above 15m.

Figure 7.1 Mean percentage time spent in the four height categories for each activity (±SD)



*p<0.01, ***p<0.001

Table 7.1 Results of post-hoc tests performed on activity and height (ground, <5m, 5-15m,>15m)

Activity	**Height**				**Mean difference**	**Significance**	**95% confidence interval for difference**	
							Lower bound	**Upper bound**
	Ground	**<5m**	**5-15m**	**>15m**				
Feed				Ground	31.32	<0.0001***	23.07	29.15
				<5m	23.00	<0.0001***	31.13	37.21
				5-15m	34.20	<0.0001***	24.32	30.40
Move	<5m				7.55	<0.0001***	-10.59	-4.51
	5-15m				5.47	<0.0001***	-8.51	-2.43
	>15m				3.68	<0.0001***	-6.72	-0.64
Rest				Ground	-8.23	0.0031**	-6.53	-0.46
				<5m	-11.92	<0.0001***	0.66	6.73
				5-15m	-8.03	<0.0001***	4.99	11.06
Social	<5m				5.33	1.0000	-3.70	2.64
		5-15m			-0.94	1.0000	-2.90	3.45
			>15m		-9.67	1.0000	-2.38	3.70

**p<0.01, ***p<0.001

Table 7.2 Results of post-hoc tests performed on activity and height (ground, <5m, 5-15m,>15m)

Height	Activity	Activity	Mean difference	Significance	95% confidence interval for difference	
					Lower bound	Upper bound
Ground	Feed	Move	1.53	1.0000	-4.56	1.52
	Feed	Rest	5.12	<0.0001***	-8.15	-2/08
	Feed	Social	8.50	<0.0001***	-11.54	-5.46
	Move	Rest	3.59	0.0046**	-6.63	-0.55
	Move	Social	6.97	<0.0001***	-10.01	-3.93
	Rest	Social	3.38	0.0117*	-6.42	-0.34
<5m	Feed	Move	1.01	1.0000	-4.05	2.03
	Move	Rest	-0.46	1.0000	-2.58	3.50
	Rest	Social	0.42	1.0000	-3.59	2.75
5-15m	Feed	Move	5.74	<0.0001***	-8.78	-2.70
	Feed	Rest	3.67	0.0033**	-6.71	-0.63
	Feed	Social	7.51	<0.0001***	-10.55	-4.47
	Move	Rest	-2.08	1.0000	-0.96	5.12
	Move	Social	1.77	1.0000	-4.80	1.28
	Rest	Social	3.84	0.0015**	-6.88	-0.80
>15m	Feed	Move	31.32	<0.0001***	-34.36	-28.28
	Feed	Rest	23.00	<0.0001***	-26.04	-19.96
	Feed	Social	34.20	<0.0001***	-37.24	-31.16
	Move	Rest	-8.32	<0.0001***	5.28	11.35
	Rest	Social	11.20	<0.0001***	-14.24	08.16

*p<0.05, **p<0.01, ***p<0.001

7.4.2 Sex, pre-release island, and age differences

7.4.2.1 Sex

The mean percentage time spent in each activity by females and males at each of the height categories were compared. Significant main effects were found for activity and height but not sex. All interactions were found to be highly significant (Table 7.3).

Table 7.3 Results of ANOVA investigating the influence of sex and activity on height (ground, <5m, 5-15m, >15m)

		df	*F*	p
Main effects	Sex	1,9	0.78	0.394
	Activity	3,27	639.25	<0.0001***
	Height	3,27	126.93	<0.0001***
Interactions	Sex*activity	3,27	4.82	0.006**
	Sex*height	3,27	13.70	<0.0001***
	Activity*height	9,80	91.29	<0.0001***
	Sex*activity*height	9,80	5.20	<0.0001***

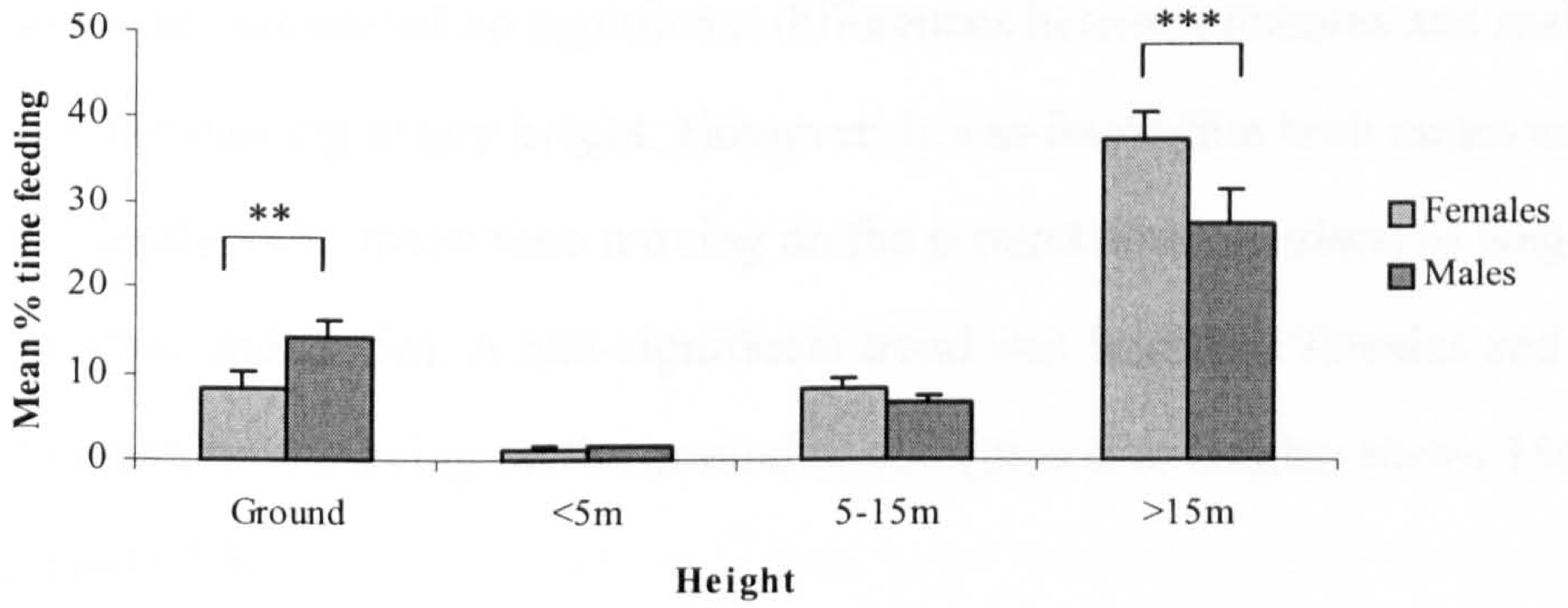
**p<0.01, ***p<0.001

Post-hoc tests revealed the following for each activity:

Feeding

Post-hoc tests revealed that males significantly fed more on the ground in comparison to females, whilst females significantly fed more above 15m than males (Table 7.4, Figure 7.2). No significant differences between the sexes were found for heights of <5m and 5-15m. Both female and male chimpanzees were found to significantly feed more on the ground in comparison to heights lower than 5m, but less than heights above 15m. Furthermore, male chimpanzees were found to significantly feed more on the ground in comparison to heights falling within the 5-15m category.

Figure 7.2 Mean percentage time spent feeding in the four height categories for females and males (±SD)



$^{**}p<0.01$, $^{***}p<0.001$

Table 7.4 Results of post-hoc tests performed on sex, feeding activity and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Feed	♀♂				-5.94	0.006**	0.73	11.15
		♀♂			-0.15	1.0000	-5.07	5.36
			♀♂		1.62	1.0000	-6.83	3.59
				♀♂	9.80	<0.0001***	-15.01	-4.59
	♀	♀			7.01	<0.0001***	-10.15	-3.86
	♀		♀		-0.13	1.0000	-3.02	3.27
	♀			♀	-28.97	<0.0001***	25.83	2.35
		♀	♀		-7.13	<0.0001***	3.99	10.27
	♂	♂			12.80	<0.0001***	-19.46	-6.14
	♂		♂		7.44	0.0088**	-14.10	-0.77
	♂			♂	-13.23	<0.0001****	6.57	19.90

**p<0.01, ***p<0.001

Moving

Post-hoc tests revealed no significant differences between females and males in the mean time spent moving at any height. However, it was found that both males and females spent significantly more mean time moving on the ground in comparison to heights of less than five metres and 5-15m. A non-significant trend was found for females and males to spend more mean time moving on the ground in comparison to heights above 15m (Figure 7.3 and Table 7.5).

Figure 7.3 Mean percentage time spent moving in the four height categories for females and males (±SD)

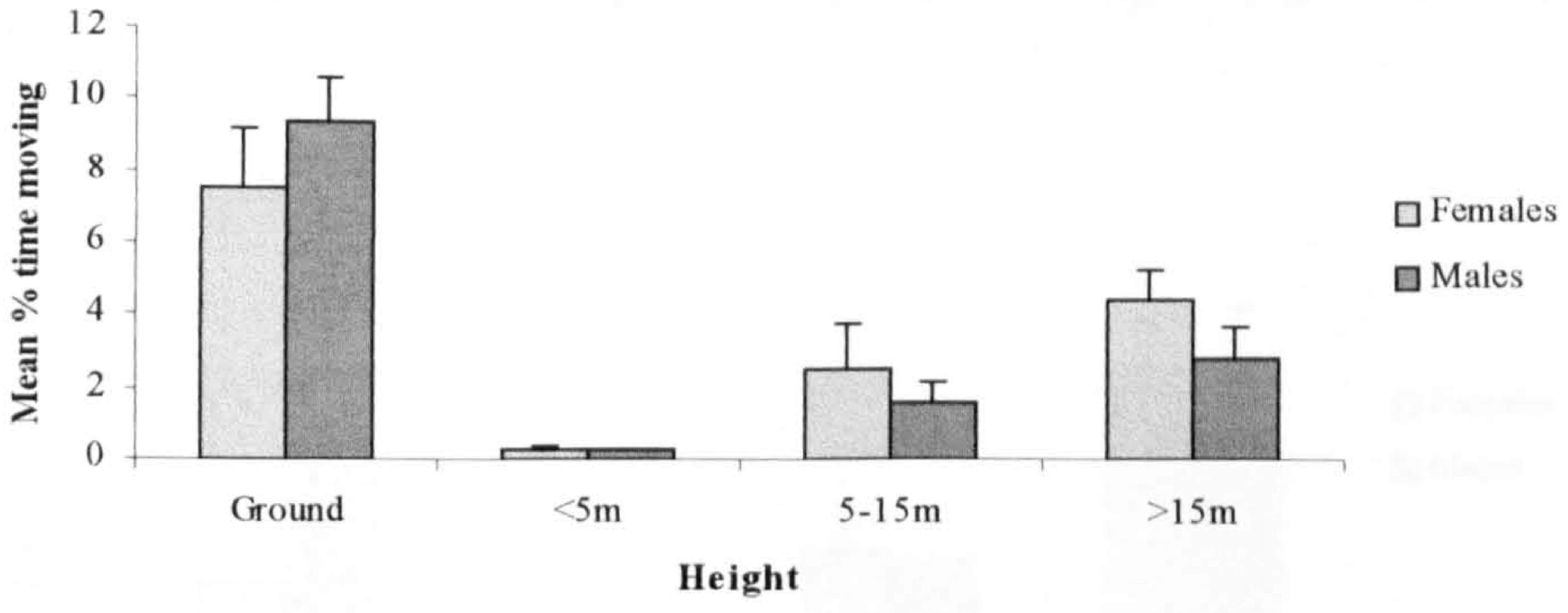


Table 7.5 Results of post-hoc tests performed on sex, height (ground, <5m, 5-15m, >15m) for the activity of move

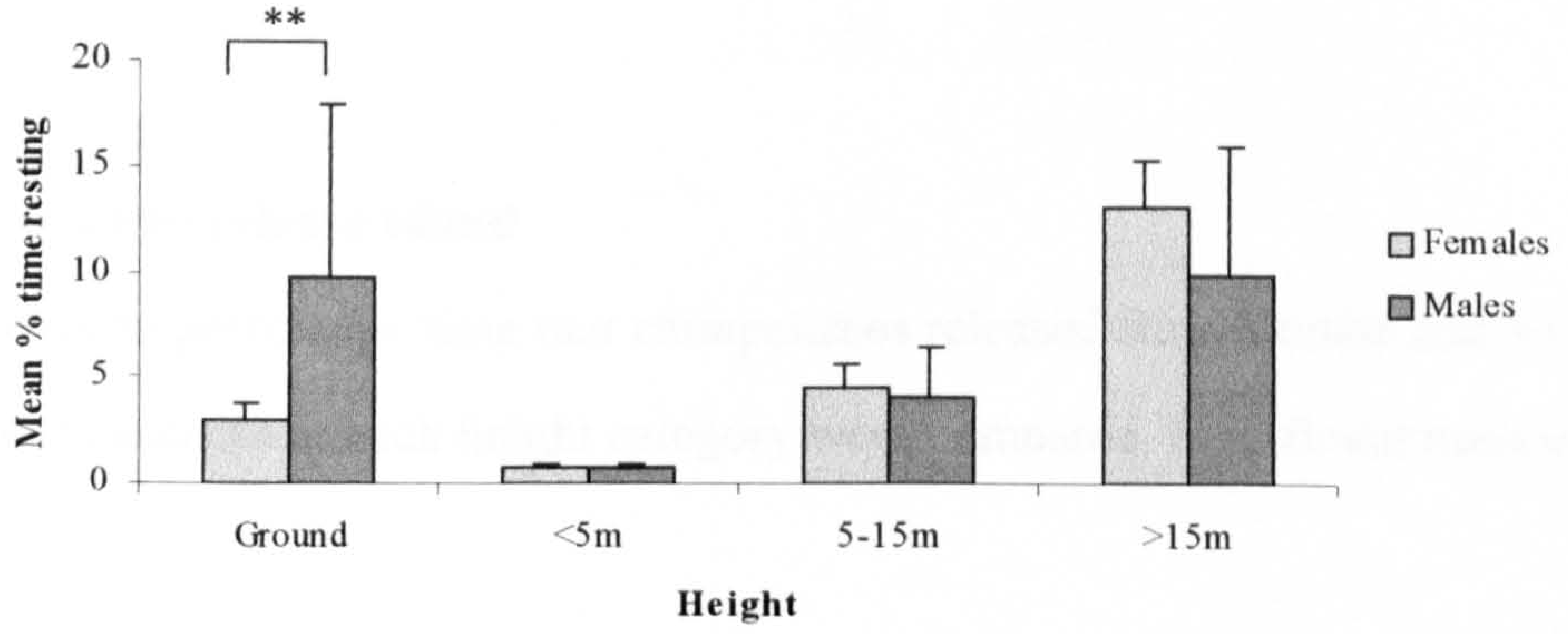
Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Move	♀♂				-1.94	1.0000	-3.29	7.13
		♀♂			-0.04	1.0000	-5.25	5.17
			♀♂		-0.95	1.0000	-6.16	4.26
				♀♂	-1.60	1.0000	-6.81	3.61
	♀	♀			7.19	<0.0001***	-10.33	-4.05
	♀		♀		4.95	<0.0001***	-8.09	-1.80
	♀			♀	3.04	0.0798	-6.18	0.12
	♂	♂			9.16	0.0001**	-15.82	-2.49
	♂		♂		7.82	0.0036**	-14.48	-1.15
	♂			♂	-6.57	0.0621	-13.23	0.10

**p<0.01, ***p<0.001

Resting

Males were found to spend significantly more time resting on the ground in comparison to females (Figure 7.4). However, females and males were not found to significantly differ in the amount of time that they spent resting at any other height. Females were found to spend significantly more time resting above 15m in comparison to all three other heights. Males were found to spend significantly more time resting on the ground in comparison to heights of less than five metres but no significant difference was found between the mean time spent on the ground in comparison to heights of 5-15m and above 15m. However, males did spend more mean time resting at heights above 15m, in comparison to heights of less than five metres (Table 7.6).

Figure 7.4 Mean percentage time spent resting in the four height categories for females and males (±SD)



**p<0.01

Table 7.6 Results of post-hoc tests performed on sex, resting activity and height (ground, <5m, 5-15m, >15m)

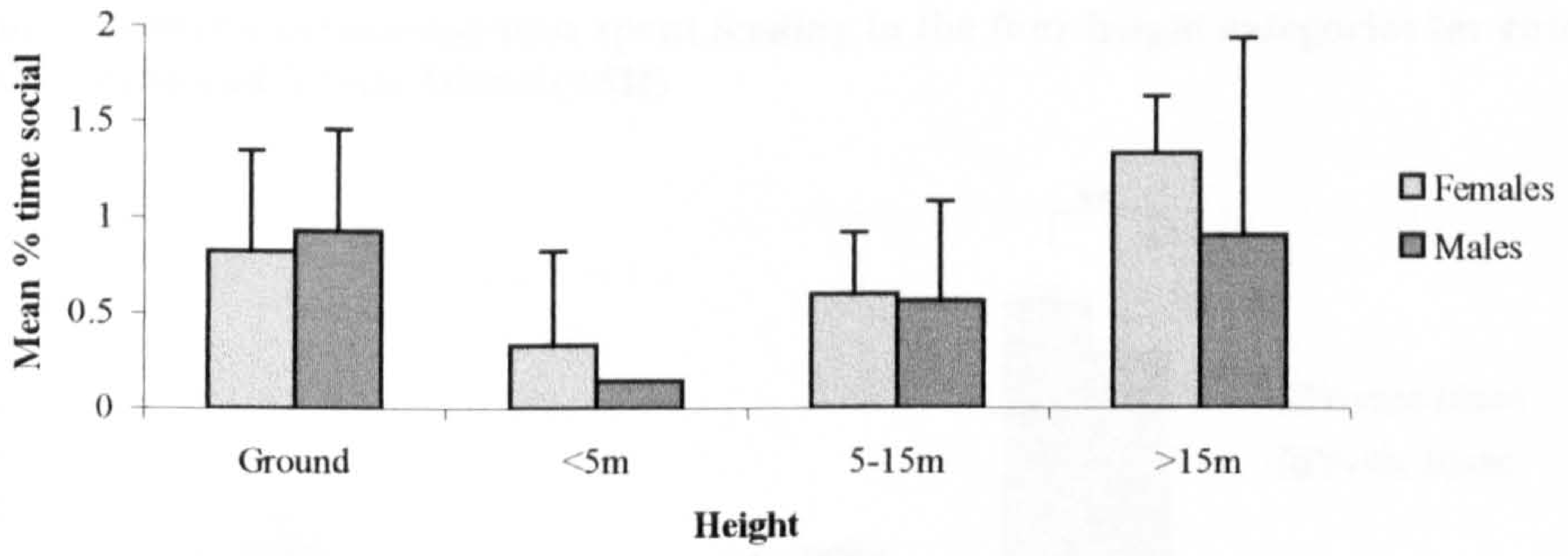
Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Rest	♀♂				-6.84	0.0004**	1.63	12.05
		♀♂			0.01	1.0000	-5.22	5.20
			♀♂		0.45	1.0000	-5.66	4.76
				♀♂	3.12	1.0000	-8.33	2.09
	♀	♀			2.25	1.0000	-5.39	0.89
	♀		♀		-1.53	1.0000	-1.62	4.67
	♀			♀	-10.04	<0.0001***	6.89	13.18
	♂	♂			9.10	0.0002**	-15.76	-2.44
	♂		♂		5.77	0.3312	-12.43	0.90
	♂			♂	0.08	1.0000	-6.59	6.74
		♂		♂	-9.18	0.0001**	2.51	15.84

**p<0.01, ***p<0.001

Social activity

Post-hoc tests found that females and males did not spend significantly any more or less time in social activity at any height in comparison to one another and each height (Figure 7.5).

Figure 7.5 Mean percentage time spent in social activity in the four height categories for females and males (±SD)



7.4.2.2 Pre-release island

The mean percentage time that chimpanzees released from Yombe and Yvette Island spent in each activity at each height category were compared. Significant main effects were found for activity and height but not island. Interactions of activity and height and island, activity and height were found to be significant (Table 7.7).

Table 7.7 Results of ANOVA investigating the influence of pre-release island, activity and height (ground, <5m, 5-15m, >15m)

		df	*F*	p
Main effects	Island	1,9	0.43	0.529
	Activity	3,27	599.22	<0.0001***
	Height	3,27	78.19	<0.0001***
Interactions	Island*activity	3,27	1.02	0.398
	Island*height	3,27	0.71	0.553
	Activity*height	9,80	126.43	<0.0001***
	Island*activity*height	9,80	3.51	0.001**

**p<0.01, ***p<0.001

Post-hoc tests revealed the following for each activity:

Feeding

Chimpanzees released from Yombe Island were found to spend significantly more time feeding at heights above 15m in comparison to chimpanzees released from Yvette Island (Figure 7.6). No significant differences were found between island at any other height category. Regardless of island all the chimpanzees spent significantly more mean time feeding at heights above 15m in comparison to all other height categories (Table 7.8).

Figure 7.6 Mean percentage time spent feeding in the four height categories for chimpanzees released from Yombe and Yvette Island (±SD)

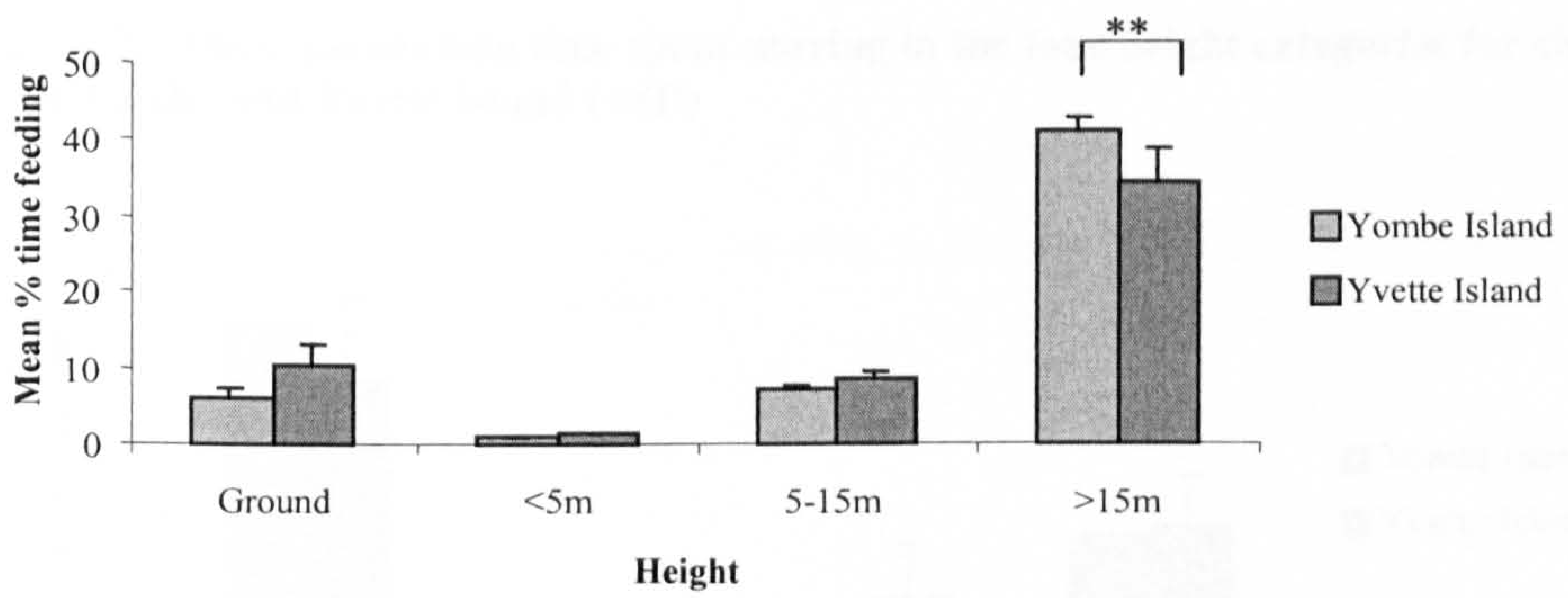


Table 7.8 Results of post-hoc tests performed on pre-release island, feeding activity and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Feed	YB YV				-4.19	1.0000	-1.37	9.74
		YB YV			-0.54	1.0000	-5.02	6.10
			YB YV		-0.99	1.0000	-4.56	6.55
				YB YV	7.06	0.0007**	-12.62	-1.51
	YB			YB	-35.32	<0.0001***	28.21	42.42
		YB		YB	-40.39	<0.0001***	33.28	47.50
			YB	YB	-33.95	<0.0001***	26.84	41.06
	YV			YV	-24.07	<0.0001***	20.72	27.42
		YV		YV	-6.89	<0.0001***	29.44	36.14
			YV	YV	-25.89	<0.0001***	22.54	29.25

YB = Yombe Island, YV = Yvette Island

**p<0.01, ***p<0.001

Moving

Chimpanzees released from Yombe and Yvette Island did not spend significantly any more or less time moving at any of the height categories (Figure 7.7). However, regardless of pre-release island, all the chimpanzees spent significantly more time moving on the ground in comparison to heights lower than 5m and at 5-15m. Chimpanzees released from Yvette Island also spent significantly more time moving on the ground in comparison to heights above 15m (Table 7.9).

Figure 7.7 Mean percentage time spent moving in the four height categories for chimpanzees released from Yombe and Yvette Island (±SD)

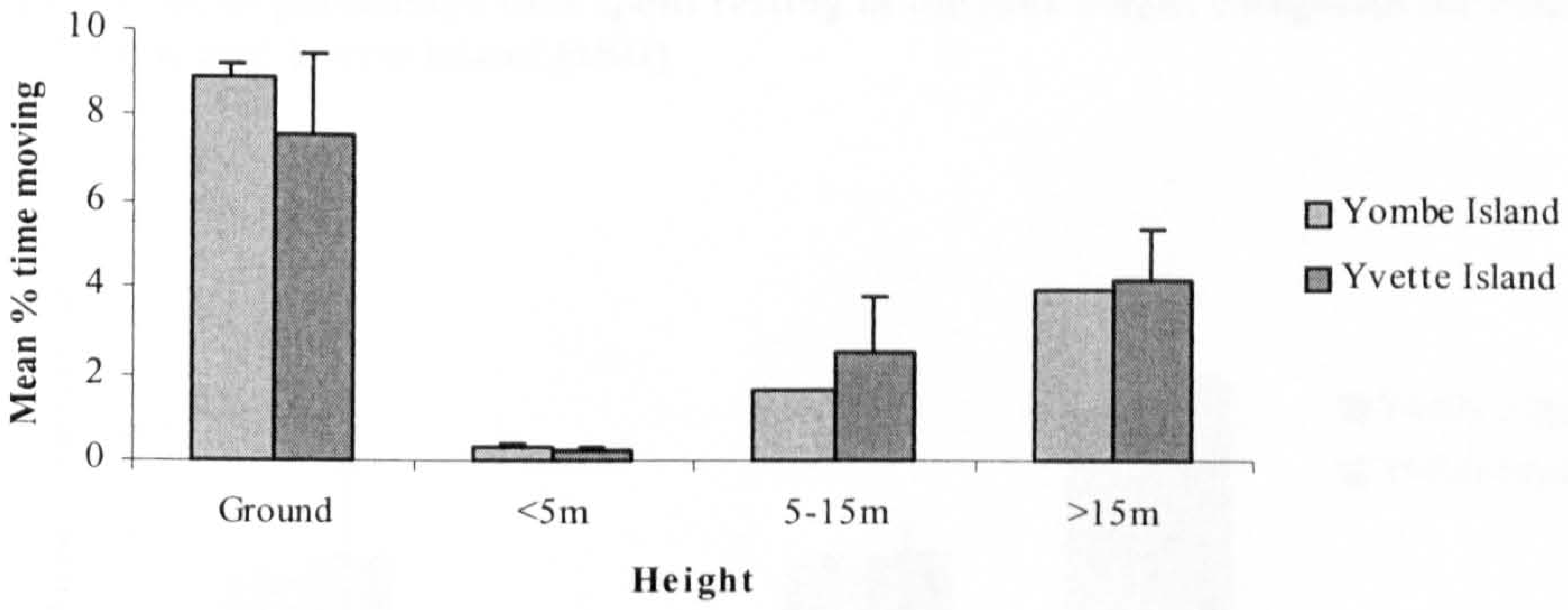


Table 7.9 Results of post-hoc tests performed on pre-release island, activity of move and height (ground, <5m, 5-15m, >15m)

Activity	**Height**				**Mean difference**	**Significance**	**95% confidence interval for difference**	
							Lower bound	**Upper bound**
	Ground	**<5m**	**5-15m**	**>15m**				
Move	YB YV				1.27	1.0000	-6.83	4.29
		YB YV			0.001	1.0000	-5.56	5.56
			YB YV		-0.88	1.0000	-4.68	6.43
				YB YV	-0.29	1.0000	-5.27	5.84
	YB	YB			8.59	0.002**	-15.69	-1.48
	YB		YB		7.23	0.0392*	-14.33	-0.12
	YB			YB	4.96	1.0000	-12.06	2.15
	YV	YV			7.32	<0.0001***	-10.67	-3.97
	YV		YV		5.08	<0.0001***	-8.43	-1.73
	YV			YV	3.40	0.0406*	-6.75	-0.05

YB = Yombe Island, YV = Yvette Island

*p<0.05, **p<0.01, ***p<0.001

Resting

As with the activity of move, when comparing the mean percentage time that chimpanzees released from Yombe and Yvette Island spent resting at the four height categories, no significant differences were found between the pre-release islands (Figure 7.8). However, chimpanzees released from both Yombe and Yvette Island spent significantly more time resting at heights above 15m in comparison to ground level and the 5-15m height category. Furthermore, chimpanzees released from Yvette island were found to spend more mean time resting at heights of 5-15m in comparison to heights lower than five metres (Table 7.10).

Figure 7.8 Mean percentage time spent resting in the four height categories for chimpanzees released from Yombe and Yvette Island (±SD)

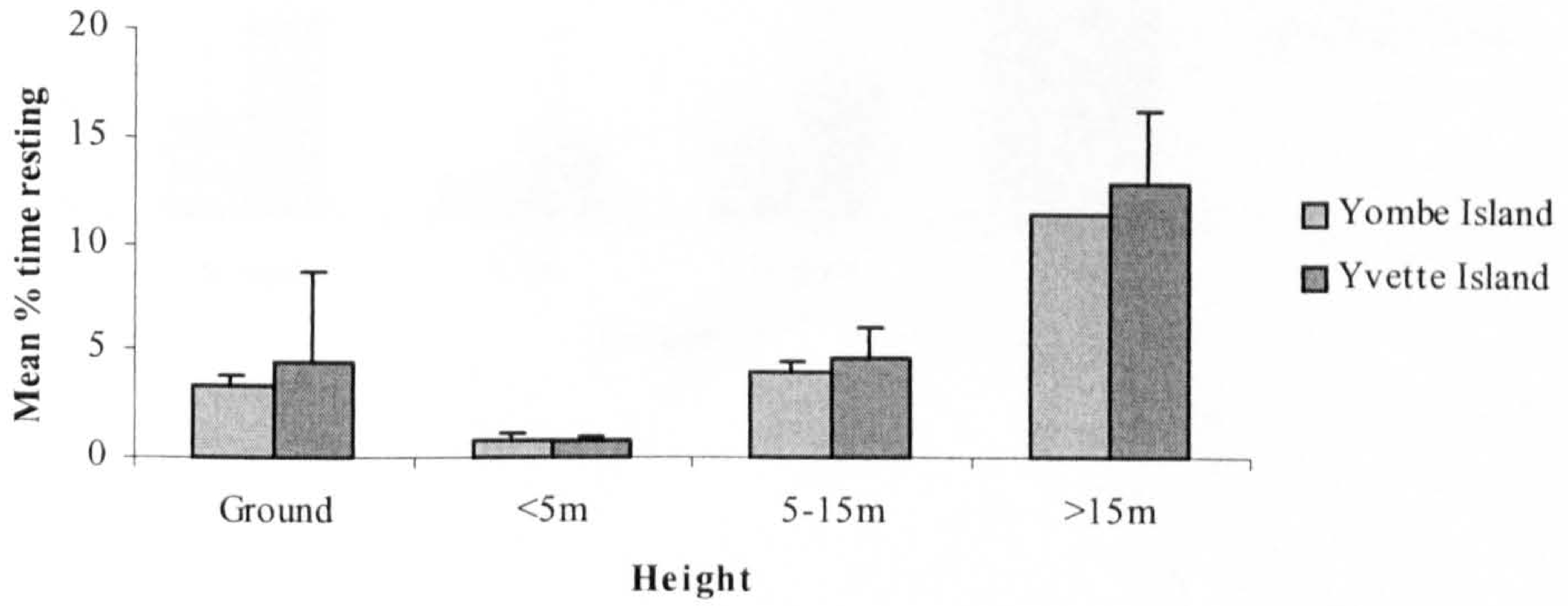


Table 7.10 Results of post-hoc tests performed on pre-release island, resting activity and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Rest	YB YV				-1.05	1.0000	-4.50	6.61
		YB YV			0.01	1.0000	-5.54	5.57
			YB YV		-0.53	1.0000	-5.03	6.08
				YB YV	-1.42	1.0000	-4.14	6.97
	YB	YB			2.65	1.0000	-9.75	4.46
	YB		YB		-0.63	1.0000	-6.48	7.74
	YB			YB	-7.93	0.0088**	0.82	15.03
		YB	YB		-3.28	1.0000	-3.83	10.38
			YB	YB	-7.30	0.0339*	0.19	14.40
	YV	YV			3.68	0.0113*	-7.03	-0.33
	YV		YV		-0.10	1.0000	-3.25	3.46
	YV			YV	-8.29	<0.0001***	4.94	11.64
		YV	YV		-3.79	0.007**	0.44	7.14
			YV	YV	-8.19	<0.0001***	4.84	11.54

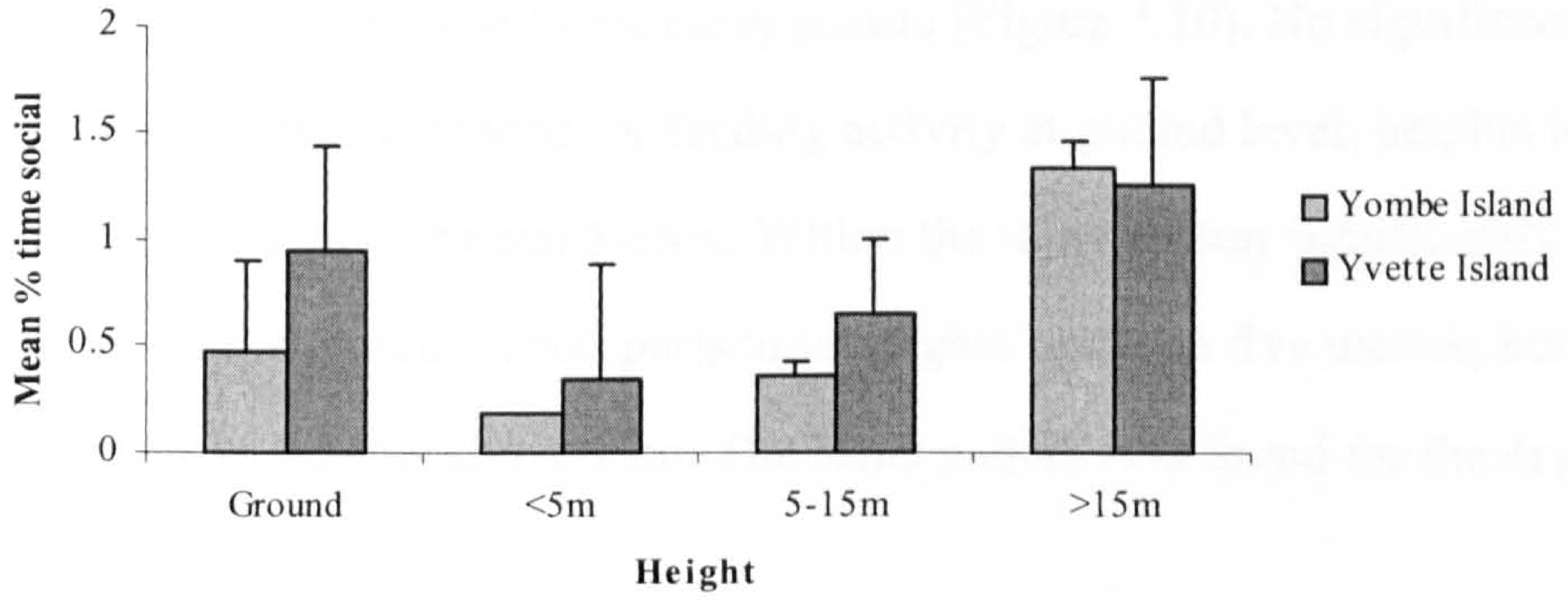
YB = Yombe Island, YV = Yvette Island

*p<0.05, **p<0.01, ***p<0.001

Social activity

Post-hoc tests found that chimpanzees released from Yombe and Yvette Island did not spend significantly any more or less time in social activity at any height in comparison to one another and each height (Figure 7.9).

Figure 7.9 Mean percentage time spent in social activity in the four height categories for chimpanzees released from Yombe and Yvette Island (±SD)



7.4.2.3 Age

A series of correlation's were run for each activity at each height against age (at release +7 months) and not surprisingly with this limited age range (6.7-9.7 years) no significant relationship was found for age with any activity at any height.

7.4.3 Environmental differences

7.4.3.1 Seasonal variation

The mean percentage time spent in each activity within the four height categories were compared across and within the rainy and dry season to examine seasonal variation of height use. All main effects and interactions were found to be significant (Table 7.11).

Table 7.11 Results of ANOVA investigating the influence of season, activity and height (ground, <5m, 5-15m, >15m)

		df	*F*	p
Main effects	Activity	3,27	482.20	<0.0001***
	Season	1,9	9.35	0.007**
	Height	3,27	418.77	<0.0001***
Interactions	Activity*season	3,27	22.17	<0.0001***
	Activity*height	9,81	184.41	<0.0001***
	Season*height	3,27	5.29	0.005**
	Activity*season*height	9,75	7.54	<0.0001***

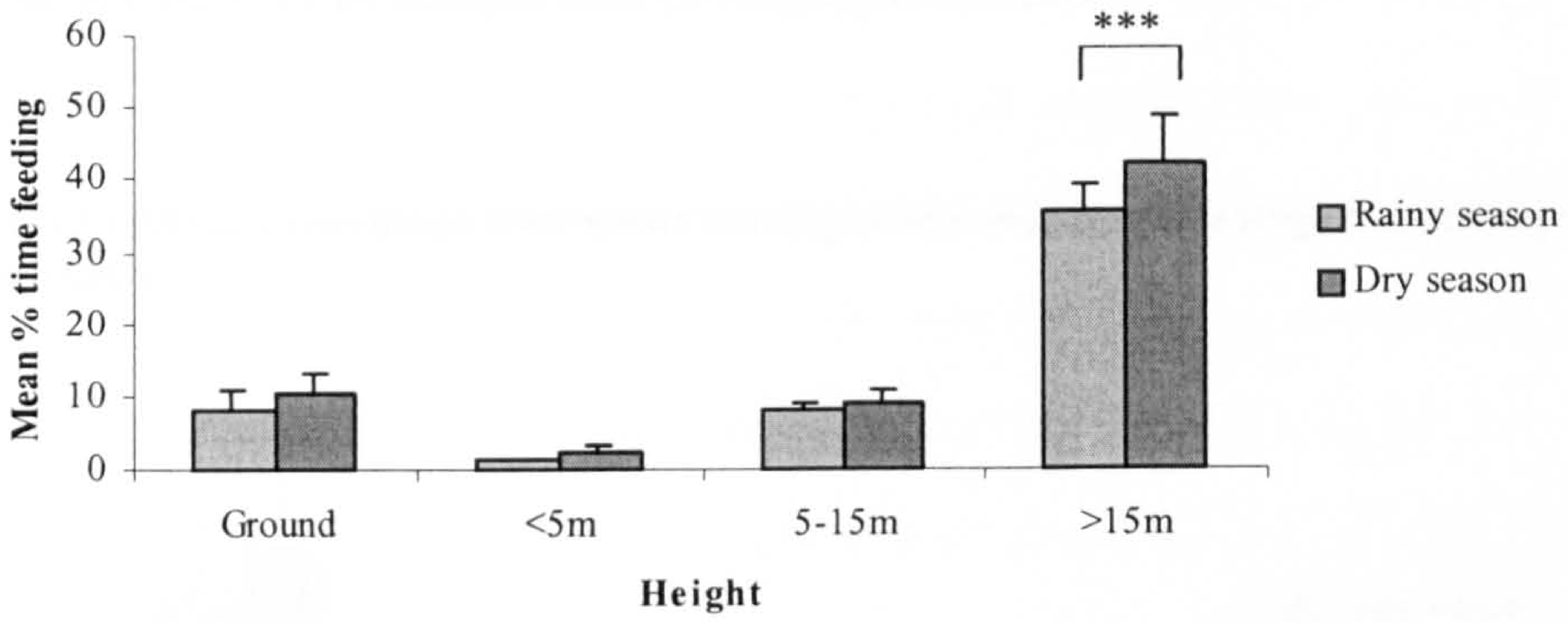
**p<0.01, ***p<0.001

Post-hoc tests revealed the following for each activity:

Feeding

A significantly higher mean percentage time was spent feeding in the dry season at heights above 15m in comparison to the rainy season (Figure 7.10). No significant differences were found between seasons for feeding activity at ground level, heights less than five metres, and heights between 5-15m. Within the rainy season significantly more feeding occurred on the ground in comparison to heights less than five metres, but less in comparison to heights above 15m. The same pattern was found for the dry season (Table 7.12).

Figure 7.10 Mean percentage time spent feeding in the four height categories during the rainy and dry season (±SD)



***p<0.001

Table 7.12 Results of post-hoc tests performed on season, feeding activity and height (ground, <5m, 5-15m, >15m)

Activity	**Height**				**Mean difference**	**Significance**	**95% confidence interval for difference**	
							Lower bound	**Upper bound**
	Ground	**<5m**	**5-15m**	**>15m**				
Feed	R D				-2.40	0.0508	-0.00	4.80
		R D			-1.32	1.0000	-1.08	3.72
			R D		-0.81	1.0000	-1.59	3.20
				R D	-6.45	<0.0001***	4.06	8.85
	R	R			6.92	<0.0001***	-9.32	-4.52
	R		R		0.02	1.0000	-2.42	2.38
	R			R	-27.34	<0.0001***	24.94	29.73
		R	R		-6.90	<0.0001***	4.50	9.29
	D	D			7.99	<0.0001***	-10.39	-5.59
	D		D		1.61	1.0000	-4.01	0.79
	D			D	-31.39	<0.0001***	28.99	33.79
		D	D		-6.38	<0.0001***	3.98	8.76

R – rainy season, D = dry season

***p<0.001

Moving

No significant differences were found between the mean percentage time spent moving in the rainy and dry season at each height (Figure 7.11 and Table 7.13). However, in both the rainy and dry season, the mean percentage time spent moving on the ground was significantly greater when compared to all other heights. Significantly more mean time was spent moving at heights above 15m in comparison to heights less than 5m in both seasons.

Furthermore, in the rainy season, significantly more mean time was spent moving at heights above 15m in comparison to heights of 5-15m.

Figure 7.11 Mean percentage time spent moving in the four height categories during the rainy and dry season (±SD)

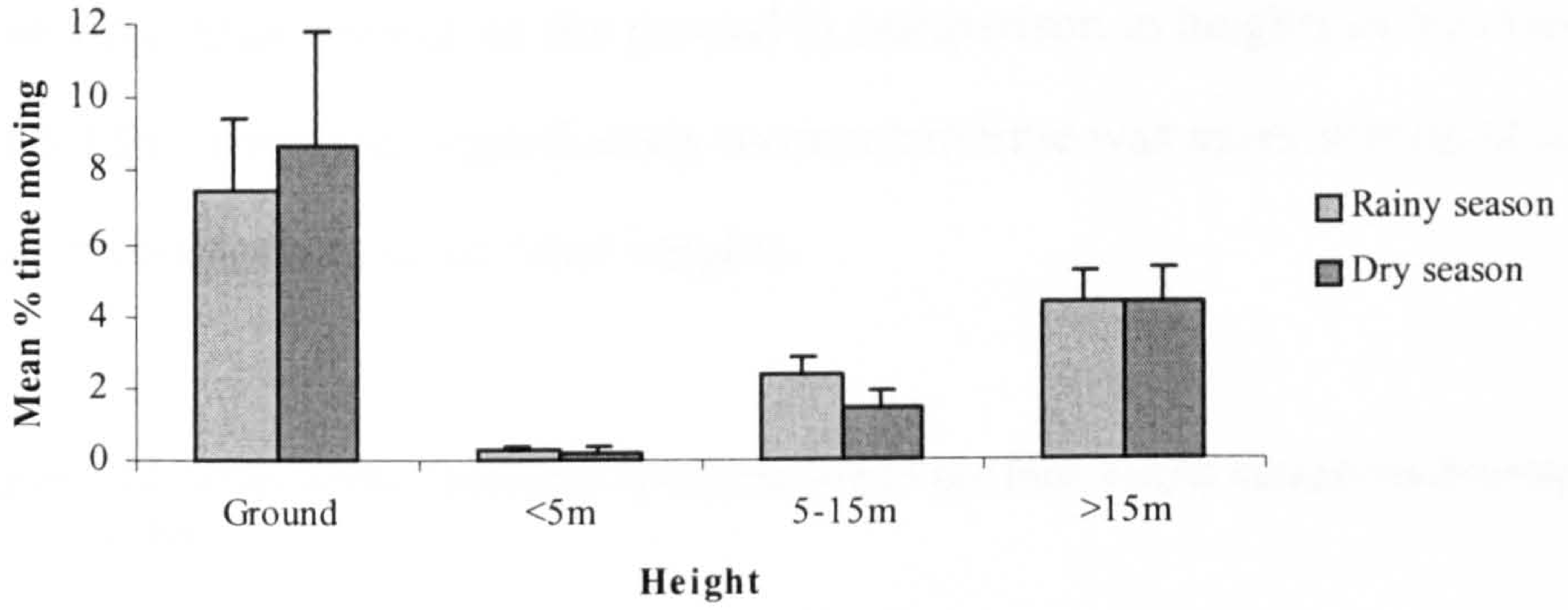


Table 7.13 Results of post-hoc tests performed on season, activity of move and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Move	R D				-1.26	1.0000	-1.14	-4.83
		R D			0.06	1.0000	-2.46	2.34
			R D		0.88	1.0000	-3.28	1.52
				R D	-0.04	1.0000	-2.44	2.36
	R	R			7.16	<0.0001***	-9.56	-4.76
	R		R		5.12	<0.0001***	-7.52	-2.72
	R			R	3.10	0.0005**	-5.50	-0.71
		R		R	-4.06	<0.0001***	1.66	6.46
			R	R	-2.02	0.4466	-0.38	4.42
	D	D			8.48	<0.0001***	-10.88	-6.08
	D		D		7.26	<0.0001***	-9.66	-4.86
	D			D	0.40	<0.0001***	-6.80	-2.00
		D		D	-4.08	<0.0001***	1.68	6.48
			D	D	-2.86	0.0027**	0.46	5.26

R = rainy season, D = dry season

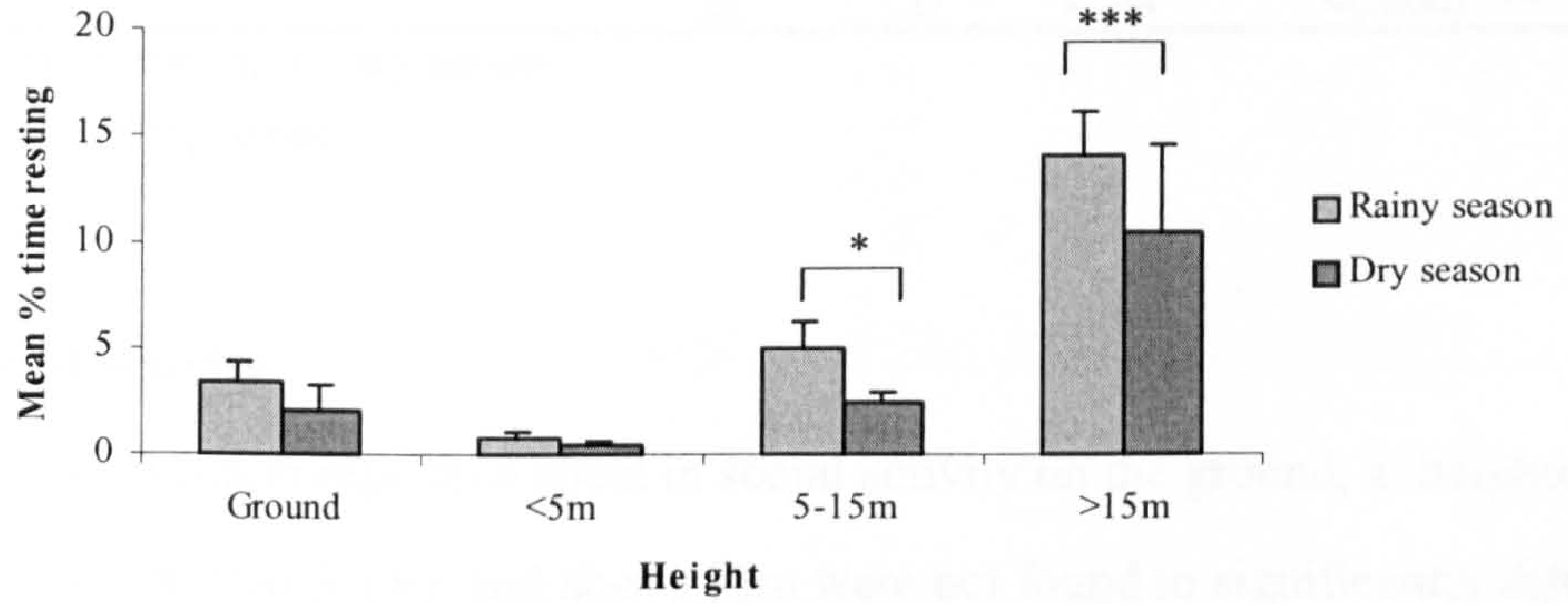
$^{**}p<0.01$, $^{***}p<0.001$

Resting

The mean percentage time that chimpanzees spent resting at heights 5-15m and above 15m were found to be significantly greater in the rainy season when compared to the dry season

(Figure 7.12). No significant differences were found between the seasons at ground level or at heights less than five metres. In the rainy season the mean percentage time spent resting both on the ground and at heights of 5-15m were significantly higher in comparison to heights of less than five metres, but significantly lower in comparison to heights above 15m (Table 7.14). In the dry season no significant differences were found between the mean time spent resting on the ground in comparison to heights of less than five metres and 5-15m. However, significantly more mean time was spent resting at heights above 15m in comparison to all other heights.

Figure 7.12 Mean percentage time spent resting in the four height categories during the rainy and dry season (±SD)



*p<0.05, ***p<0.001

Table 7.14 Results of post-hoc tests performed on season, height (ground, <5m, 5-15m, >15m) and the activity of rest

Activity	**Height**				**Mean difference**	**Significance**	**95% confidence interval for difference**	
							Lower bound	**Upper bound**
	Ground	**<5m**	**5-15m**	**>15m**				
Rest	R D				1.36	1.0000	--3.76	1.04
		R D			0.34	1.0000	-2.74	2.06
			R D		2.52	0.0244*	-4.92	-0.12
				R D	3.57	<0.0000***	-5.97	-1.17
	R	R			2.66	0.0100*	-5.06	-0.26
		R	R		-4.18	<0.0001***	1.78	6.58
	R			R	-10.51	<0.0001***	8.11	12.90
		R		R	-13.16	<0.0001***	10.76	15.56
			R	R	-8.99	<0.0001***	6.59	11.39
	D	D			1.63	1.0000	-4.03	0.77
	D		D		-0.37	1.0000	-2.03	2.77
	D			D	-8.30	<0.0001***	5.90	10.70
		D		D	-9.94	<0.0001***	7.54	12.33
			D	D	-7.94	<0.0001***	5.54	10.33

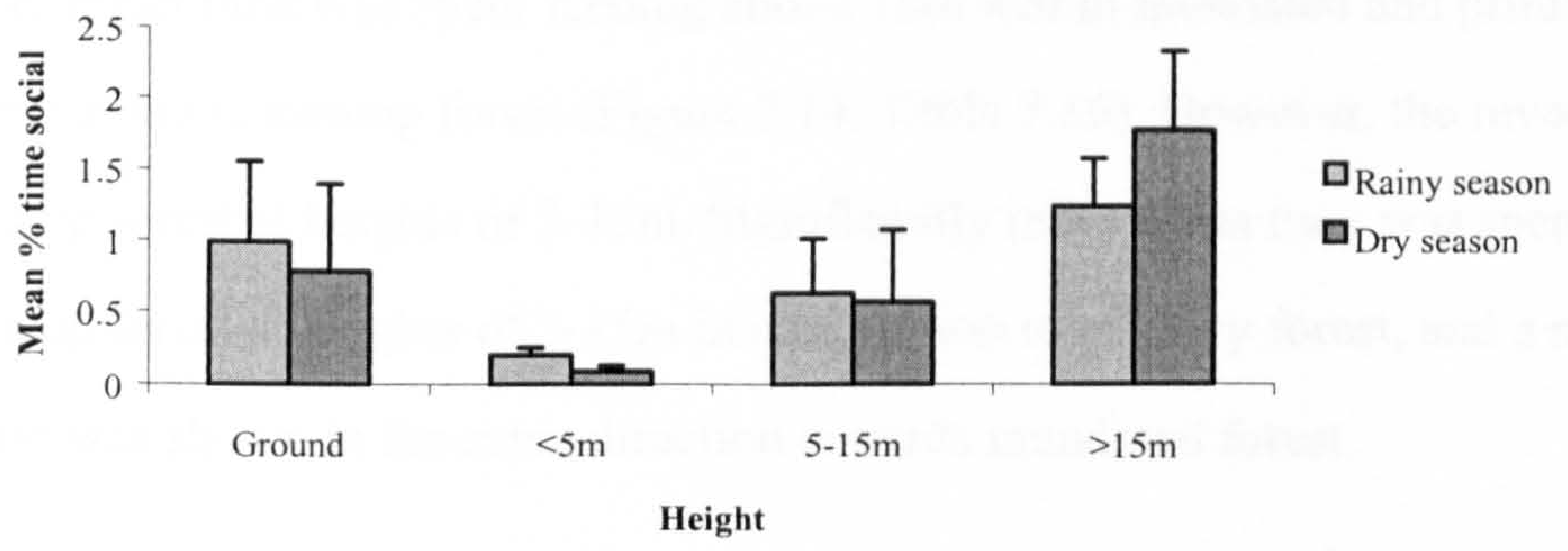
R = rainy season, D = dry season

*p<0.05, ***p<0.001

Social activity

The mean percentage time spent in social activity on the ground, at heights less than five metres, between 5-15m and above 15m were not found to significantly differ between and within the dry and rainy season (Figure 7.13).

Figure 7.13 Mean percentage time spent in social activity in the four height categories during the rainy and dry season (±SD)



7.4.3.2 Forest type

The mean percentage time spent in each activity within the four height categories were compared across and within the three forest types (inundated, swamp and primary) to examine its possible influence on height of activity. In the present analyses social activity has not been included due to missing cases, and the number of subjects has been reduced to nine for the same reason. Significant main effects were found for activity and height but not forest, and significant interactions were found for all comparisons except activity and forest (Table 7.15).

Table 7.15 Results of ANOVA investigating the influence of forest type, activity and height (ground, <5m, 5-15m, >15m)

		df	*F*	p
Main effects	Activity	2,16	276.81	<0.0001***
	Forest	2,16	0.73	0.484
	Height	3,24	344.72	<0.0001***
Interactions	Activity*forest	4,32	0.70	0.136
	Activity*height	6,48	171.89	<0.0001***
	Forest*height	6,48	12.70	<0.0001***
	Activity*forest*height	12,93	5.49	<0.0001***

***p<0.001

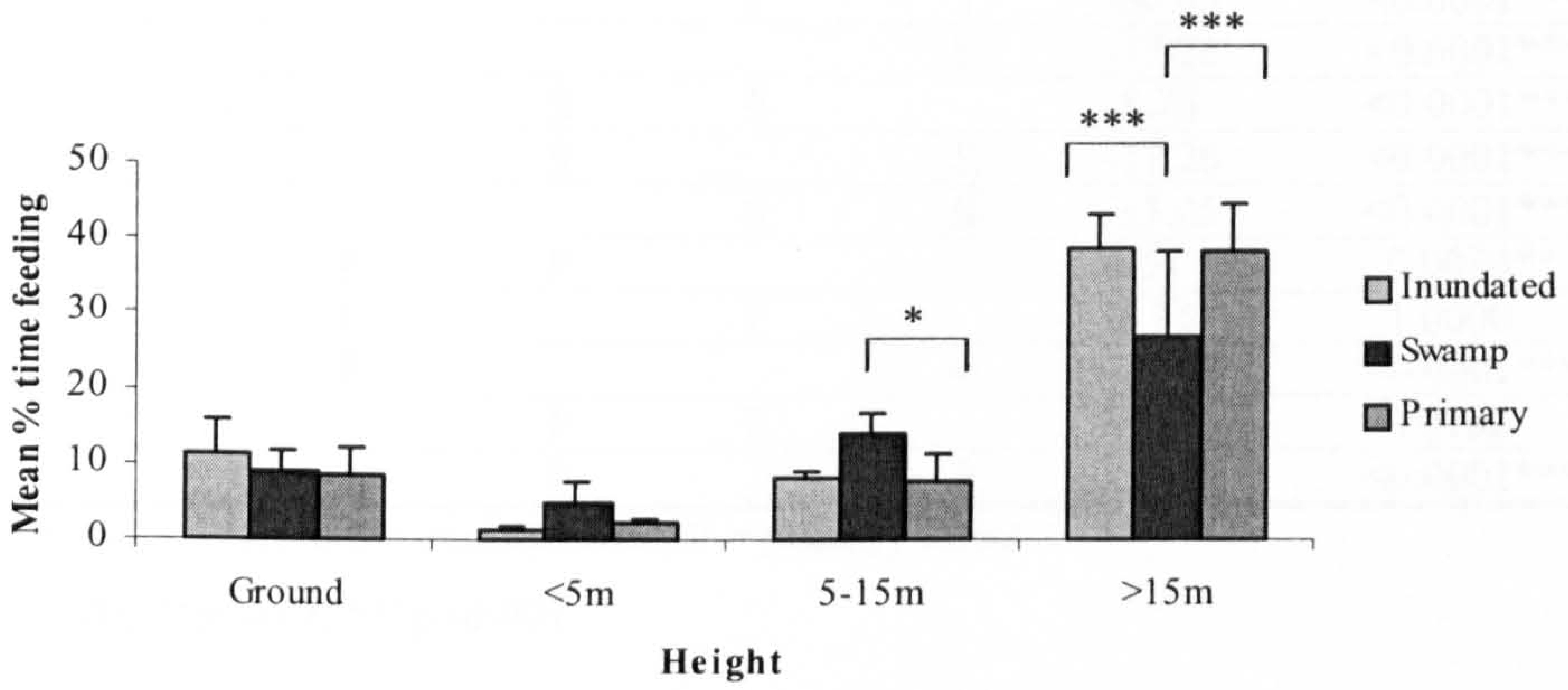
Post-hoc tests revealed the following for each activity:

Feeding

Earlier comparisons highlighted that significantly more mean time was spent feeding at heights above 15m regardless of forest type. Present analyses revealed that significantly more mean time was spent feeding above 15m within inundated and primary in comparison to swamp forest (Figure 7.14, Table 7.16). However, the reverse was true for swamp forest at heights of 5-15m. Significantly more mean time was spent feeding in the swamp forest at heights of 5-15m in comparison to primary forest, and a non-significant trend was shown in the same direction towards inundated forest.

Within inundated forest, significantly more feeding activity occurred on the ground in comparison to heights lower than five metres, but less than heights above 15m. No significant difference was found between the level of feeding activity on the ground and at 5-15m, but significantly less feeding activity occurred at 5-15m in comparison to heights above 15m. In swamp forests, significantly more feeding activity occurred at heights above 15m in comparison to all other heights, and furthermore, significantly more feeding occurred at heights of 5-15m in comparison to heights less than five metres. As with swamp forest significantly more feeding activity occurred at heights above 15m in comparison to all other heights in primary forest. Furthermore, significantly more feeding activity occurred on the ground and at heights of 5-15m in primary forest in comparison to heights lower than five metres.

Figure 7.14 Mean percentage time spent feeding in the four height categories in inundated, swamp and primary forest (±SD)



*p<0.05, ***p<0.001

Table 7.16 Results of post-hoc tests performed on forest type, feeding activity and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Feed	I S				1.70	1.0000	-8.17	4.77
	I P				2.64	1.0000	-8.57	3.29
	S P				0.94	1.0000	-7.40	5.53
		I S			-3.56	1.0000	-2.37	9.49
		I P			-0.55	1.0000	-5.38	6.48
		S P			3.01	1.0000	-8.94	2.92
			I S		5.88	0.0569	-0.05	11.81
			I P		0.12	1.0000	-6.05	5.81
			S P		6.00	0.0417*	--1.93	-0.07
				I S	12.03	<0.0001***	-17.96	-6.10
				I P	0.59	1.0000	-6.52	5.34
				S P	-11.43	<0.0001***	5.50	17.37
	I	I			9.80	<0.0001***	-15.73	-3.87
	I		I		3.37	1.0000	-9.30	2.56
	I			I	-27.58	<0.0001***	21.65	33.52
			I	I	-30.95	<0.0001***	25.02	36.88
	S			S	-17.26	<0.0001***	10.79	23.73
		S	S		-8.75	<0.0001***	2.82	14.68
		S		S	-17.26	<0.0001***	15.86	27.73
			S	S	-13.05	<0.0001***	7.11	18.98
	P	P			6.61	0.0084**	-12.54	-0.68
	P		P		-0.85	1.0000	-6.78	5.08
	P			P	-29.63	<0.0001***	23.70	35.60
		P	P		-5.75	0.0782	-0.18	11.69
		P		P	-36.24	<0.0001***	30.31	42.17

I =inundated forest, S = swamp forest, P = primary forest

*p<0.05, **p<0.01, ***p<0.001

Moving

No significant differences were found between forest type and the mean percentage time spent moving at each height category (Figure 7.15). Furthermore, regardless of forest type significantly more mean time was spent moving on the ground in comparison to all other heights (Table 7.17).

Figure 7.15 Mean percentage time spent moving in the four height categories in inundated, swamp and primary forest (±SD)

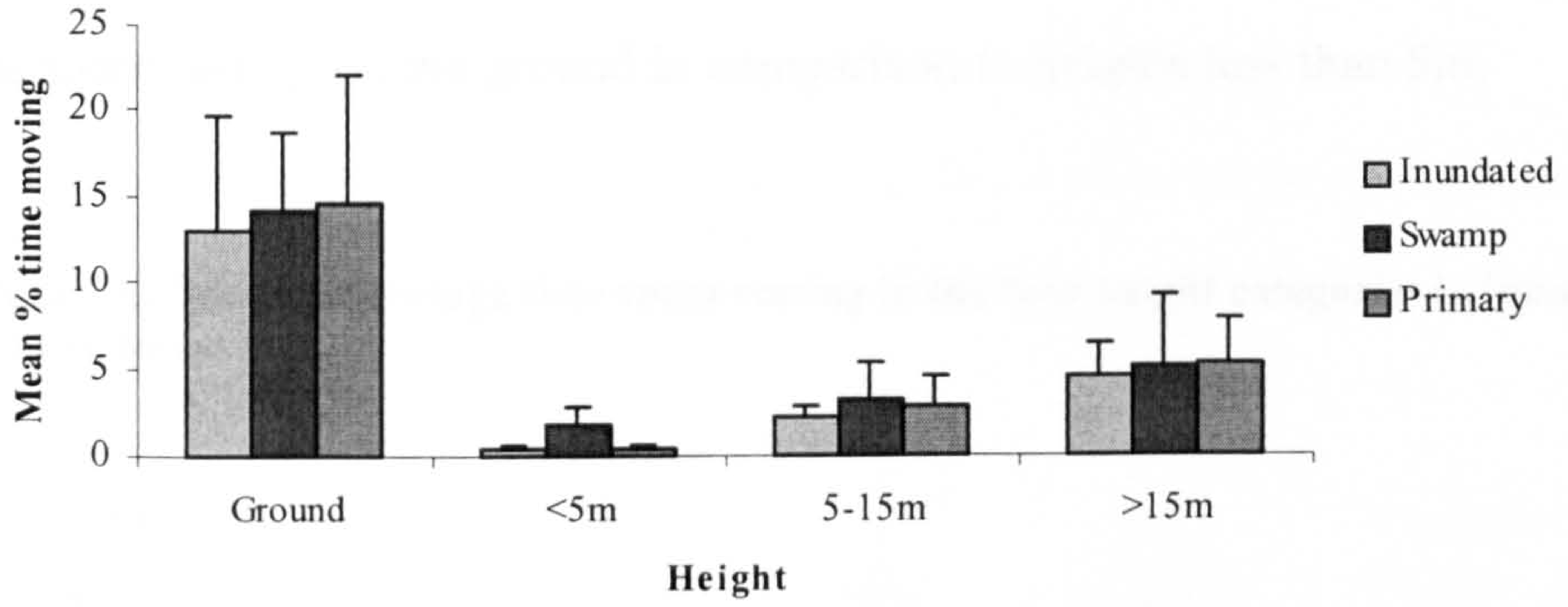


Table 7.17 Results of post-hoc tests performed on forest type, activity of move and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	**<5m**	**5-15m**	**>15m**				
Move	I	I			12.67	<0.0001***	-18.60	-6.74
	1		I		10.95	<0.0001***	-16.88	-5.02
	I			I	8.49	<0.0001***	-14.42	-2.56
	S	S			12.55	<0.0001***	-18.48	-6.62
	S		S		11.14	<0.0001***	-17.07	-5.21
	S			S	9.06	<0.0001***	-14.99	-3.13
	P	P			15.14	<0.0001***	-21.61	-8.67
	P		P		11.70	<0.0001***	-17.63	-5.77
	P			P	9.11	<0.0001***	-15.05	-3.18

I = inundated forest, S = swamp forest, P = primary forest

***p<0.001

Resting

As with the activity of move, no significant differences were found between forest type and the mean percentage time spent moving at each height category (Figure 7.16). However, within inundated forest significantly more mean time was spent resting at heights above 15m in comparison to ground level, although no significant differences were found between the mean time spent resting on the ground, in comparison to heights less than five metres and 5-15m. In swamp forest, the chimpanzees showed no significant difference in the heights at which they rested in this forest type (Table 7.18). In primary forest significantly more mean time was spent resting at heights above 15m in comparison to heights below five metres and ground level. Furthermore, significantly more mean time was spent resting on the ground in comparison to heights less than 5m.

Figure 7.16 Mean percentage time spent resting in the four height categories in inundated, swamp and primary forest (±SD)

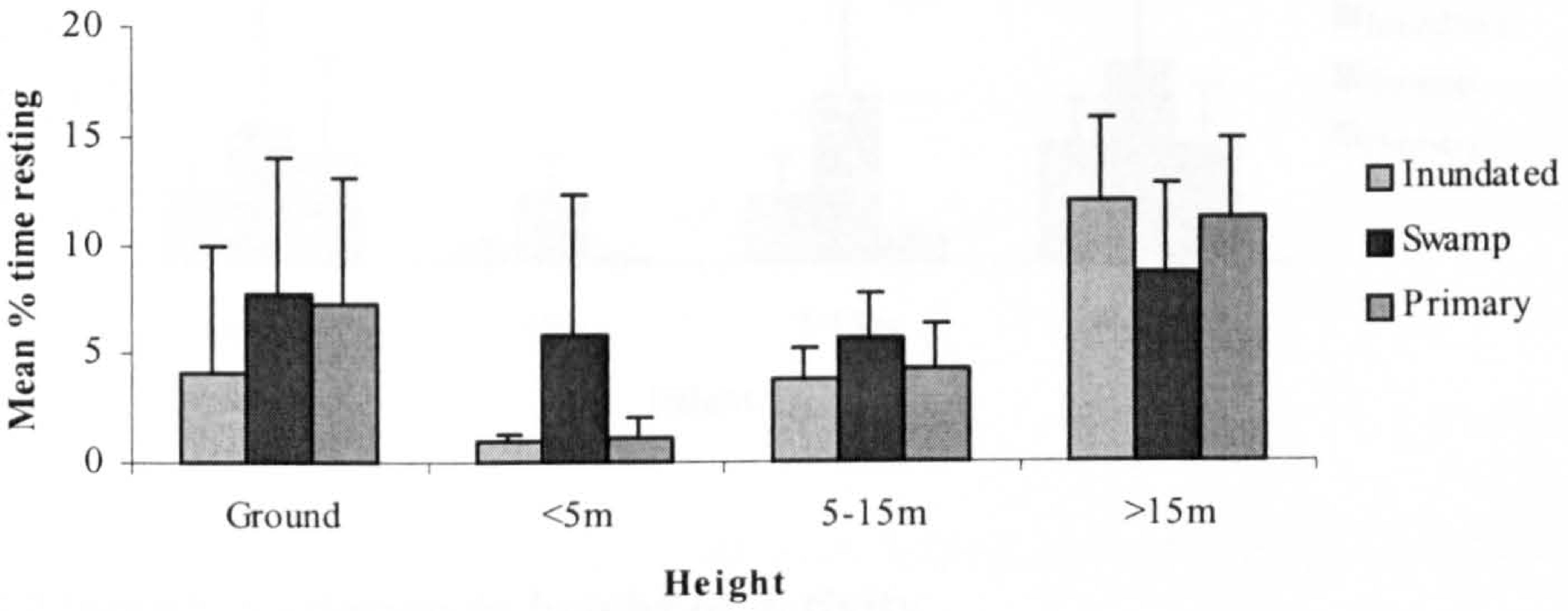


Table 7.18 Results of post-hoc tests performed on forest type, resting activity and height (ground, <5m, 5-15m, >15m)

Activity	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Rest	I	I			3.19	1.0000	-9.12	2.74
	I		I		0.25	1.0000	-6.18	5.68
	I			I	-7.89	0.0002**	1.96	13.82
	S	S			2.69	1.0000	-9.15	3.78
		S	S		1.96	1.0000	-5.74	7.19
			S	S	-0.99	1.0000	-2.98	8.88
	P	P			6.13	0.0295*	-12.07	-0.20
		P		P	-10.01	<0.0001***	4.08	15.94
			P	P	-6.90	0.0038**	0.97	12.83

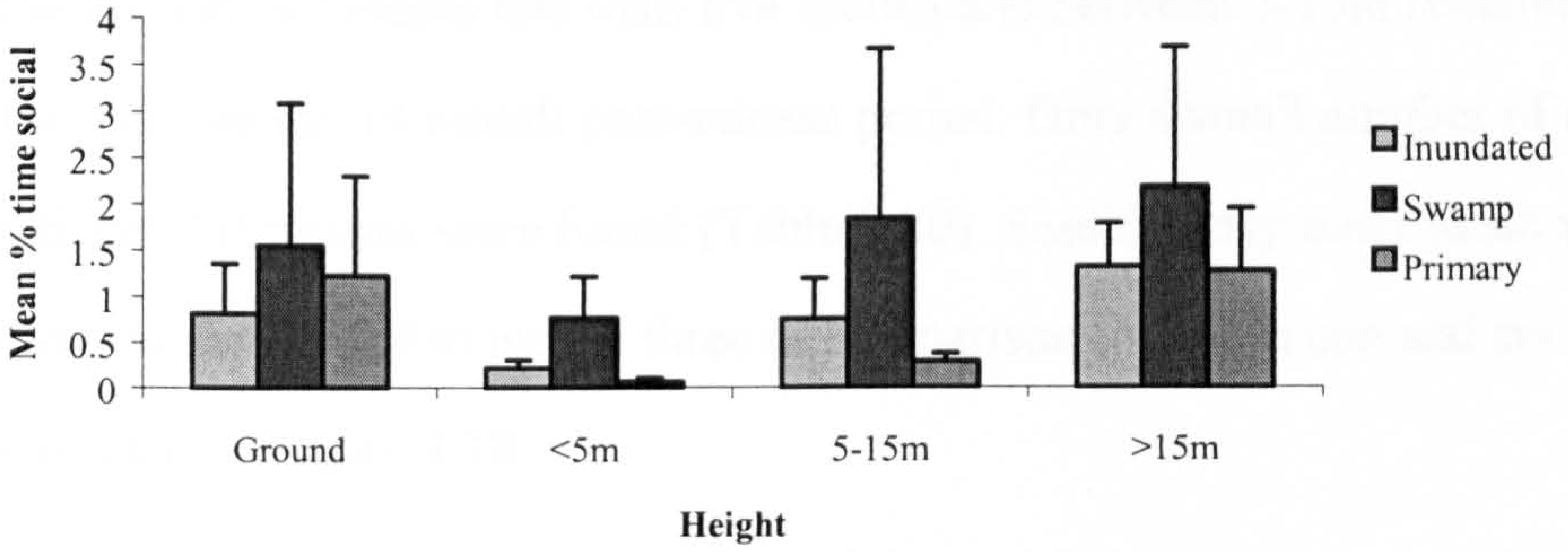
I = inundated forest, S = swamp forest, P = primary forest

*p<0.05, **p<0.01, ***p<0.001

Social activity

Due to missing values it was not possible to include social activity in statistical analyses. Although the means indicate that more time was spent in social activity in swamp forest at all height categories the overall levels of this activity are so low it is not possible to discuss further (Figure 7.17).

Figure 7.17 Mean percentage time spent within social activity in the four height categories in inundated, swamp and primary forest (±SD)



7.4.4 Monthly variation in height of activity

To examine any possible variation in height of activity across the study period, the mean monthly time spent within each activity either on the ground, at heights less than 5m, 5-15m and above 15m were compared. Social activity was excluded from analyses due to missing values. Analyses produced highly significant main effects and interactions for all factors and combinations (Table 7.19).

Table 7.19 ANOVA investigating the influence of month post-release on height (ground, <5m, 5-15m, >15m) of activity

		df	***F***	**p**
Main effects	Activity	2,20	422.89	<0.0001***
	Month	13,130	5.30	<0.0001***
	Height	3,30	107.43	<0.0001***
Interactions	Activity*month	26,260	13.15	<0.0001***
	Activity*height	6,60	136.22	<0.0001***
	Month*height	39,390	5.86	<0.0001***
	Activity*month*height	78,726	5.55	<0.0001***

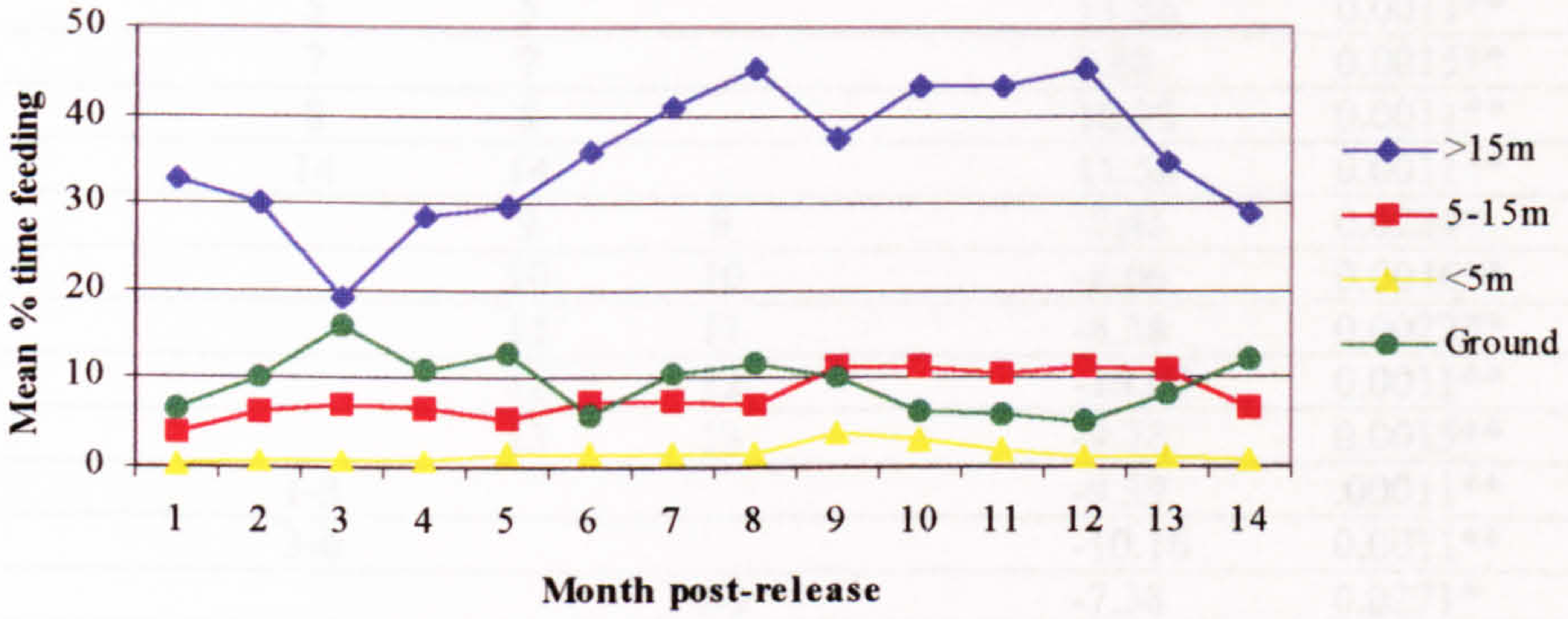
***p<0.001

Post-hoc tests revealed the following for each activity:

Feeding

In all 14 months post-release significantly more feeding activity was observed at heights above 15m in comparison to all other heights (Figure 7.18). The mean time spent feeding on the ground, at heights less than five metres and between 5-15m remained relatively uniform across the 14 month post-release period. Only a small number of statistically significant differences were found (Table 7.20). Significantly more mean time was spent feeding on the ground in month three in comparison to month one and six which can be clearly seen in Figure 7.18.

Figure 7.18 Monthly mean percentage time spent feeding on the ground, at heights less than 5m, 5-15m and above 15m



At heights above 15m a pattern was evident. Significantly more mean time was spent feeding in months 7-12 in comparison to months 2-4 indicating an increase in feeding activity at this height. No significant differences were found between months 8-12 indicating a feeding activity plateau at heights above 15m. Furthermore, months 1-2 were not found to significantly differ in the mean time spent feeding in comparison to months 13-14. However, significantly less feeding activity occurred in months 13-14 in comparison to months 10-12, indicating that the level of feeding activity at this height was subsequently decreasing to approximately the same level as found in months1-2.

Table 7.20 Results of post-hoc tests performed on month post-release, feeding activity and height (ground, <5m, 5-15m, >15m)

	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Month post - release	1			1	-26.11	0.0011**	18.98	33.24
		2		2	-29.31	0.0011**	22.17	36.43
			3	3	-12.11	0.0011**	4.98	19.24
	4			4	-17.53	0.0011**	10.40	24.66
		5		5	-28.41	0.0011**	21.28	35.55
			6	6	-28.60	0.0011**	21.46	35.73
	7			7	-30.70	0.0011**	23.57	37.84
		8		8	-44.06	0.0011**	36.92	51.19
			9	9	-26.09	0.0011**	18.96	33.22
	10			10	-37.27	0.0011**	30.14	44.41
		11		11	-41.19	0.0011**	34.05	48.32
			12	12	-34.06	0.0011**	26.93	41.19
	13			13	-26.63	0.0011**	18.35	34.92
		14		14	-28.51	0.0011**	20.99	36.04
	2	2			9.19	0.0012**	-16.32	-2.06
	3	3			15.37	0.0011**	-22.88	-7.86
	4	4			10.23	0.0011**	-17.37	-3.10
	5	5			11.56	0.0011**	-18.69	-4.24
	7	7			8.68	0.0015**	-15.81	-1.55
	8	8			10.22	0.0011**	-17.35	-3.09
	14	14			11.58	0.0011**	-19.11	-4.06
		9	9		-7.45	0.0224*	0.32	14.58
		10	10		-8.06	0.0046**	0.93	15.19
		11	11		-8.38	0.0022**	1.25	15.51
		12	12		-10.09	0.0011**	2.96	17.22
		13	13		-9.78	0.0015**	1.78	17.79
	1-3				-9.39	.00011**	2.26	16.52
	3-6				-10.16	0.0011**	-17.29	-3.03
			1-9		-7.38	0.0271*	0.25	14.51
			1-10		-7.24	0.0384*	0.11	14.37
			1-12		-7.24	0.0390*	0.10	14.37
				2-7	-10.93	0.0011**	3.80	18.06
				3-8	-26.13	0.0011**	18.99	33.26
				4-9	-9.01	0.0012**	1.88	16.14
				2-10	-13.23	0.0011**	6.10	20.36
				3-11	-23.96	0.0011**	16.83	31.10
				4-12	-9.01	0.0012**	9.71	23.97
				8-10	2.03	1.0000	-9.17	5.10
				9-11	-5.85	1.0000	-1.28	12.99
				10-12	-1.85	1.0000	-5.28	8.98
				1-13	-2.02	1.0000	-5.11	9.16
				2-13	-4.74	0.9875	-2.39	11.87
				1-14	3.85	1.0000	-10.98	3.28
				2-14	1.13	1.0000	-8.26	6.00
				10-13	8.49	0.0019**	-15.62	-1.36
				11-14	14.23	0.0011**	-21.37	-7.10
				12-14	16.21	0.0011**	-23.34	-9.08

*p<0.05, **p<0.01

Moving

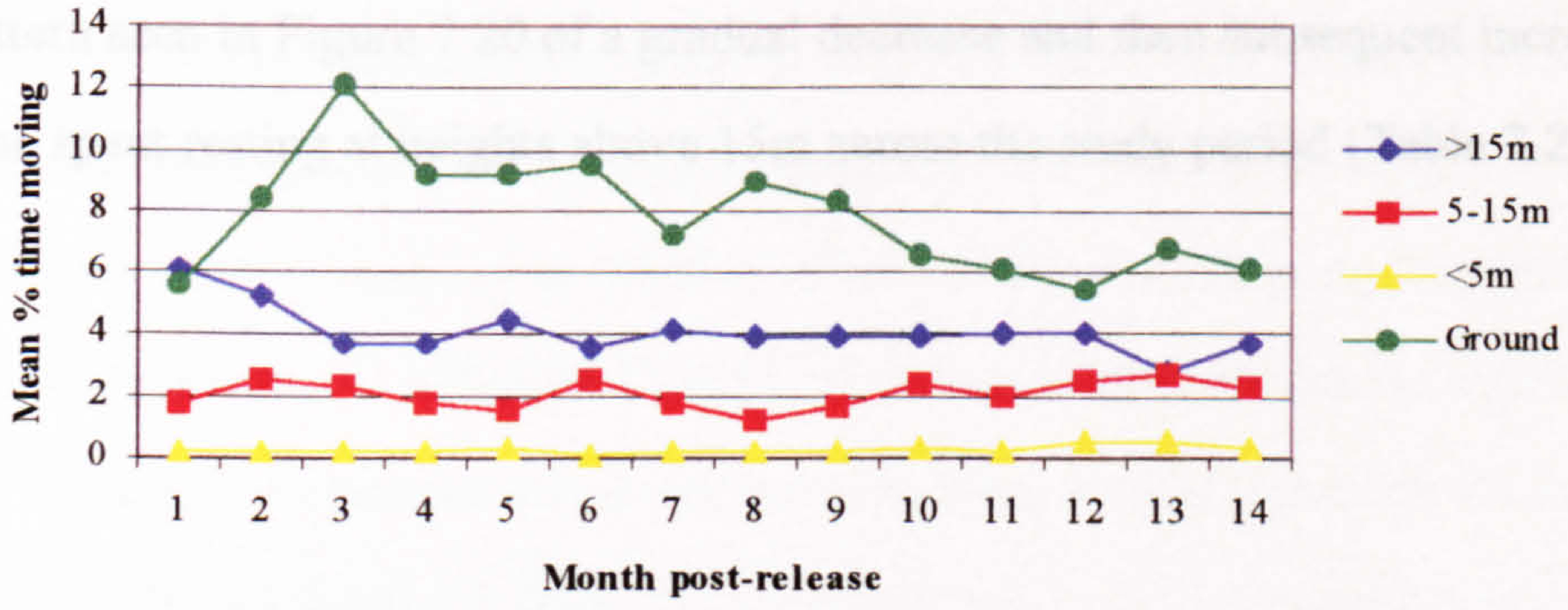
Statistical analyses comparing the amount of mean time spent moving at the four heights within each month did not produce many significant results, but the pattern revealed that overall more time was spent moving on the ground in all except one month (Table 7.21). Only in month three where a peak of moving at ground level can clearly be seen (Figure 7.19) was this found to be significantly greater than the mean time spent moving at heights above 15m.

Table 7.21 Results of post-hoc tests performed on month post-release, activity of move and height (ground, <5m, 5-15m, >15m)

	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Month post - release	3	3			11.87	0.0011**	-19.01	-4.74
	3		3		9.96	0.0011**	-17.00	-2.72
	3			3	8.37	0.0023**	-15.51	-1.24
	4	4			9.05	0.0186*	-17.64	-0.47
	4		4		7.40	0.0256*	-14.53	-0.27
	5	5			9.12	0.0016**	-16.63	-1.61
	5		5		7.60	0.0153*	-14.73	-0.47
	6	6			9.21	0.0103*	-17.69	-0.73
	8	8			8.94	0.0185*	-17.42	-0.47
	8		8		7.72	0.0109*	-14.86	-0.59

*p<0.05, **p<0.01

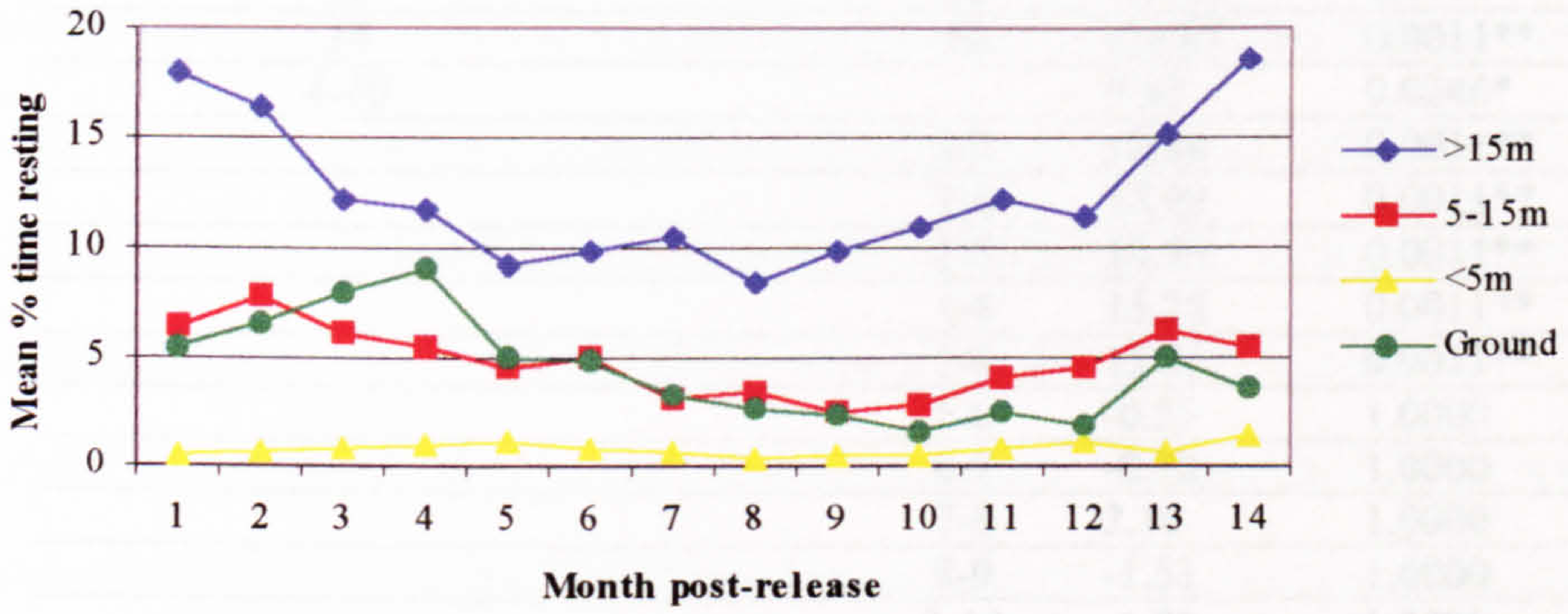
Figure 7.19 Monthly mean percentage time spent moving on the ground, at heights less than 5m, 5-15m and above 15m



Resting

Significantly more mean time was spent resting at heights above 15m in comparison to ground level in nine out of the 14 months. The remaining months showed the same pattern (Figure 7.20) but not to statistical significance. No significant differences were found between all other height comparisons within any month.

Figure 7.20 Monthly mean percentage time spent resting on the ground, at heights less than 5m, 5-15m and above 15m



Analyses comparing the mean percentage time spent resting at each height across the 14 month study period produced no significant differences between months at heights less than five metres and 5-15m. Furthermore only one significant result was found at ground level; significantly more mean time was spent resting on the ground in month four in comparison to month 10 and this can be clearly seen in Figure 7.20. At heights above 15m a clear pattern emerged. Significant and non-significant differences support the clear pattern seen in Figure 7.20 of a gradual decrease and then subsequent increase in mean time spent resting at heights above 15m across the study period (Table 7.22).

Table 7.22 Results of post-hoc tests performed on month post-release, resting activity and height (ground, <5m, 5-15m, >15m)

	Height				Mean difference	Significance	95% confidence interval for difference	
							Lower bound	Upper bound
	Ground	<5m	5-15m	>15m				
Month	1			1	-12.45	0.0011**	5.32	19.59
post -	2			2	-9.81	0.0011**	2.68	16.94
Release	7			7	-7.15	0.0481*	0.02	14.28
	9			9	-7.52	0.0186*	0.39	14.66
	10			10	-9.14	0.0011**	2.28	16.55
	11			11	-9.63	0.0011**	2.50	16.76
	12			12	-9.85	0.0013**	1.89	17.81
	13			13	-11.08	0.0011**	2.78	19.37
	14			14	-16.87	0.0011**	8.91	24.83
	4-10				7.42	0.0246*	-14.55	-0.28
				1-5	12.86	0.0011**	-15.80	-1.54
				1-6	13.00	0.0011**	-15.25	-0.99
				1-7	14.55	0.0011**	-14.53	-0.27
				1-8	15.28	0.0011**	-16.64	-2.37
				1-9	15.50	0.0011**	-15.11	-0.85
				5-6	-0.55	1.0000	-6.59	7.68
				6-7	-0.72	1.0000	-6.41	7.85
				7-8	2.10	1.0000	-9.24	5.03
				8-9	-1.53	1.0000	-5.60	8.66
				9-10	-1.09	1.0000	-6.04	8.22
				5-14	-9.38	0.0011**	2.25	16.51
				6-14	-8.83	0.0013**	1.70	15.96
				7-14	-8.76	0.0012**	0.98	15.24
				8-14	-10.22	0.0011**	3.08	17.35
				9-14	-8.69	0.0015**	1.55	15.82
				10-14	-7.60	0.0152*	0.47	14.73
				12-14	-7.26	0.0368*	0.13	14.39

*p<0.05, **p<0.01

7.5 Discussion

7.5.1 Overview

The reintroduced chimpanzees spent over 70% of their time in activities above the ground and over three quarters of this was at heights above 15m, illustrating that not only were the chimpanzees well adapted to function in arboreal zones, but complied with behaviour seen in wild populations. Although Teleki (1977) found chimpanzees at Gombe to be predominately terrestrial, this is not found in other studies (although they are few in number and not detailed). However, as mentioned in the introduction this is likely to be influenced by the nature of the terrain and Gombe is a relatively dry grassland-woodland forest. In comparison, the Triangle release zone is characterised by three main forest types, two of which are either temporarily or permanently water logged (periodically inundated and swamp forest).

Analyses revealed that significantly more feeding and resting took place at heights above 15m in comparison to all other heights. These significant differences occurred in every month post-release for feeding and for two thirds of the months for rest with the remainder showing the same pattern but not to statistical significance. Furthermore, significantly more time was spent moving on the ground in comparison to all other heights. These results support those of Teleki (1977) who found that feeding was primarily arboreal and travel primarily terrestrial in wild chimpanzees. A study of reintroduced chimpanzees in Gabon also found that foraging occurred primarily in mid-canopy rather than on the ground (Hladik, 1977). However, in contrast Teleki (1977) found rest to be primarily terrestrial (66%) whereas in the present study significantly more time was spent resting above the ground and specifically at heights above 15m. As mentioned earlier the Gombe site is a relatively drier habitat in comparison to the release zone and which may help to explain this discrepancy. A further consideration is the high proportion of time spent interacting by the Gombe chimpanzees in this particular study, a behaviour found to be primarily terrestrial (84%) (Teleki, 1977). A significant negative correlation between rest and interact Teleki (1977) suggested, was indicative that some of the time devoted to rest was a function of time (and perhaps energy) expended on interaction. Therefore, the highly social nature of the Gombe group may have resulted in the activity of rest being a primarily terrestrial activity in comparison to the reintroduced chimpanzees that exhibited low levels of sociality and a pattern of arboreal resting.

7.5.2 Sex, pre-release island, and age differences

Sex

Both females and males spent more time feeding above the ground in comparison to on the ground but specifically females spent significantly more time feeding at heights above 15m in comparison to males, and males spent more time feeding on the ground in comparison to females. No comparable data exist on differential height use by female and male wild chimpanzees. However, that both sexes spent more time feeding above the ground may simply reflect the extent of food species available in arboreal zones in comparison to herbaceous ground vegetation. The finding that females spent more time feeding at heights above 15m and males spent more time feeding on the ground may be a reflection of differential nutritional requirements. Very little is known about primate nutrition but the selection of natural food substances can be related to their content in primary nutrients (soluble carbohydrates, lipids and protein) (Hladik, 1978). However, there is some evidence (see Chapter 6, p.168) to suggest that differential energy requirements and costs exist between females and males, for example, females have to be able to achieve a minimum body condition in order to be able to ovulate. A sudden reduction of cycling females was found following a sharp decline in food supply for free-living baboons (Hall, 1963) and macaques (Loy, 1970). Furthermore, Gautier-Hion (1977) found a significant shift in the diet of female guenons to foods with a high protein content (young leaves, insects) during the part of the year when females were pregnant or lactating. Although males do not have to bear these costs, they do have to compete with each other for access to females and patrol boundaries and this inevitably requires a heavy expenditure of energy. However, none of this can be substantiated without detailed nutritional analysis of consumed feeding species, and caution should be taken in interpreting these results as the small number of males in contrast to females may not be representational.

The physical size of a chimpanzee (i.e., an adult male in comparison to an adult female) may influence who can access the higher flimsier branches in a feeding tree. In the present study the age of the chimpanzees all fell within the categories of childhood or early adolescence as defined by Goodall (1986), and were perhaps not of sufficient size to have a great influence on access to particular feeding branches.

Pre-release island

As expected, due the greater proportion of overall mean time spent feeding above ground, chimpanzees released from either island spent significantly more mean time feeding above the ground, and specifically heights above 15m. Furthermore, chimpanzees released from Yombe Island were found to spend significantly more time feeding at heights above 15m in comparison to chimpanzees from Yvette Island. Although no surveys have been conducted on either island, Yombe Island is almost twice the size as Yvette Island and from a number of tours made around the periphery seem to contain not only more trees and dense vegetation, but taller trees (personal observation). Possible explanations as to why chimpanzees released from Yombe Island fed significantly more at heights above 15m may be a consequence of familiarity with particular feeding species available on the island or more experience of climbing and feeding in taller trees. Furthermore, as Chapter 6 (p.146) revealed that chimpanzees released from Yombe Island were significantly older upon release, increasing age may be related to increasing levels of confidence. However, this prior exposure to potentially more feeding species and taller trees seems to have conferred no advantage to chimpanzees released from Yombe Island as at the time of writing the physical condition of the chimpanzees released from both islands are good.

Chimpanzees from both islands spent more mean time moving on the ground in comparison to all other heights (some significantly) and spent significantly more time resting at heights above 15m than on the ground and at heights 5-15m. These results indicate that both islands (the pre-release training environment) facilitated the development of locomotor activities at appropriate heights.

Age

As mentioned in the methods section, analyses also compared the amount of mean time spent in each activity on and above the ground but only analyses comparing the four height categories are presented. As a consequence chimpanzees from Release 4 were excluded from analyses; these chimpanzees all originated from Yombe Island and as mentioned earlier were older at release than chimpanzees from Yvette Island. It was not surprising then that the detailed analyses did not find any significant correlation between age and height of activity. However, comparison of activity at ground and above ground heights extended the age range of reintroduced chimpanzee (i.e., was able to include chimpanzees from Release 4) and found that chimpanzees spent significantly more time moving on the ground with increasing age. Although the age range is not great in the present study animals, this may simply reflect the ease of moving on the ground as body weight and size increases with age.

7.5 3 Environmental variables

Season

At feeding heights above 15m, significantly more time was spent feeding in the dry season. This is a surprising result as one may expect that in the dry season, a period characterised by relatively scarce resources, for more feeding activity to occur on the ground as a consequence of having to eat more herbaceous ground vegetation. However, Chapter 6 found that overall, more time was spent feeding in the dry season, implying that either more time was being spent eating lower quality food items in the dry season and/or that different plant species were being consumed. This together with the finding that more feeding was occurring specifically at heights above 15m in the dry season lends this argument support. However, a non-significant trend was also shown in the same direction for feeding at ground level and the means reflected the same for heights <5m and 5-15m. Consequently this result may be an artefact of more time overall being spent in feeding activity in the dry season.

Within each season significantly more mean time was spent moving on the ground which implies that regardless of water level, this activity remained largely terrestrial and that moving at ground level even within wet environments was not problematic. It was also found that significantly more time was spent resting at heights 5-15m and above 15m in the rainy season. As with feeding this may be an artefact of the overall higher proportion of time spent resting in the rainy season as the means for ground level and <5m show the same pattern. However, chimpanzees have been found to build their nests higher and with reduced canopy cover in the rainy season with the suggestion being that the height and openness reduces discomfort from dripping vegetation (Baldwin, Sabater Pi, McGrew and Tutin, 1981). A similar explanation may explain this finding.

Forest

Chimpanzees spent more time feeding above ground and specifically at heights above 15m in all forest types. However, more time was spent feeding in swamp forests at height 5-15m in comparison to primary and inundated forest (latter non-significant trend only), and more time was spent feeding at heights above 15m in primary and inundated forest in comparison to swamp forest. This is likely to be factor of available feeding species and their height; see Chapter 9 (p.304) for a comparison of tree height in each forest type.

Regardless of forest type, significantly more mean time was spent moving on the ground. This together with the earlier result that regardless of season, more time was spent moving on the ground, suggests that the hydrophobia that normally characterises chimpanzees is not readily apparent in the reintroduced chimpanzees due to their prior experience on their water bound islands (Plate 7.2). As mentioned in Chapter 3 and 4, at feeding time the chimpanzees on Yombe Island readily wade into the water to collect their tins of Cerelac. However, chimpanzees on Yvette Island, although habituated to the water surrounding the island have not been fed in the same manner. Possibly as a consequence of this, some differences have been observed post-release in how the chimpanzees behave in and around water. Chimpanzees released from Yombe Island have been frequently observed to cross swamps and small rivers by wading through them. In contrast, chimpanzees released from Yvette Island, in preference will search for a place to cross (i.e. by overhanging branches) in an attempt to avoid getting wet (J. Paredes, former HELP manager, personal communication, 2001). This behaviour may therefore facilitate access to some areas that wild chimpanzees and chimpanzees from Yvette Island may not utilise, but to date does not seem confer any long-term benefits to survival.

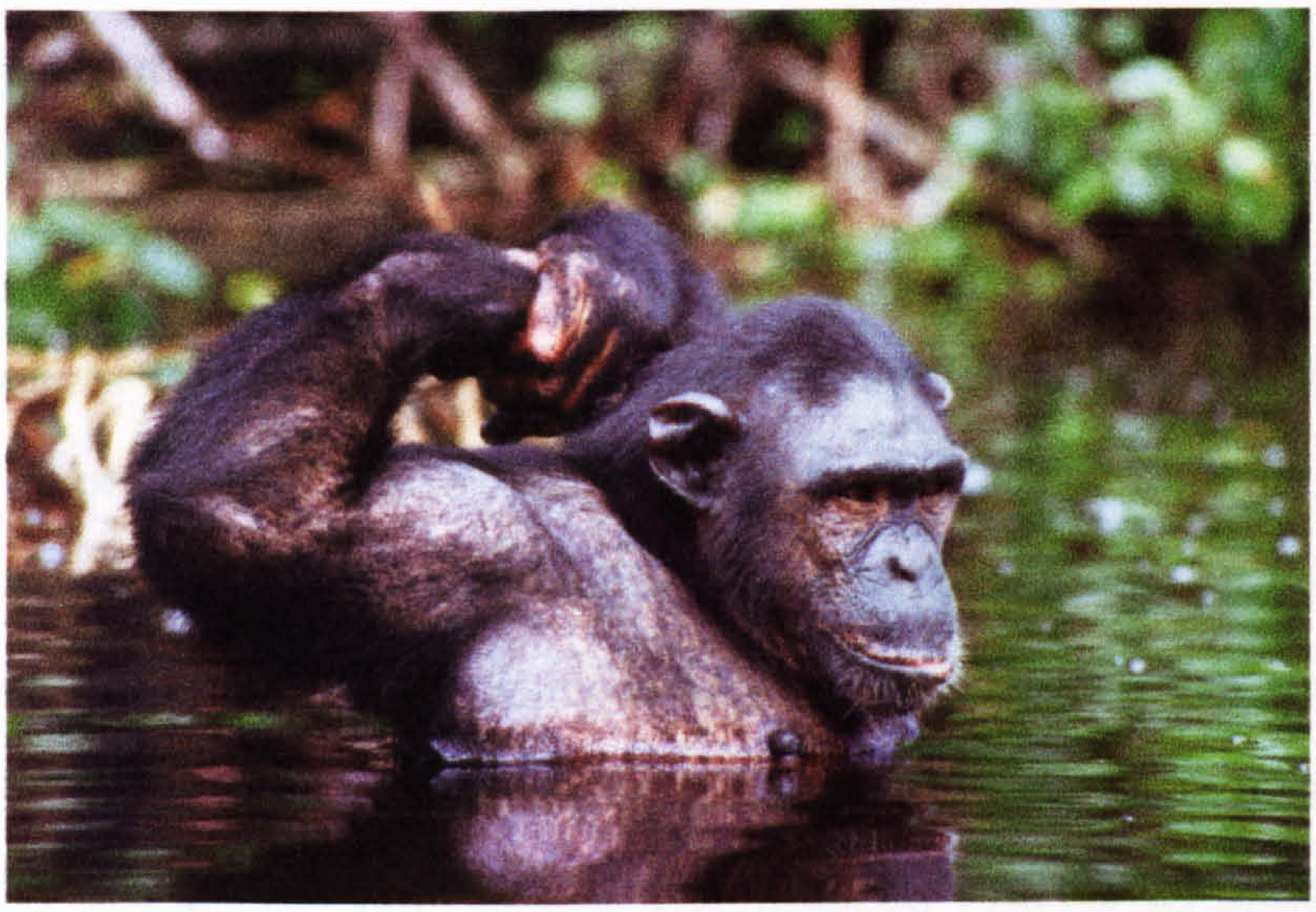


Plate 7.2 Emmanuelle wading in the water surrounding Yombe Island

7.5.4 Monthly variation

The monthly pattern of feeding and resting at heights above 15m reflect those seen previously in monthly comparisons regardless of height. Due to the high proportion of time that was spent feeding and resting not only above the ground, but also specifically at heights above 15m, this is not surprising. The pattern reflected appears to be one of seasonal variance; more time is spent feeding and less time spent resting in the dry season.

7.6 Conclusions

- The reintroduced chimpanzees spent more time feeding and resting in arboreal zones but moved more on the ground reflecting patterns seen in some studies on wild chimpanzees but differences may reflect adaptation to particular habitat types.
- Both males and females spent more time feeding in arboreal zones but females spent more time feeding at heights above 15m whilst males spent more time feeding on the ground. This may be a consequence of different nutritional requirements.
- Regardless of pre-release island the chimpanzees spent more time feeding and resting in arboreal zones but more time moving terrestrially. However, chimpanzees from

Yombe Island spent significantly more time feeding at heights above 15m. This may be explained by differing experiences on the islands but these differences seem to have conferred no advantage in terms of survival.

- More time was spent moving on the ground with increasing age. This may be explained by increasing size and body weight and consequent ease of movement in terrestrial zones.
- At heights above 15m more time was spent feeding in the dry season and this is probably related to feeding strategies (see Chapter 8). More time spent resting in higher arboreal zones in the rainy season may reflect pursuit of drier zones.
- Feeding heights in different forest zones probably reflects available plant species.
- Changes seen in the heights of feeding and resting activity over the course of the 14-month study corresponded approximately with the dry season. Furthermore, that no other distinctive pattern of vertical strata use was seen over the post-release period confirms that the chimpanzees were able to immediately adapt.
- Teleki (1977) has presented the only detailed data set on the extent of arboreal and terrestrial behaviour in wild chimpanzees. However, he did not specify or categorise the height at which the arboreal behaviour was being performed. Therefore the present data set is unique and hopefully will encourage other researchers to describe the vertical dimensions of chimpanzee activity to facilitate further comparison.
- Overall, analyses of height use indicate that the chimpanzees were able to adapt to utilising both arboreal zones and terrestrial zones in response to a variety of environmental conditions. This will be addressed further in the following chapter that investigates the diet and feeding behaviour of the reintroduced chimpanzees.

Chapter 8

Diet and feeding behaviour

8.1 Introduction

Chapter 6 provided data to show that the activity budgets of the reintroduced chimpanzees resembled those of their wild conspecifics; the chimpanzees spent most of their feeding. The crucial importance of feeding for primates to maintain themselves and reproduce has already been discussed; all primates need to acquire energy, amino acids, minerals, vitamins, water and certain fatty acids to survive (Oates, 1987). Habitat defines the potential diet of each species and as mentioned in Chapter 6, food availability can change seasonally and annually producing wide variation in primate diets (Harding, 1981). However, despite this eclecticism, three broad categories have been recognised; faunivores, frugivores and folivores (Chivers and Hladik, 1980) that emphasise the distribution of different food categories (e.g., fruit, leaves, insects etc.,) in primate diet.

Plant parts consumed

Chimpanzees have been described as frugivores; all studies of wild populations to date have found that fruit dominates the diet both qualitatively (total foods) and quantitatively (feeding time and mass ingested). Fruit consumption has been known to constitute 57-79% of total dietary intake (Wrangham, 1977; Sabater-Pi, 1979; Ghiglieri, 1984; McGrew, Baldwin and Tutin, 1988; Tutin et al.,1991; Wrangham, Chapman, Clark-Arcadi and Isabirye-Basuta, 1996; Tutin, Ham, White and Harrison, 1997; Newton-Fisher, 1999). Although the major component of chimpanzee diet is fruit, significant proportions of leaves, insects, seeds, flowers and mammalian prey have also been described in their diet. Feeding on fruit pulp alone will not provide a complete diet and arguments have focused on the use of the term frugivorous (Harding, 1981; Teleki, 1981). Fruits are typically rich in simple sugars but deficient in protein and fats and all frugivorous primates must supplement their diet with insects or leaves or both (Hladik, 1973). Overall, the diet of chimpanzees includes the following broad categories; leaves, shoots, stem pith (Plate 8.1) buds, blossoms, fruits, berries, grains, seeds, husks, pods, nuts, reeds, grasses, vine stems, barks, resins, lichens, galls, larvae, ants, termites, caterpillars, cocoons, birds and birds eggs, honey, various mammals, minerals and water (Goodall, 1986; Sugiyama and Koman, 1987; Moutsambоté, Yumoto, Mitani, Nishihara, Suzuki and Kuroda, 1994; Tutin, White, Williamson, Fernandez and McPherson, 1994; Yumoto, Yamagiwa, Mwanza and Maruhashi, 1994). An itemised list would include hundreds of floral and faunal species exploited by wild chimpanzees.

Plate 6.1 Agathe eating stem pith from the herbaceous plant *Marantaceae* spp.

Plant species

Food lists are not the best indicators of chimpanzee dietary patterns of feeding habits but they can be useful in formulating a rough index of diet diversity, which can then be used to compare results obtained from other species and populations (Teleki, 1981). The number of identified plant species from which chimpanzees feed ranges from 43 to 203 and differences in plant species consumed exists between sites (Wrangham, 1977; Sabater-Pi, 1979; Nishida and Uehara, 1983; Ghilgieri, 1984; McGrew et al., 1988;

Tutin et al. 1991; Tutin and Fernandez, 1993; Moutsambotè et al. 1994; Tutin et al. 1994; Yumoto et al. 1994; Newton-Fisher, 1999). Whilst the diet of chimpanzees is quite diverse, they normally rely heavily upon a small number of feeding species (Wrangham et al. 1996; Tutin and Fernandez, 1993; Newton-Fisher, 1999; Fawcett, 2000). This selection may reflect density and distribution of some plant species and hence value. In the light of recent evidence of differences in material and behavioural cultures between different sub-species and different study populations of the same sub-species (Whiten, Goodall, McGrew, Nishida, Reynolds, Sugiyama, Tutin, Wrangham and Boesch, 1999) it is interesting to compare diversity of diet.

Animal food

a. Invertebrate prey

All populations of chimpanzee studied to date consume a variety of insects; termites, ants, bees, caterpillar, wasps, beetle grubs, crickets, larvae and insect eggs (Goodall, 1986; Tuttle, 1986, Uehera, 1982). Insects supply protein especially amino acids and some vitamins lacking in plant foods (Hladik, 1977; Redford, 1987). Fishing for termites *Macrotermes* sp. (Goodall, 1970, 1986) and driver ants *Dorylus nigricans* (McGrew, 1974) has been described in some detail although not all insects are obtained by tool use; chimpanzees also lick insects directly off environmental substrates and their bodies (Goodall, 1963). At Lopé, chimpanzees pluck the weaver ant (*Oecophylla longinoda*) nest from the tree, crush it to kill as many of the ants as possible and then lick the ants and larvae off before discarding the nest (Tutin and Fernandez, 1992).

Although social insects form a significant component of chimpanzee diet (Goodall, 1986; Uehara, 1982) patterns of insect eating reported from different populations vary both in species and in feeding techniques, and studies have focused on the methods used to obtain insects rather than the prey themselves (McGrew 1974, 1983a, 1992; Nishida, 1973; Nishida and Hiraiwa, 1982; Uehara, 1982; Sugiyama, Koman and Bhoye Sow, 1988; Yamagiwa, Yumoto, Ndunda and Maruhashi, 1988; Whiten et al., 1999).

Variation in tool use and other behaviours suggest that there is significant cultural variation in behavioural repertoires between field studies (Goodall, 1986; Nishida, 1990; McGrew, 1992; Wrangham, 1994). Existence, prevalence and technique of nut cracking have also been found to vary between sites (Sugiyama and Koman, 1979; Goodall, 1986; Nishida, 1990; Matsuzawa, 1994; McGrew, Ham, Goodall and Uehera, 1997). Humle and Matsuzawa (2001) recently compared four neighbouring chimpanzee field sites and found variations in species cracked, tool choice and technique applied. For a recent review comparing presence and absence of behaviour patterns across chimpanzee study sites, refer to Whiten et al. (1999). Recent research indicates that there is a strong influence of prey (*Dorylus* sp.) characteristics, for example their aggressiveness and gregariousness upon tool length and technique employed which may reshape some of the culture literature to include environmental influences (Humle and Matuszawa, submitted).

b. Vertebrate prey

Wild chimpanzees have been seen to consume at least 32 species of mammal (Wrangham and Bergmann Riss, 1990). Explanations as to why chimpanzees hunt range from nutritional requirements (Stanford, 1998) and increasing mating opportunities (Teleki, 1973; Stanford, 1998), to facilitating the development and maintenance of social relationships with other males (Mitani and Watts, 2001). Observed prey differs in size and weight ranging from mice, rats and small birds to primates, bushpigs and bushbuck (Goodall, 1986; Wrangham and Bergmann Riss, 1990). As with plant inventories and invertebrate prey, differences exist in the predatory behaviour of chimpanzees across sites; the frequency of predation, prey selection, hunting success and co-operation amongst chimpanzee predators (Wrangham, 1975; Nishida, Takasaki and Takahata, 1990; Kawanaka, 1982; Goodall, 1986; Boesch and Boesch, 1989; Uehera, Nishida, Hamai, Hasegawa, Hayaki, Huffman, Kawanaka, Kobayashi, Mitani, Takahata, Takasaski and Tsukahara, 1992; Stanford, Wallis, Mpongo and Goodall, 1994; Hosaka, 1995; Mitani and Watts, 1999).

Influence of sex and life history on food consumption

Differences in sex and life history may influence nutritional requirements. There is some evidence to suggest that males and females consume different quantities of plant parts (Doran, 1997) and that ripeness may be a factor (Fawcett, 2000). However, not all studies agree (Boesch and Boesch, 1981; Hunt, 1989). There does however, seem to be a female sex bias in tool use and efficiency, and suggestions why have focused on the preference of male chimpanzees for social contact in contrast to performing solitary activities (Boesch and Boesch, 1981,1984).

Data investigating sex differences in dietary preference primarily concentrate on animal foods (invertebrate and vertebrate). A female bias in insect consumption (Nishida, 1973, 1977; McGrew, 1979) and termite fishing (McGrew, 1979) has been widely observed. Hiraiwa-Hasegawa (1989) reported female bias in ant consumption in adults, adolescents, juveniles but not infants. That no differences were found for the time spent eating ants between infant males and females would reflect a time when both sexes would still primarily be dependent and close to their mother. However, following weaning, male infants tend to spend more and more time with adult males than with their mothers.

Furthermore, female state of sexual receptivity may influence insect consumption as a consequence of time constraints (Uehera, 1982; Hiraiwa-Hasegawa, 1989; McGrew, 1992). Social and (normally) terrestrial insects are an important resource of animal matter (high in protein content) for a female with dependant offspring. Females in oestrous may however, have less time for gathering ants as they range longer distances and wider areas with males seeking opportunities to mate. In contrast to the female bias in insect feeding, male chimpanzees have been found to be the predominant hunters and consumers of vertebrate prey (Goodall, 1968; Teleki, 1973; McGrew, 1979; Wrangham and Bergmann Riss, 1990; Boesch and Boesch-Achermann, 2000). Explanations for the female concentration on insects and the male concentration on mammals have focused on mammalian physiology and sexual dimorphism (McGrew, 1992). However, Goodall (1986) argues that females eat more meat than previously thought. Meat consumption does not appear evenly distributed between group members and as its occurrence varies greatly from one population to the next this implies that it is not critical for survival of chimpanzees or normal growth (Boesch and Boesch-Achermann, 2000). However, meat is not only a source of energy but also highly nutritious, and even if the daily amount obtained is minimal (i.e., an estimated 25g per day for females at Tai), it may still play a role in balancing diet (Boesch and Boesch-Achermann, 2000).

Diurnal rhythms in food selection

The charting of chimpanzee feeding activities across the hours of the day can highlight trends in food intake. Different foods and food parts tend to be eaten at different times of the day. A general pattern seen is one of fruit eaten earlier in the day than leaves (Wrangham, 1977; Teleki, 1981; Newton-Fisher, 1999). Wrangham (1977) suggests that this overall trend may be related to digestive processes. Moist, fleshy foods with a high sugar content may be consumed at the start of an active day when energy requirements are high, whilst more fibrous foods that are less easily digested are eaten mainly in the afternoon and evening, before chimpanzees retire into night nests (Teleki, 1981). Wrangham (1977) has also suggested that diurnal variation in item quality may explain some fluctuation because alkaloids and other compounds can vary during the day and this has been known to affect food selection in other mammals. Comparison of time spent feeding on insect resources and predatory episodes has also revealed a considerable diurnal overlap (a distinct morning peak) in mammal hunting and insect-collecting. As plant foods are central to chimpanzee diet, exploitation of fauna might be expected to peak at a time when energy requirements are still high but some basic level of satiation has been achieved; for example, late morning and midday periods (Teleki, 1981).

Seasonal influence

The availability and abundance of fruit for the highly frugivoral chimpanzee is likely to have a major influence on diet composition and diversity. Reduction in food availability may result in animals increasing the time spent searching for food or reducing selectively to feed on a broader range of lower quality items (Suzuki, 1969; McGrew et al. 1988; Isabirye-Basuta, 1989; Tutin et al., 1991; Wrangham, Conklin, Chapman and Hunt, 1991; Doran, 1997; Fawcett, 2000). For example, Doran (1997) found that chimpanzees at Tai increased the time they spent feeding and fed on lower quality food items such as leaves and fibrous fruits during a period of food scarcity. Figs and terrestrial herbaceous vegetation (THV) have been described as main fallback foods for chimpanzees during periods of food scarcity. The particular foods that constitute THV vary but four plant species are prominent; *Marantaceae*, *Zingiberaceae*, *Gramineae* and *Acanthaceae*. The parts eaten include stem pith, leaf-shoots, leaves and fruits (Wrangham et al., 1996). However, THV has also been found to be an important component of chimpanzee diet after arboreal fruits. The Kanyawara chimpanzee community (Uganda) were often seen to leave fruit-rich trees to eat THV in the evening and the authors argued that THV may play a nutritional role beyond being a fallback food (Wrangham et al., 1996). In some cases chimpanzees maintain a diet of some fruit by increasing consumption of, for example *Duboscia macrocarpa*, a fruit available throughout the year but only consumed when other fruit is scarce (Tutin et al. 1991). Food choice is complex. Strong preferences for certain species exist which explains why foliage scores are not consistently related to fruit density (Isabirye-Basuta, 1989; Tutin et al. 1991; Fawcett, 2000) and may reflect nutritional balancing (Isabirye-Basuta, 1989). Seasonal variation in fruit availability has also been found to influence insect eating, hunting rate and consumption of mammalian prey (Goodall, 1968; Baldwin, 1979; Takahata et al., 1984; Boesch and Boesch, 1989; Tutin and Fernandez, 1992; Stanford et al., 1994; Stanford, 1998; Mitani and Watts, 1999; Boesch and Boesch-Achermann, 2000; Mitani and Watts, 2001).

Drinking

Data is scarce on drinking behaviour but overall chimpanzees have been observed drinking more in the dry season (Nishida, 1980; Goodall, 1986) and late afternoon (Nishida, 1980). Chimpanzees may crouch down and suck water with their lips for a few seconds at a time (Nissen, 1931; Nishida, 1980; Ghiglieri, 1984; Goodall, 1986). Water may also be drunk from hollows in tree trunks; if this cannot be reached with the lips then a 'sponge' is used. A handful of leaves are chewed briefly (crumbling them and making them more absorbent) inserted into the water, withdrawn, and the liquid is sucked from the crumbled leaves. This behaviour has been described as occurring regularly at Bossou, Tai, Gombe, Kibale and Budongo (Whiten et al.,1999). Chimpanzees also suck or lick raindrops from their own hair (Nishida, 1980; Goodall, 1986).

Coprophagy and uriposia

Coprophagy, the ingestion of faeces by apes, has been observed in their natural and captive environment. However, due to the prevalence of this behaviour in captivity, explanations have focused on boredom (Maple, 1979; Hoff, Forthman and Maple, 1994) and diet deficiency (Hill, 1966; Erwin and Deni, 1979; Akers and Schildkraut, 1985; Fritz, Nash, Martin and Matevia, 1992) as to reasons why this 'abnormal' behaviour occurs (Nash, Fritz, Alford and Brent, 1999). However, coprophagy also occurs in wild populations and may be correlated with boredom and/or the need to eat something warm (Fossey and Harcourt, 1977; Harcourt and Stewart, 1978), the need to increase fibre intake (Hladik, 1978), reflect diet deficiency, medical problems, or occurs as a result of ageing individuals unable to climb trees with wide girths or travel far (Goodall, 1986).

Urine drinking, or uriposia is uncommon in wild primates and a literature search revealed no descriptions of wild or captive apes performing this behaviour, although it seems likely that captive apes have performed uriposia. Following an appeal on Allo-primate (a global email list) an anecdotal observation on captive gorillas was revealed.

Hand reared gorillas living in impoverished conditions have been observed drinking urine and in one case one female performed uriposia 10% of the time she was observed (K. Gold, personal communication, 2001). As with coprophagy, uriposia has been described as an abnormal behaviour in captive primates (Leathers and Schedewie, 1980) and is one indicator used to assess psychological well-being of non-human primates in laboratories by National Institute Health investigators (Bayne, 1989). However, Lambert (2000) recently described a case of uriposia in wild red tail monkeys *Cercopithecus ascanius* and suggested that its performance may serve to balance nitrogen in animals that are protein deficient. Urine-drinking is also used by some veterinarians in the diagnosis of diabetes in primates, however, not all animals exhibiting this behaviour are found to be diabetic (Levanduski, Bayne and Dexter, 1992).

Diet and feeding behaviour of introduced and reintroduced chimpanzees

In the wild, infant chimpanzees learn which foods to eat primarily through observation of their mothers (Goodall, 1968). Mothers will share food with their offspring and prevent them from eating unsuitable foods (Goodall, 1968; Hiraiwa-Hasegawa, 1989). However, orphaning deprives the young animal of critical maternal input in the food learning process (Russon, 2002). The diet provided in most captive environments does not contain a wide range of natural feeding species, and individuals destined for reintroduction may need to be trained to recognise and process natural foods. Chapter 1 highlighted that training can take place in various locations but regardless of place, environmental challenges are needed to stimulate natural patterns of behaviour (Box, 1991a).

When the first golden lion tamarin reintroduction took place in 1984, it was evident that they lacked critical survival skills (Stoinski, 2000). The majority had been raised in traditional cage environments with standard husbandry routines; food was provided in fixed locations at relatively fixed times of the day, food was cut or processed and live prey, for example crickets, were often immobilised to ensure they were easy to capture (Stoinski, 2000). Upon release the tamarins displayed two types of foraging deficiencies; they showed recognition problems and adopted a strategy of waiting rather than searching for food (Kleiman et al., 1986). Consequently, later training incorporated hiding food, presenting uncut and unpeeled fruits, and a wide range of mobile invertebrate and vertebrate prey (Beck et al., 1991).

Chapter 1 highlighted that only two projects that have attempted to introduce chimpanzees onto islands resulted in nutritional independence. None of the chimpanzees placed onto Rubondo Island were provided with any kind of pre-release training and due to their aggressive nature they were not followed or provided with any post-release support apart from a small amount of initial provisioning (Grzimek, 1971; Borner, 1985). Consequently, there are no data on diet although recently direct foraging was observed on four plant species and seeds of two identified in faeces (Moscovice and Huffman, 2001). The continued survival of some of these chimpanzees indicates that some were able to successfully locate, select and process sufficient amounts of food.

The study of chimpanzees released onto Ipassa Island has provided the most comprehensive nutritional analysis of chimpanzee diet to date (Hladik 1973, 1977, 1981). Diversity of vegetation in the area was high; over 900 plant species were identified (Hladik and Halle, 1973 cited in Hladik, 1977). The chimpanzees were seen consuming parts from 141 identified plant species, 33 animal foods (insect and small mammal prey) and 5 mineral foods (a further 144 samples could not be identified). Bananas were provided at an artificial feeding site and the chimpanzees obtained approximately 30% of their annual diet from this except during the dry minor season when fruits were abundant. Hladik (1973) used estimates of food ingested to calculate the annual diet of the chimpanzees and found that the chimpanzees like wild conspecifics were primarily frugivorous and showed diurnal and seasonal patterns of feeding. On the basis of chemical analyses of nutrients and alkaloids in foods eaten by the chimpanzees, Hladik (1977) concluded that chimpanzees need to combine different food categories to obtain a balanced diet. Energy is obtained from the glucids in fruits and lipids in certain seeds and arils. However, fruits, seeds and arils are low in protein, and seeds and arils are also not available in sufficient amounts. In contrast leaves and stems are common and have high protein content. Leaves also provide calcium and animal foods are a good source of potassium (Hladik, 1977). The ability to be able to correctly select and process feeding species containing all the necessary nutrients is a challenge for chimpanzees reared in captive conditions on unnatural diets.

Hladik (1973) also described the drinking behaviour of the released chimpanzees and found that they too, drank more in the hot dry season. The chimpanzees would either drink directly from streams or from tree trunks by sucking water from their digits or make wadges of leaves (sponges) to soak up water.

Chimpanzees that were released onto islands in Liberia were initially provided with the same amount of food that they were given in the laboratory. However, soon after release, the chimpanzees began to forage and eat naturally occurring leaves and fruits (Hannah and McGrew, 1991). When more animals were released, they closely watched the others eating and tasted the same leaves and fruits (Hannah, 1989). None of the newcomers ate much on the first day of release but gradually increased their intake. However, chimpanzees placed with others released previously accepted wild foods more readily than individuals released first. When all the chimpanzees were on the islands, the amount of supplementary food provided was gradually reduced from seven to three days per week. This minimum level of artificial provision was necessary, as the islands were not large enough to meet all the nutritional requirements of the released chimpanzees. There is no published data on the number and type of plant species and parts consumed and attention was focused on their consumption of insects and nut cracking behaviour. Hannah (1989) described the behaviour of a female chimpanzee consuming weaver ants. The female first ate the ants that were moving out of the nest onto her hand, she picked them from her hand directly with her lips, then she peeled the leaves from the nest, ate the ants and larvae inside and discarded the leaf nest. Within a week, two other chimpanzees were seen using the same method to eat weaver ants. In contrast wild chimpanzees crush the nest first to stop the ants from streaming out of the nest in defence (Goodall, 1986; Tutin and Fernandez, 1992) (see p.219). Hannah and McGrew (1991) also detailed the transmission of nut cracking behaviour on the islands. On the first day of release one female exhibited nut-cracking behaviour. Nut-cracking was subsequently shown by other chimpanzees already on the island who up until that time had shown no interest in palm nuts or tool-use even though available. Another female chimpanzee on her first day of release was seen using the surface root of a tree at the feeding site as an anvil. The next day another female attempted to do the same and eventually other surface roots on the islands were used as anvils and this allowed the chimpanzees to crack nuts in many more locations.

In contrast to the release of chimpanzees onto islands, Brewer (1978) attempted to release chimpanzees into a natural environment in Senegal. All the chimpanzees had spent a period of time at Abuko Nature Reserve (The Gambia) prior to being transferred to Niokola Koba National Park and later to Mt. Asserik (Senegal). It was at the Abuko Nature Reserve that chimpanzees arriving from Europe experienced their first change of diet from temperate climate fruit or commercially produced feed pellets to wild African fruits and vegetation (Marsden, née Brewer, 1998). The chimpanzees were very conservative about their diet and hesitant to try new foods. Brewer actively demonstrated which foods to eat and how to eat them when introducing new foods to the chimpanzees. Exaggerated food grunts were made and sometimes a small amount of food was placed on the lips or into the mouth of the chimpanzee if they showed no curiosity to taste the food. Brewer found that the period to accept new foods varied but normally after a week of watching both human and other chimpanzees feeding on the food, was sufficient for the chimpanzees to finally eat the food. Recent research has indicated that chimpanzees in captivity prefer familiar foods (Remis, 2002). All the chimpanzees were taken for daily walks to locations where edible fruit was known to occur and the more experienced chimpanzees provided examples for the more inexperienced by food grunting at the sight of food and quickly climbing to feed. Five years post-release the chimpanzees diet contained over 90 different types of vegetable matter and included insect and mammal prey. The nests of weaver ants were crushed to render the aggressive ants harmless (Brewer, 1976) and as mentioned previously (see p.219) this is a technique also performed by wild chimpanzees at Lopé (Tutin and Fernandez, 1992) but not by practised by introduced chimpanzees to islands in Liberia (Hannah, 1989) (see p.228). Despite the chimpanzees becoming increasingly nutritionally self-sufficient the chimpanzees were moved onto secure islands on the River Gambia due to violent encounters between the 'rehabilitants' and wild conspecifics during periods of food scarcity (Marsden, née Brewer, 1998). Carter (1981) also moved both wild and captive-born chimpanzees onto the same islands. On all the islands the chimpanzees are nutritionally self-sufficient but they are fed every few days to facilitate contact and monitor their health and progress. There are no published data on the islands vegetation or island diet of the chimpanzees.

A young female chimpanzee named Bahati was observed for three weeks prior to contact with wild conspecifics and diet data were collected continuously whenever she ingested an item (Treves and Naughton-Treves, 1994, 1997). Initially, provisioning was performed two to three times a day then subsequently reduced to once per day. Typically food was placed out of sight to encourage foraging. Overall, Bahati sampled over 27 species of wild foods during the study period. Some plant foods that were frequently eaten by Kanyawara chimpanzees were ignored by Bahati and likewise some foods eaten by Bahati were not recorded items in the diets of wild chimpanzees. Bahati did not have to be shown which foods were edible, except in the case of two fruits that researchers deliberately led her to as they were known to be important seasonal foods for local chimpanzees. Although Bahati was able to sustain herself nutritionally post-release, she was found begging for food at a nearby village during a period of food scarcity. Unlike wild conspecifics she had no fear in approaching humans and was placed in a local zoo.

Overview

The work of Hladik (1973, 1977) revealed that food choice is complicated and affected by variation in levels of specific nutrients in foods. Studies of wild chimpanzee diet reveal the diversity of species consumed and the variation between sites and populations. Knowledge of wild chimpanzee feeding species has important implications for reintroduction. As highlighted in Chapter 4, in the present study detailed vegetative surveys were conducted on potential release sites in the Conkouati-Douli National Park. The selection of the present release site was based on surveys that qualified and quantified feeding species (their diversity and abundance) and identified keystone and fallback feeding species. Based on the assumption that the variety of foods eaten by wild chimpanzees are adequate for a minimum level of nutrition (indeed there is little or no mention of malnourished wild chimpanzees at any major study site), the comparison of diet and feeding behaviour between reintroduced and wild chimpanzees may provide another measure (see Chapters 6, 7 and 9) of their behavioural adaptability. This chapter presents the first long-term systematically collected data set on the diet and feeding behaviour of reintroduced chimpanzees.

8.2 Aims

- To describe the diet of the reintroduced chimpanzees in comparison to published data on the diet of wild chimpanzee populations and one reintroduced population
- To investigate the influence of sex, pre-release island, diurnal hour, ecology and time post-release on diet and feeding behaviour
- To describe any anecdotal feeding and drinking behaviours

8.3 Method

8.3.1 Pre-release diet

Chapter 5 highlighted that due to the presence of some aggressive chimpanzees it had not been possible to enter the islands pre-release to collect behavioural data. Likewise, no detailed vegetative surveys were conducted. However, occasionally chimpanzees were observed eating naturally occurring plant species in addition to the supplementary food provided, and these were noted. Furthermore, tours were made by boat around the periphery of Yombe and Yvette Island and known plant species were noted to provide an indication of pre-release exposure to edible feeding species. A list of plant species that the chimpanzees were observed consuming and potential feeding species are presented in table format to facilitate comparison to plant species and parts consumed by wild chimpanzees, and one other reintroduced chimpanzee group (Appendix D). Refer to section 8.3.2.2 (p.233) for the rationale behind which wild chimpanzee data were included. There are no data as to the amount of time spent consuming the different plant species and parts, only an indication that they were consumed. It is also not known which chimpanzee consumed what; consumption is identified to island only.

8.3.2 Post-release diet

8.3.2.1 Overview

As described in Chapter 5, when visible, each individual's activity post-release were recorded every 10 minutes using scan sampling with instantaneous recording. When the activity recorded was feeding, the plant species and part being consumed were noted. If the plant species could not be identified a sample was collected, numbered and preserved (either pressed or preserved in spirit) for later identification. Not all plant parts consumed could be identified to a specific plant species and where necessary the plant genera, family or life form are used for descriptive purposes. To provide an indication of the number of species consumed, those identified to genera, family or life form are counted as one species based on the assumption that a minimum number of one species was being consumed. Such a rigorous method probably under estimates the number of species being consumed. Plant parts were categorised into fruit, leaf, stem pith, flower, sap, shoots, bark and liquid. Categories were determined by the direct observation of the chimpanzees feeding and cross referenced with published data on wild populations (e.g., Tutin et al., 1994; Moutsamboté, et al., 1994; Yumoto, et al., 1994). The category of liquid has not been used in any study on wild chimpanzees (no equivalent could be found) and refers specifically to the fluid found inside *Strychnos congolana*. These data were used to determine the relative contribution of each plant species and part to the diet. Diet was therefore measured in terms of time spent feeding on each food type, plant species and part.

Throughout this chapter the terms plant species, plant part and food type are employed and defined as:

Plant species:	the taxonomic species of plant being consumed
Plant part:	the part of the plant, for example, fruit, leaf, etc., being consumed
Food type:	includes plant parts, invertebrate and vertebrate prey

The number of feeding observations collected per individual varied. Therefore as with activity budget analyses, unless otherwise stated overall means and medians are based on the mean number of observations for each chimpanzee divided by the number of months during which observations were made.

Feeding data were analysed for the first 14 months post-release except in the case of Koutou and David. Only 12 months post-release data were included for Koutou as he was missing during months 2 and 13. David disappeared during the fourth month post-release and was present in the rainy season only. Therefore, data collected from David have been included in all analyses except seasonal and dietary richness, diversity and evenness. Analyses of seasonal variation and indices of dietary richness, diversity and evenness employed calendar months and not month post-release.

8.3.2.2 Comparison to wild chimpanzee diet

Throughout this chapter the diet of the reintroduced chimpanzees is compared to wild chimpanzee diet. The three wild chimpanzee sites were selected on the basis of similar habitat type to Conkouati; all lowland tropical forest within central Africa. The data from these surveys were all published in a 1994 Tropics journal in the same format, facilitating comparison.

The three sites are:

(a) Lopé Reserve, Gabon (Tutin, White, Williamson, Fernandez and Pherson, 1994)
(b) Nouabalé-Ndoki, Republic of Congo (Moutsambotê, Yumoto, Mitani, Nishihara, Suzuki & Kuroda, 1994)
(c) Itebero region in Kahuzi-Biega, Democratic Republic of Congo (Yumoto, Yamagiwa, Mwanza & Maruhashi, 1994)

In the same paper as the Itebero region, data were also presented on a survey that was conducted in a montaine area of Kahuzi-Biega (Yumoto et al., 1994) and only nine plant species were found in both regions indicating the influence of habitat and vegetation type on diet diversity. Although long-term studies have been conducted at Gombe, the study site has a drier and more mountainous habitat (Goodall, 1965) and would not present a suitable comparison of diet.

The three studies detailing the diet of wild chimpanzees specified not only plant species eaten but also provided a full list of plant species found in the area. This offered the opportunity to compare plant species present at all the sites whether eaten or not, and to make further comparisons to what was and was not eaten and available to the reintroduced chimpanzees at Conkouati.

The diet of chimpanzees reintroduced to Ipassa Island, an area of lowland tropical forest in Gabon, was also included on the table for comparative purposes (Hladik, 1973,1977).

This study has produced the most comprehensive analyses conducted on the diet of chimpanzees living in natural habitat (see introduction). Unfortunately the study only published a list of plant species consumed and did not include species available but not consumed.

8.3.2.3 Botanical surveys conducted in the Conkouati-Douli National Park

As mentioned earlier, throughout this chapter the diet of the reintroduced chimpanzees is compared to wild chimpanzee diet. To provide an indication of feeding species available to the reintroduced chimpanzees, plant species identified within the Triangle release zone and eastern/western parts of the Conkouati-Douli National Park were cross-referenced with those species known to be consumed by wild chimpanzees at the three sites mentioned earlier. Four surveys conducted within the Conkouati-Douli National Park (Doumenge, 1992; Hecketsweiler and Ikonga, 1992; Sita, 1996; Moutsambote, 1997) were used to provide a full range of possible feeding species available to the reintroduced chimpanzees. The inclusion of surveys conducted in areas of the park outside of the Triangle release site is because the chimpanzees move in and out of the Triangle. A table was constructed to list the plant species, its life form, presence/absence and part eaten by the three wild populations and reintroduced chimpanzee group at Ipassa in comparison to the chimpanzees at Conkouati (Appendix E). Only species identified in one of the four surveys from Conkouati were included in the table.

8.3.2.4 Primary plant species consumed

To evaluate if the reintroduced chimpanzees concentrated their feeding on some plant species and parts more than others, species that were consumed for more than 0.5% or more of feeding time were examined in detail. Due to the overall large number of species consumed, the figure 0.5% was used to refine the list and produced the top 25 plant species consumed.

8.3.2.5 Hourly variation in plant part consumption

To investigate temporal variation in levels of plant part consumption across the day, proportions of time spent consuming the main parts consumed; fruit, leaf and stem pith were examined on a hourly basis. As with activity budgets, the day was divided into hourly segments. No feeding activity was observed to occur in hour one (05h00-05h55) and only two chimpanzees, Bougnoule (n=1) and Jeanette (n=2) were observed feeding in hour 15 (19h00-19h55), accounting for a mean respective 0.008% of feeding activity. Consequently only feeding data observed in hours 2-14 were included in analyses. Refer to Table 6.3 (p.134) for a description of actual time each numbered hour refers to.

8.3.2.6 Seasonal variation in diet

To examine seasonal variation in plant species and parts consumed the same rationale and allocation of calendar months to dry and rainy season were used in the present chapter as with Chapter 6 and 7.

The richness, diversity and evenness of the chimpanzee's plant diet were calculated for each consecutive month for each post-release period. These indices have been used to calculate dietary diversity in a range of primate species; from chimpanzees (Newton-Fisher, 1999) to saddleback (*Saguinus fuscicollis*) and moustached tamarins (*Saguinus mystax*) (Smith, 1997). The dietary richness was calculated using the Margalef (1958) index (R') and is based on the number of feeding species exploited and feeding records. Dietary diversity was calculated from the Shannon diversity index (H'); this is a sensitive measure of dietary diversity as it accounts for the relative proportion of each plant species in the diet. Dietary evenness (E') was calculated from dietary diversity (see Begon, Harper and Townsend, 1990) and is a measure of how equally an animal distributes its feeding time between plant species.

Richness $R' = \frac{(S-1)}{\ln n}$

Diversity $H' = -\Sigma(p_i \ln p_i)$

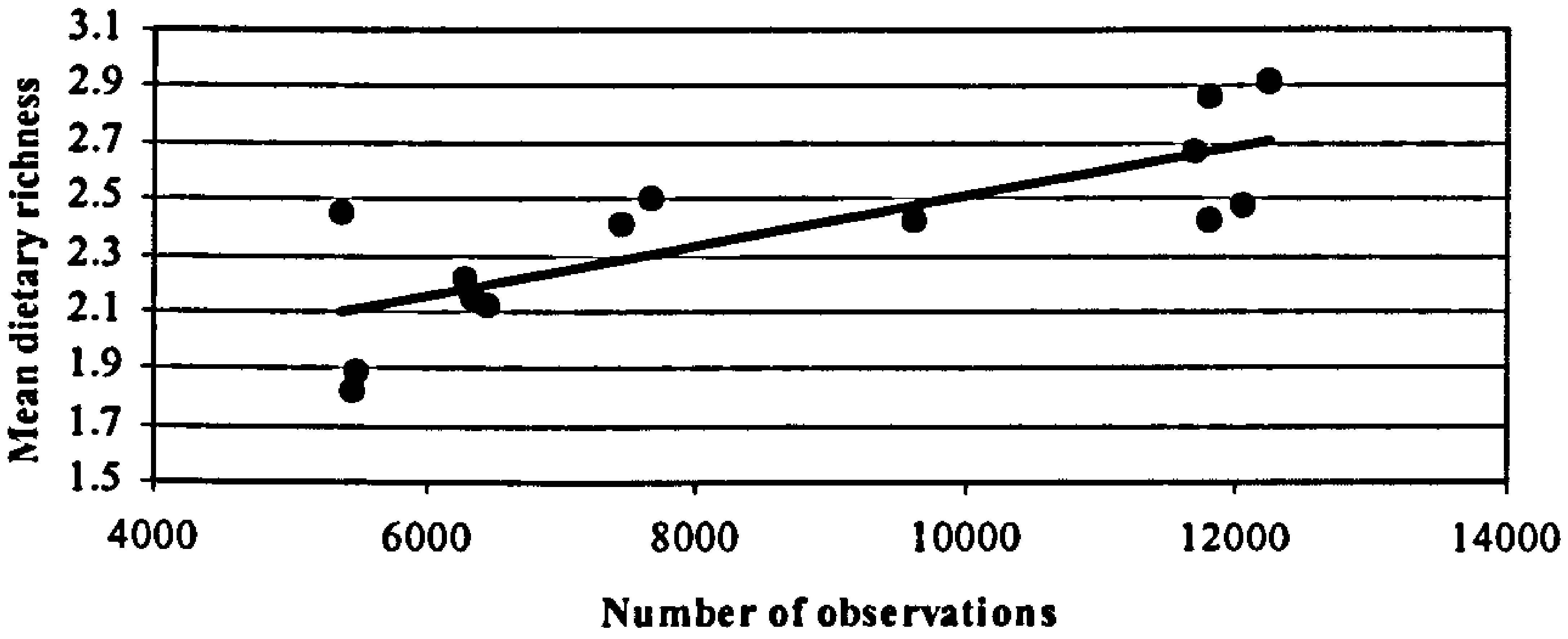
Evenness $E' = \frac{H'}{\ln S}$

Where: S = total number of food species
n = total number of feeding records
pi = proportion of feeding records for each plant species
ln = natural log

The dietary richness, diversity and evenness for each chimpanzee were calculated and plotted onto three separate graphs. To make sense ecologically the data were plotted for each calendar month for each post-release period, for example, ranging from November 1996 to March 2000. In the case of three chimpanzees data were missing for one month. For Massabi (C7 on Figures 8.7, 8.8 and 8.9) and Mossendjo (C9) very little data were available for the calendar month of January 1998 (month two post-release for both chimpanzees) due to illness (see Chapter 4, p.101). Koutou (C16) was missing in February 2000 and likewise has no data for that month. Therefore for presentation purposes so that the graph could be viewed as a continuous line, indices from each month either side of the missing month were summed and divided by two (the number of months) to provide an approximate figure. Indices for Agathe, Sophie and Koutou start from calendar month March 1999 (month two post-release). Data were collected for Agathe and Sophie from mid February 1999, not a full calendar month and consequently indices were calculated and presented from March 1999. No data were collected for Koutou in February 1999 (month one post-release) because he disappeared immediately post-release (see Chapter 4 p.100). Consequently indices for 13 calendar months are presented for Agathe and Sophie and 12 for Koutou.

Caution must be taken when interpreting the results from the indices due to the possible effect that the varying number of observations may have on the indices. However, although this should be taken into account for indices of richness (calculations of which are based on the number of plant species and feeding records) this is less of a problem with diversity that is based on proportions. Indices of dietary evenness are calculated from diversity and as therefore as with evenness (although not to the same extent urging some degree of caution in interpretation) is less effected by the number of observations. This can be clearly seen in scatterplots (Figures 8.1, 8.2 and 8.3) and results from Pearson's product moment correlation (Table 8.1) performed on the number of observations and indices of richness, diversity and evenness for each chimpanzee.

Figure 8.1 Relationship between number of observations and indices of dietary richness



***p<0.01

Figure 8.2 Relationship between number of observations and indices of dietary diversity

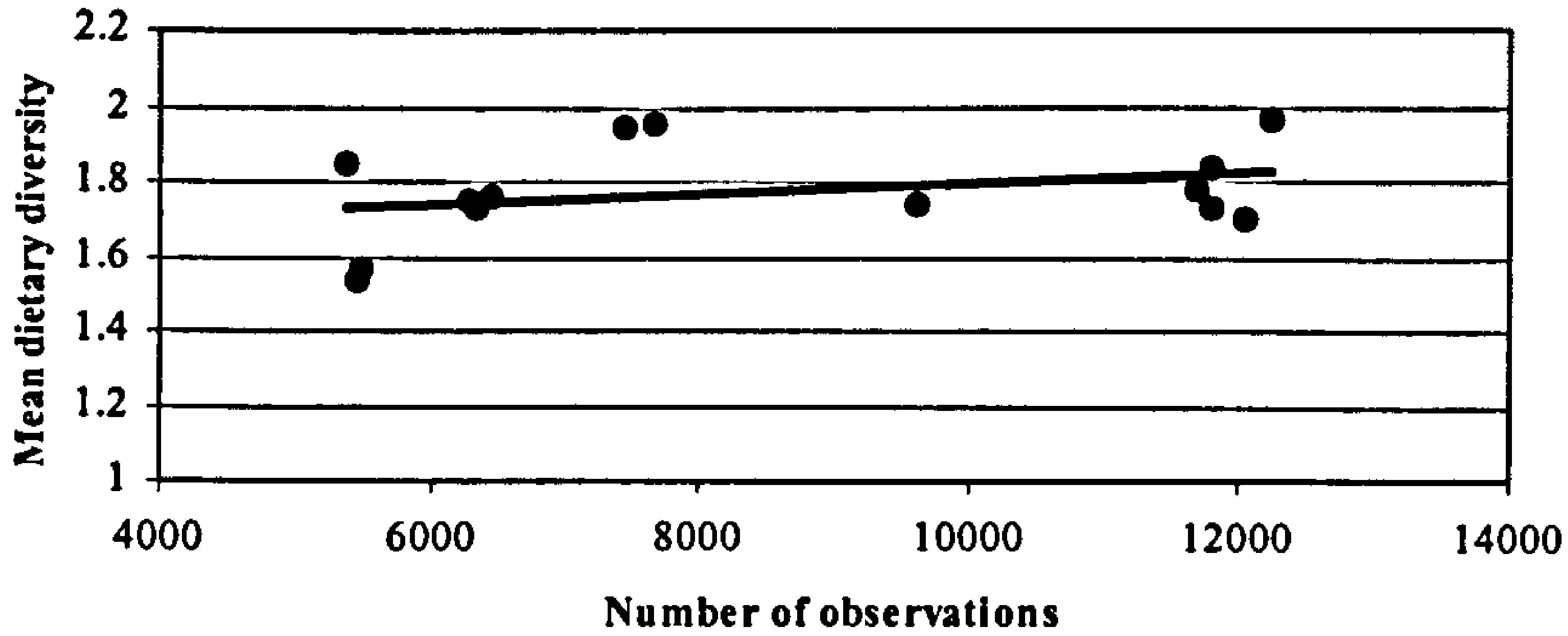


Figure 8.3 Relationship between number of observations and indices of dietary evenness

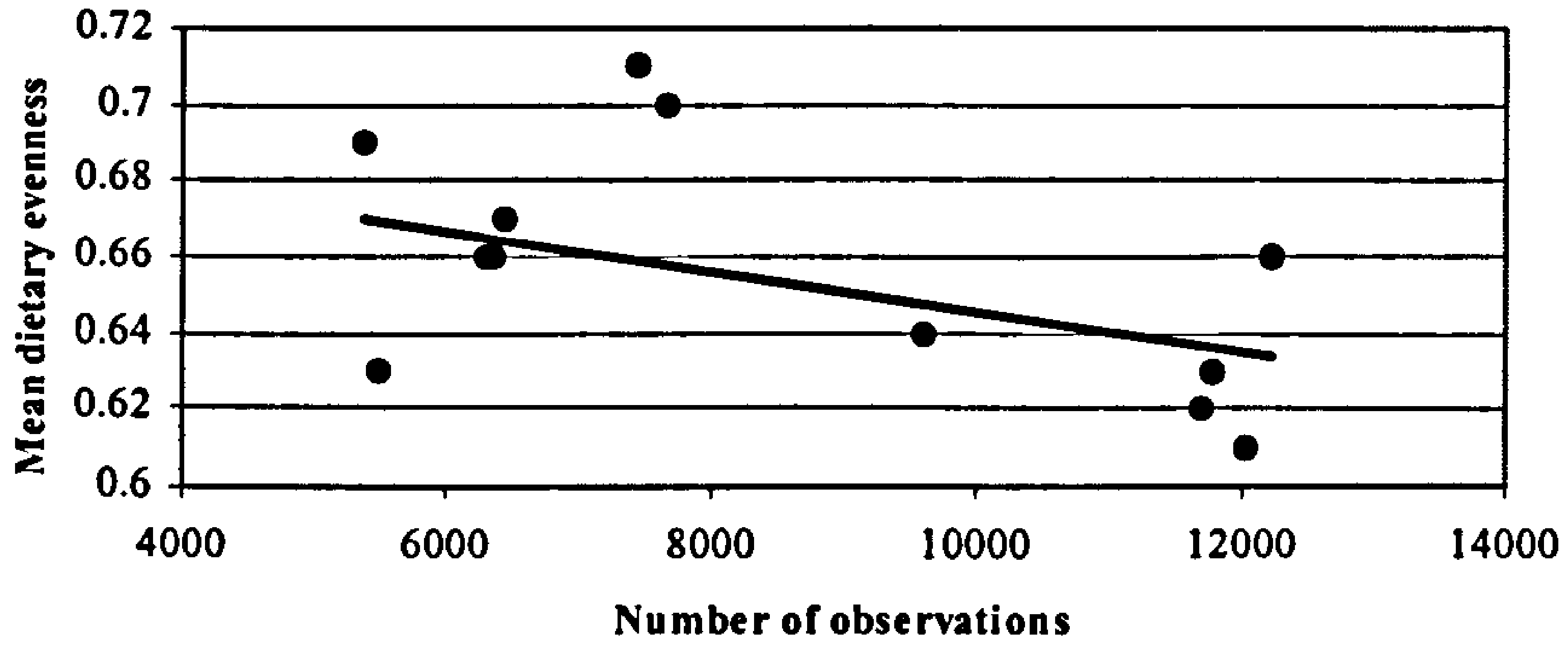


Table 8.1 Results of Pearson's product moment correlation's performed on the number of observations and indices of dietary richness, diversity and evenness

	r	n	p
Richness	0.79	14	0.001**
Diversity	0.32	14	0.295
Evenness	-0.48	14	0.086

**p<0.01

Chimpanzees were released in stages (in different months and years). The 14-month post-release study period includes very little overlap for chimpanzees released at different times except for a period of two months; December 1997 and January 1998. These months constitute the last two months of the study period for chimpanzees released at the end of November 1996 (R1) and the first two calendar months for chimpanzees released at the end of November 1997 (R3). As a comparison, the mean levels of dietary diversity and evenness were compared using an independent t-test for each month and release group. Mean levels of dietary richness were compared using a two-way ANOVA as this test provides the opportunity to weight the indices of dietary richness against the number of observations. Comparison of indices for December 1997 included five chimpanzees, but due to missing data in January 1998 only three chimpanzees were included.

As outlined in Chapter 5, analyses have included data collected during the first 14 months post-release (for the majority of chimpanzees) to provide a long-term perspective on post-release behaviour. Furthermore, a 14-month period provides the opportunity to compare the first and last two months post-release; a period comparable in calendar months to exactly one year later. Consequently to compare dietary richness, diversity and evenness at the beginning and end of the study period, the indices for months 1 and 14 were compared and months 1 and 2 with months 13 and 14. Indices for months 1 and 2 were summed and divided by the number of months (n=2); the same method was applied to months 13 and 14. The number of chimpanzees included in analyses was 11 for months 1 and 14, and 9 for months 1-2 and 13-14 for the reasons as outlined above. For Agathe, Sophie and Koutou, indices of month 2 were compared to month 14 corresponding to calendar months March 1999 and March 2000. Paired t-tests were used to compare mean levels of dietary diversity and evenness between months and a two-way ANOVA for dietary richness due to the aforementioned problem of the number of observations influencing results.

8.3.3 Statistical analyses

As with Chapter 6 and 7 all analyses have been performed on mean percentage scores unless otherwise stated. Variables were analysed using a variety of parametric; repeated measures ANOVA, Bonferroni post-hoc tests, t-tests (2-tailed), Pearson's product moment correlation and non-parametric tests; Mann Whitney *U*-test. Means (with standard deviation) and median (with inter-quartile range) were likewise employed according to normality of data. Due to the large number of post-hoc tests generated by the ANOVA analyses, only results illustrating a pattern of activity are presented.

8.4 Results

8.4.1 Pre-release diet

Pre-release chimpanzees were seen consuming 23 parts of a minimum 14 plant species (see Appendix D). Ten were identified to species level; *Alchornea cordifolia*, *Borassus aethiopum*, *Dracaena arborea*, *Elaeis guinnensis*, *Haplormosia monophylla*, *Mangifera indica*, *Odyendyea gabonensis*, *Psidium guajava*, *Terminalia superba* and *Vitex* *doniana*. Parts were also consumed of plants identified to two genus; *Cola* and *Aframomum* sp., from the life form liana and from a shrub species known locally as Palétuvier (scientific name not known).

Parts consumed of plants identified to genus only, the species *Elaeis guinnensis*, and the shrub Palétuvier were consumed by chimpanzees on all three islands. Chimpanzees on Yombe Island were also seen eating parts from a further three identified species and from the life form liana. Chimpanzees from Yvette Island were seen consuming plant parts from an additional five species, and one species on Pepere Island. The palm *Borassus aethiopum* was identified on both Yombe and Yvette Island but only chimpanzees on Yvette Island were seen consuming its fruit.

The following identified species: *Sacoglottis gabonensis*, *Symphonia globulifera*, *Tetracera podotrich* and genera: *Dialium*, *Klainedoxa*, *Pterygota* and *Salacia* were available on some islands pre-release but the chimpanzees were only seen consuming parts of these plants post-release. Parts of two plant species; *Vitex doniana* and *Elaeis guineensis*, from the genus *Aframomum* and *Cola*, and life form liana were eaten both pre- and post-release. The chimpanzees were never seen consuming *Milletia comosa* pre-release although available on all three islands. However, the fruit, leaf, and flowers of this liana were consumed post-release; (it is listed as one of the top 25 species consumed, see Table 8.8, p.250)

Plant parts of two species; *Musanga cecropiodes* and *Sacoglottis gabonensis* and five identified to genus; *Dialium*, *Costus*, *Klainedoxa*, *Marantaceae* and *Palisota*, are known to be consumed by wild chimpanzees and were consumed post-release. However, although available pre-release, there were no accounts of the chimpanzees consuming any parts of these species on any island. Chimpanzees at Ipassa also consumed plant parts from the species *Musanga cecropiodes*.

Plant parts from two species consumed on the islands; *Mangifera indica* and *Vitex doniana*, and from the genus *Cola* are consumed by wild chimpanzees at Lopé; *Vitex doniana* has also been identified at Nouabalé-Ndoki but is not known to be consumed by chimpanzees. The following plant species consumed on the islands; *Terminalia superba*, *Alchornea cordifolia*, *Dracaena arborea* and *Elaeis guinnensis* were all identified at Nouabalé-Ndoki but not consumed by wild chimpanzees. Likewise *Alchornea cordifolia and Odyendyea gabonensis* were identified at Lopé but not consumed by wild chimpanzees. Plant parts from the genus *Aframomum* were consumed by wild chimpanzees at Lopé and Nouabalé-Ndoki; these were consumed pre- and post-release and by reintroduced chimpanzees at Ipassa. In the case of *Macaranga* sp. this was available pre- and post-release but never consumed, available to wild chimpanzees at Lopé, Nouabalé-Ndoki and Kahuzi-Biega and never consumed, but eaten by chimpanzees reintroduced to the island of Ipassa.

8.4.2 Post-release diet

8.4.2.1 Plant species, life forms and parts consumed

Appendix E lists the plant species and parts consumed by the reintroduced chimpanzees at Conkouati in comparison to three studies on wild chimpanzees and one study on a reintroduced population. It includes all the data described below. The reintroduced chimpanzees consumed parts of 62 identified plant species that belong to 3 orders, 39 taxonomic families and 55 genera. Plant parts of a further 22 identified by genera only (2 orders, 17 families) brings the total number consumed to 84. Furthermore, the consumption of plant parts from 38 unidentified species (no genus/family distinction) increases the total number of species consumed to a minimum 122.

Of the 62 species identified, 45 were trees, 8 liana, 5 herb, 3 palm and 1 fern. Of those identified by genera only; 11 were trees, 4 liana, 5 herb, 1 palm, and 1 shrub. Of the non-identified species consumed, 8 were known to be liana and 1 a tree – no life form descriptions are available for the remainder. Fungi were also eaten but it is not known if this comprised of one or more species.

Table 8.2 compares the number of species (genera, taxonomic family and order), life form and number of plant parts consumed by two reintroduced and three wild chimpanzee populations. The reintroduced chimpanzees at Conkouati ate a minimum of 239 plant parts of at least 122 species, showing that many of the plants were sampled (although not regularly consumed, see Table 8.8, p.250) for more than one part. At Ipassa (Hladik, 1973,1977) and Lopé (Tutin et al., 1994) chimpanzees consumed more species from more life forms in comparison to chimpanzees at Nouabalé-Ndoki (Mousambote et al., 1994) and Kahuzi-Biega (Yumoto et al., 1994). The reintroduced chimpanzees at Conkouati consumed a smaller number of species and life forms (a minimum of 122 species that included 93 life forms) in comparison to chimpanzees at Ipassa and Lopé but greater than chimpanzees at Nouabalé-Ndoki and Kahuzi-Biega . Wild chimpanzees at Nouabalé-Ndoki and Kahuzi-Biega consumed approximately less than half the number of species in comparison to Ipassa, Lopé, and the present data set. The reintroduced chimpanzees at Conkouati consumed more plant parts in comparison to all other populations presented, approximately four times more than the wild populations at Nouabalé-Ndoki and Kahuzi-Biega.

Table 8.2 Number of plant order, family, genera, species and life form of parts consumed by reintroduced and wild chimpanzees

		Reintroduced chimpanzees		Wild chimpanzees		
Reference		**Present data**	**Hladik, 1973, 1977**	**Tutin et al., 1994**	**Moutsambo te et al., 1994**	**Yumoto et al., 1994**
Site		**Conkouati**	**Ipassa**	**Lopé**	**Nouabalé-Ndoki**	**Kahuzi-Biega**
Year (length) of study		**1996-2000 (14 mths per chimpanzee)**	**1971-1972**	**1983 - ongoing**	**1988-1992**	**1987-1991**
Diet (n)	Order	3	2	2	2	3
	Family	39	38	36	28	28
	Genera	55	90	85	49	41
	Number of species	**122**	**151**	**141**	**64**	**48**
Life form (n)	Tree	57	92	98	47	33
	Herb	10	12	14	7	5
	Liana	20	27	13	9	4
	Shrub	1	3	5	1	3
	Epiphyte	0	0	8	0	1
	Palm	4	4	2	0	1
	Fern	1	0	0	0	1
	Total	**93**	**138**	**140**	**64**	**48**
Parts eaten (n)	Fruit	101	116	116	53	39
	Leaves	62	18	21	2	4
	Seeds	19	16	16	5	1
	Stem/pith	19	6	11	4	8
	Flower	17	7	7	2	-
	Sap	16	-	-	-	-
	Shoots	4	10	-	-	-
	Bark	Yes (n=?)	1	4	-	1
	Liquid	1	-	-	-	-
	Galls	-	-	1	-	-
	Total	**239**	**174**	**176**	**66**	**53**

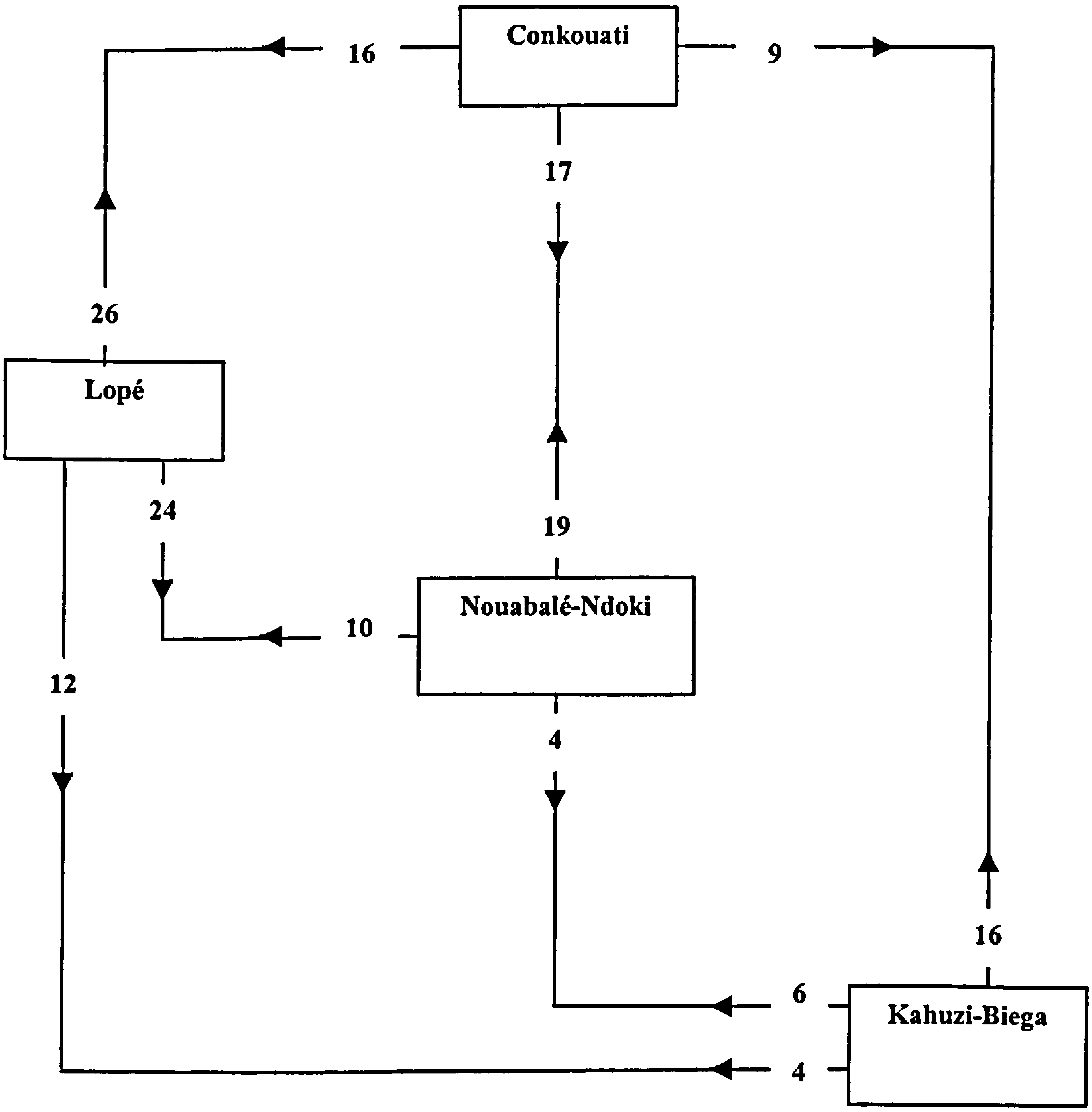
8.4.2.2 Presence and absence of plant species between sites and diet comparability

Appendix E also provides the opportunity to compare the presence and absence and plant species and parts consumed at all five sites in relation to the vegetative surveys conducted at Conkouati. Of the 312 plant species listed (274 identified by species or genera and 38 non-identified), 39% (n=122) of species were consumed at least once by the reintroduced chimpanzees. One hundred and nineteen of these species were also identified at Lopé, 116 at Nouabalé-Ndoki and 58 at Kahuzi-Biega. At Lopé wild chimpanzees are known to consume 73 of the listed species found at Conkouati, 46 at Nouabalé-Ndoki and 28 at Kahuzi-Biega.

By comparing plant species consumed across the sites we can examine similarity or dissimilarity in diet. The reintroduced chimpanzees at Conkouati consumed 27 plant species (plus 18 identified by genera only) that are also known to be eaten by wild chimpanzees at least one of the mentioned field-sites. Eight plant species were consumed by the reintroduced chimpanzees and by wild chimpanzees at two sites (plus seven identified by genera) and one (plus five identified by genera) at all three. The reintroduced chimpanzees at Conkouati and wild chimpanzees at Lopé consumed plant parts from 23 of the same species (and parts from species non-identified from a further 14 genera). In comparison, plant parts from 10 of the same species were consumed at Nouabalé-Ndoki (plus species from a further 12 genera) and four species at Kahuzi-Biega (plus species from a further 9 genera). The reintroduced chimpanzees at Ipassa and Conkouati consumed plant parts from 19 of the same species (and species non-identified from 10 genera).

The reintroduced chimpanzees at Conkouati did not always consume the same plant species as wild chimpanzees despite being available. Likewise, some plant species consumed by the reintroduced chimpanzees at Conkouati were available to wild chimpanzees but not consumed (data extracted from Appendix E and displayed in Figure 8.4). In Figure 8.4 the numbers placed closest to each box represent plant species eaten at that site yet not eaten at the linked site despite being available. For example, 16 plant species eaten by the reintroduced chimpanzees were available to chimpanzees at Lopé but not consumed. Twenty-six plant species consumed at Lopé were available at Conkouati but not consumed by the reintroduced chimpanzees (Figure 8.4). A similar pattern was found for comparisons made between the reintroduced chimpanzees and wild populations at Nouabalé-Ndoki and Kahuzi-Biega and similarly between wild populations (Figure 8.4). For example, wild chimpanzees at Lopé consumed 24 plant species that were available to, yet not consumed by chimpanzees at Nouabalé-Ndoki. Chimpanzees at Nouabalé-Ndoki consumed 10 species that were available yet not consumed by chimpanzees at Lopé.

Figure 8.4 Comparison of common plant species available that are and are not eaten by reintroduced and wild chimpanzees



Key: The numbers placed closest to each box represent plant species eaten at that site yet not eaten at the linked site despite being available.

8.4.2.3 Composition of diet

Fruit dominated the diet of the reintroduced chimpanzees followed by leaf and stem pith that together constituted a major component of the diet (Table 8.3). Leaves were primarily consumed in trees whilst stem pith were mainly consumed on the ground (Table 8.4). In all cases when stem pith was consumed above the ground, it was the pith of the palm *Elaeis guinnensis*. Sap, seed, shoots and liquid were all eaten in small amounts. One chimpanzee consumed bark from an unidentified tree. Non-plant food was consumed at some point by each chimpanzee and consisted primarily of invertebrate prey and parts (e.g., ant nest, honey). Although all chimpanzees received some supplementary food, overall this amount constituted a very small proportion of the diet.

Table 8.3 Mean percentage time (±SD) spent feeding on plant parts at Conkouati

Food part	Overall mean %	SD	Mean n observation	SD	n (chimpanzee)
Fruit	54.97	8.28	356.95	143.46	15
Leaf	19.27	4.61	129.27	55.75	15
Stem	16.87	4.69	101.13	25.40	15
Flower	2.03	2.48	10.74	10.54	15
Seed	0.85	1.07	5.09	7.63	15
Sap	0.68	0.53	5.54	6.12	15
Shoots	0.07	0.05	0.53	0.43	9
Liquid	0.07	0.02	0.20	0.02	4
Fungi	0.02	0.07	0.54	0.66	2
Bark	0.01	-	0.14	-	1
Invertebrate prey and associated parts	2.13	1.25	15.67	16.56	15
Vertebrate prey and associated parts	0.07	0.06	0.47	0.41	9
Supplementary food provided by observers	0.79	1.13	2.01	1.64	15
Not known	0.59	0.47	3.42	3.75	14

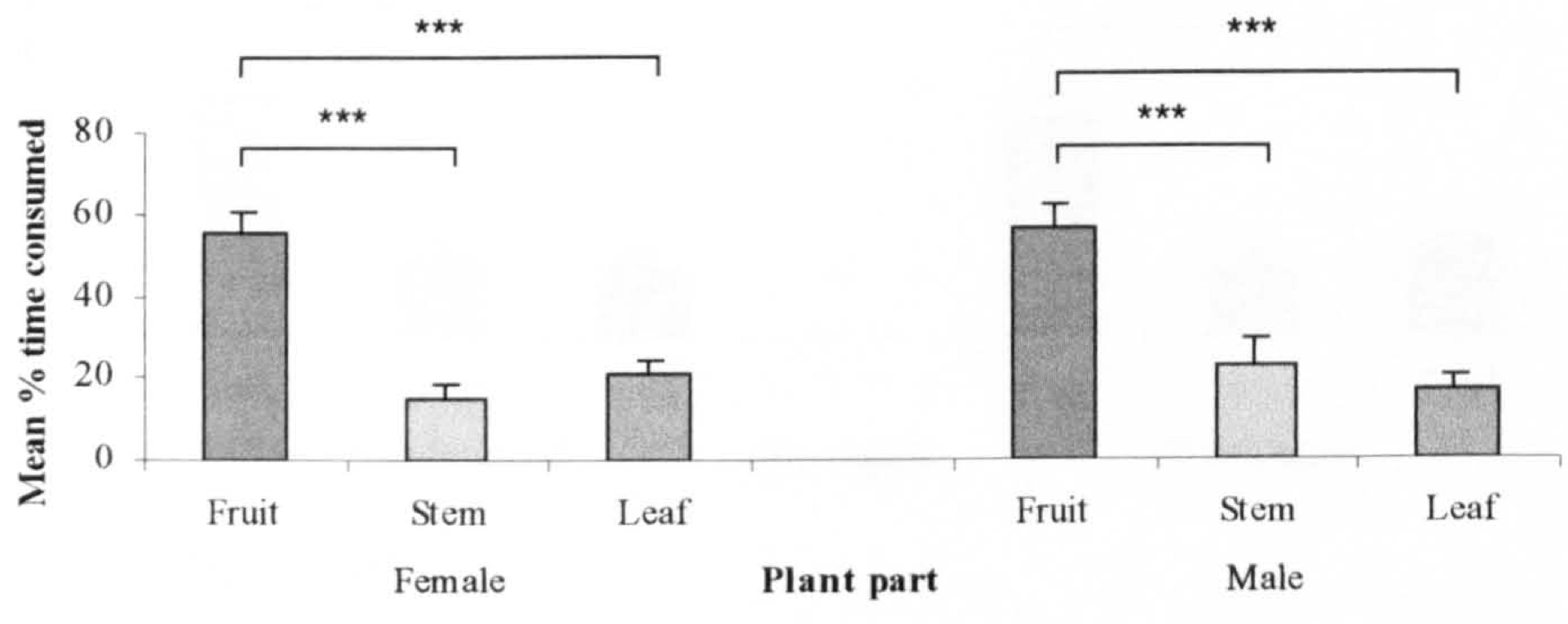
Table 8.4 Mean percentage time spent consuming leaf and stem pith on and above ground level

Plant part and height	Overall mean % (±SD)	Mean n observations (±SD)	n (chimpanzee)
Stem pith - ground	75.24 (10.71)	79.91 (26.23)	15
Stem pith – above ground	24.71 (10.60)	28.07 (11.95)	15
Leaf – ground	4.54 (4.09)	7.04 (5.38)	15
Leaf – above ground	95.46 (4.09)	122.56 (46.23)	15

The mean percentage of time that each sex spent feeding on fruit, stem pith and leaf were compared. The main effect of food type was found to be significant (*F* (2,26) = 193.71, p<0.001) but not sex (*F* (1,13) = 3.99, p=0.067); both females and males ate more fruit in comparison to stem pith and leaf (Figure 8.5). This is not surprisingly due to the overall high proportion of fruit consumed in comparison to both leaf and stem pith consumption (Table 8.5). A significant interaction between sex and food type

(*F* (2,26) = 4.08, p=0.029) was found. This is probably because females ate more leaf and less stem pith in comparison to males and males ate more stem pith and less leaf in comparison to females (Figure 8.5). However, post-hoc tests did not reveal any significant results (Table 8.6).

Figure 8.5 Mean percentage time (±SD) females and males spent consuming fruit, stem pith and leaf



***p<0.0001

Table 8.6 Results of post-hoc tests performed on sex and plant part consumed

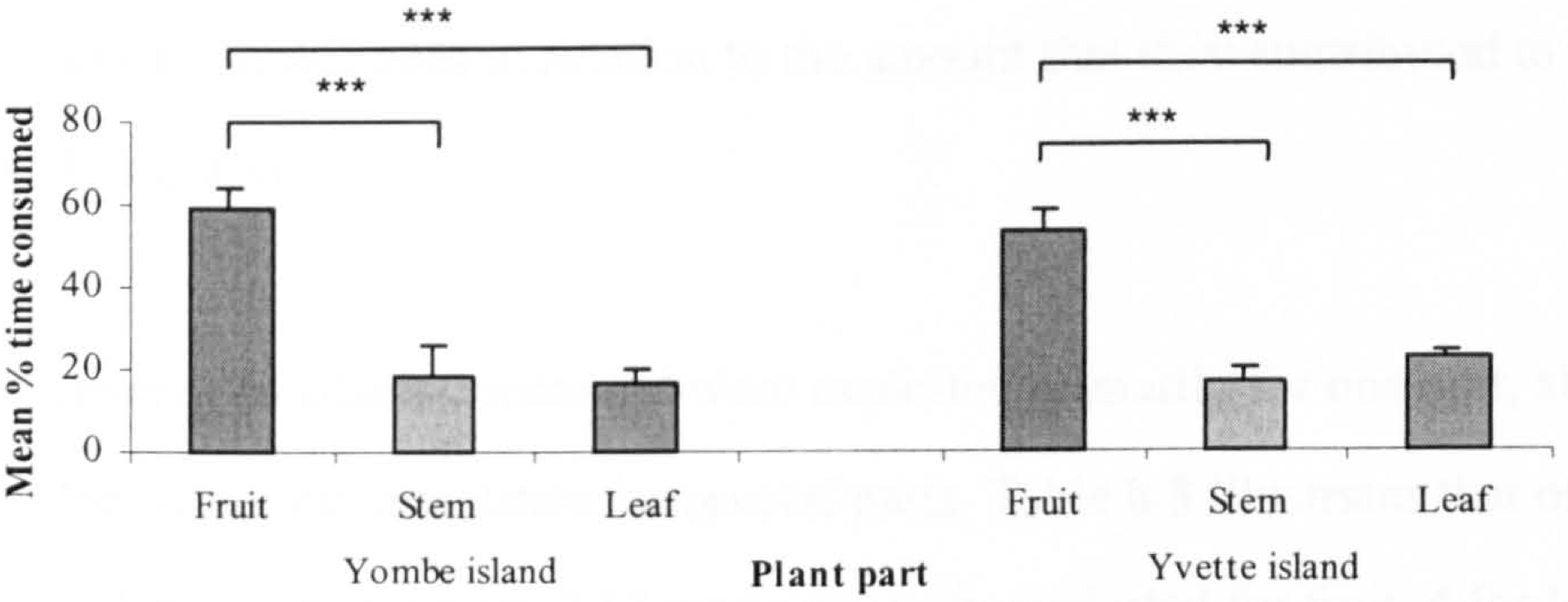
Plant part		Sex		Mean difference	Significance	95% confidence interval for difference	
						Lower bound	Upper bound
Fruit	Stem	♀	♀	40.21	<0.0001***	-47.44	-32.97
Fruit	Leaf	♀	♀	34.03	<0.0001***	-41.26	-26.80
Fruit	Stem	♂	♂	33.66	<0.0001***	-45.65	-21.66
Fruit	Leaf	♂	♂	39.86	<0.0001***	-51.85	-27.87
Fruit	Fruit	♀	♂	-0.93	1.0000	-8.97	10.84
Stem	Stem	♀	♂	-7.48	0.3258	-2.42	17.39
Leaf	Leaf	♀	♂	4.90	1.0000	-14.80	5.01
Stem	Leaf	♀	♂	-1.28	1.0000	-8.62	11.18

***p<0.0001

When the same comparisons were made between chimpanzees released from Yombe and Yvette island a similar pattern was found. The main effect of food type was found to be significant (*F* (2,26) = 238.94, p<0.001) but not island (*F* (1,13) = 1.14, p=0.305); chimpanzees from both islands ate more fruit in comparison to stem pith and leaf (Figure 8.6). A significant interaction between island and food type was found (*F* (2,26)

= 3.45, p=0.047) but as with sex, the interaction appears to be due to differences (non-significant) in the proportions of stem pith and leaf in the diet of chimpanzees from the two islands (Table 8.7).

Figure 8.6 Mean percentage time spent consuming fruit, stem pith and leaf for each pre-release island (±SD)



***p<0.0001

Table 8.7 Results of post-hoc tests performed on pre-release island and plant part consumed

Plant part		Island		Mean difference	Significance	95% confidence interval for difference	
						Lower bound	Upper bound
Fruit	Stem	Yombe	Yombe	40.40	<0.0001***	-50.38	-30.42
Fruit	Leaf	Yombe	Yombe	41.73	<0.0001***	-51.71	-31.75
Fruit	Stem	Yvette	Yvette	37.17	<0.0001***	-45.31	-29.02
Fruit	Leaf	Yvette	Yvette	31.49	<0.0001***	-39.64	-23.34
Fruit	Fruit	Yombe	Yvette	5.11	1.0000	-14.22	4.00
Stem	Stem	Yombe	Yvette	1.88	1.0000	-10.99	7.23
Leaf	Leaf	Yombe	Yvette	-5.13	1.0000	-3.98	14.24
Stem	Leaf	Yombe	Yvette	-3.80	1.0000	-5.31	12.91

***p<0.0001

8.4.2.4 Primary plant species and parts consumed

Table 8.8 lists the median percentage time that the chimpanzees fed on plant species (or species from the genus, family or form if not specifically identified) for 0.5% or more of feeding time. The majority of time spent feeding (>70%) was accounted for by consumption of species from the life form liana, the family *Marantaceae*, the genus *Vitex* and the following species: Dialium no.47 (exact species not identified), *Elaeis guinnensis*, *Irvingia gabonensis*, *Scytopetalum klaineanum* and *Staudia gabonensis*. Not all plants listed in Table 8.8 were exploited by all chimpanzees but despite this in some cases accounted for a larger proportion of overall median time spent feeding than perhaps expected. For example in the case of *Scytopetalum klaineanum* only four chimpanzees consumed the parts of this species (from R4) but this accounted for an overall 6.75% of median time spent feeding on plants. Similarly *Dialium* no. 47, *Grewia cororiacea* and other species from the genera *Grewia* were consumed by a small number of chimpanzees in relation to the amount that they contributed to the overall diet (Table 8.8).

The majority of plants consumed were exploited primarily for one part, although were sampled in smaller quantities for several parts. Table 8.8 illustrates that of the 25 species listed (or genus etc.,) 17 were primarily exploited for fruit, 4 for leaf and 3 for stem pith, and 1 (*Elaeis guinnensis*) for an almost equal amount of fruit and pith.

Table 8.8 Plant species, genus, family and form accounting for 0.5% or more of feeding time and primary parts consumed

Species (genus, family and form if not identified)	Median % time feeding (±IQR)	Plant parts consumed	Primary part consumed	Median % of primary part consumed	n chimpanzees consuming plant	Mean n observations (±SD)	Median n observations (±IQR)
Liana (form)	**17.70 (6.90)**	L,F,ST,SD,SP, B, FW	Leaf	91.20 (5.00)	15	*105.32 (38.19)	100.43 (39.97)
Marantaceae (family)	**11.00 (4.10)**	ST, F, L, F, SH, LQ	Stem	99.70 (1.00)	15	*62.95 (23.63)	55.86 (46.57)
Vitex (genus)	**10.10 (15.50)**	F, L, SP, FW, ST	Fruit	99.40 (7.10)	15	72.94 (73.09)	166.68 (83.10)
Dialium no. 47	**9.90 (1.03)**	F, SD, L, SP	Fruit	99.15 (0.35)	6	*82.04 (9.46)	85.25 (12.97)
Elaeis guinnensis	**7.60 (5.30)**	F, ST, L, FW, SD	Fruit	50.40 (39.30)	15	53.67 (31.82)	48.21 (71.28)
			Stem	48.20 (34.30)			
Scytopetalum klaineanum	**6.75 (2.87)**	F	Fruit	100	4	*33.00 (14.85)	36.97 (26.27)
Irvingia gabonensis	**5.50 (5.90)**	F, SD, FW, L, ST	Fruit	98.20 (9.90)	15	*39.11 (26.36)	41.97 (46.72)
Staudia gabonensis	**5.03 (2.04)**	F, ST, L	Fruit	100 (0.40)	14	*29.08 (8.81)	26.39 (12.64)
Grewia (genus)	4.20	F	Fruit	100	3	18.30 (8.22)	22.43
Nauclea (genus)	3.40 (5.40)	F, L, SD	Fruit	99.50 (1.10)	9	*18.31 (13.52)	17.15 (29.24)
Grewia cororiacea	3.10	F, SP	Fruit	98.60	3	*15.58 (0.99)	15.43
Grewia obigoneura	2.70 (5.10)	F, ST, SD, SP	Fruit	100 (0.48)	15	23.15 (26.04)	14.18 (33.49)
Milletia comosa	1.80 (1.35)	F, L, FW	Leaf	68.20 (38.98)	14	*9.64 (3.07)	10.57 (5.43)
Dacroydes igananga	1.60 (2.20)	F.L	Fruit	95.20 (8.55)	8	40.06 (84.64)	17.64 (23.00)
Liana no.10 (form)	1.40 (3.90)	F, L	Fruit	99.20 (1.70)	11	17.35 (16.90)	29.71 (32.40)
Warnecka (genus)	1.10 (1.70)	F, SH	Fruit	100	13	*9.09 (6.01)	9.50 (8.29)
Nauclea diderrichii	1.10 (1.90)	F. L	Fruit	100 (0.08)	14	*7.97 (6.63)	5.04 (10.02)
Aframomum (genus)	1.00 (0.80)	F, ST, FW	Stem	77.95 (29.90)	15	*8.76 (5.34)	7.93 (6.51)
Santiria trimera	0.90 (0.55)	F, L, ST	Fruit	100 (1.05)	9	6.17 (1.81)	6.57 (1.14)
Non-identified tree	0.65 (1.30)	SP, L, ST, SH, FW	Leaf	65.25 (26.08)	14	5.88 (5.34)	11.82 (7.62)

Table 8.8 continued............Plant species, genus, family and form accounting for 0.5% or more of feeding time and primary parts consumed

Species (genus, family and form if not identified)	Median % time feeding (±IQR)	Plant parts consumed	Primary part consumed	Median % of primary part consumed	n chimpanzees consuming plant	Mean n observations (±SD)	Median n observations (±IQR)
Pacypodanthium staudii	0.60 (0.20)	F, L, ST	Fruit	98.50 (2.25)	9	*3.87 (1.84)	4.50 (3.68)
Ficus (genus)	0.50 (0.75)	F, ST, SP	Fruit	100	15	*3.09 (2.84)	3.75 (3.69)
Hexalobus crispiflorus	0.50 (2.60)	F	Fruit	100	15	5.72 (5.44)	4.91 (10.49)
Maccata (*Cola* genus)	0.50 (0.35)	F, L	Leaf	97.40 (6.70)	9	2.71 (1.92)	4.54 (4.27)
Marantachola (genus)	0.50 (0.64)	ST	Stem	100	9	*2.66 (2.46)	1.97 (2.57)

Key: F = fruit, ST = stem, SD = seed, SP = Sap, L = leaf, FW = flower, B = bark, SH = shoots, LQ = liquid

Notes:
Mean and median number of observations made are presented as some data were judged normal and others not. * represent data judged normal
Where there are no IQR's, this is due to a small number of chimpanzees contributing scores
Fruit and stem pith of *Elaeis guinnensis* were consumed in almost equal amounts
Figures in bold in the column two (median % time spent feeding) together constitute over 70% of feeding time on plant species

Species consumed from the genus *Vitex*, *Dialium* no. 47 and *Scytoptealum klaineanum* accounted for over a third (43.85%) of all fruit consumed (Table 8.9). Over two thirds of leaf consumption (78.45%) could be accounted for from the life form liana and the species *Milletia comosa* (Table 8.10) and similarly for stem pith consumption (79.40%) from the family *Marantaceae* and species *Elaeis guinnensis* (Table 8.11).

Table 8.9 Main plant species accounting for the fruit component of post-release diet

Species	Fruit		n chimpanzees
	Median % consumed	IQR	
Vitex (genus)	16.80	26.50	15
Dialium no. 47	15.65	3.05	6
Scytopetalum klaineanum	11.40	7.10	4
Staudia gabonensis	9.80	6.60	15
Irvingia gabonensis	8.40	6.70	15
Nauclea (genus)	5.80	9.80	9
Elaeis guinnensis	4.20	7.10	15
Grewia obigoneura	4.00	8.60	15
Liana (life form) no. 10	2.70	6.20	11
Warnecka (genus)	1.80	3.65	13
Total median %	**80.55**	-	-

Table 8.10 Main plant species accounting for the leaf component of post-release diet

Species	Leaf		n chimpanzees
	Median % consumed	IQR	
Liana (life form)	73.70	17.60	15
Milletia comosa	4.75	4.08	14
Unidentified tree	1.90	2.70	15
Maccata (genus *Cola*)	1.85	1.48	10
Pterygota bequaerti	1.50	5.20	15
Epiphyte (life form) no.8	1.30	5.60	11
Total median %	**85**	-	-

Table 8.11 Main plant species accounting for the stem pith component of post-release diet

Species	Fruit		n chimpanzees
	Median % consumed	IQR	
Marantaceae (family)	60.90	12.80	15
Elaeis guinnensis	18.50	18.10	15
Aframomum (genus)	5.30	3.50	15
Marantachola (genus)	3.10	2.00	11
Palisota (genus)	1.80	2.45	14
Costus albus	1.20	4.50	15
Raphia (genus)	1.00	4.28	14
Total median %	**91.80**	-	-

8.4.2.5 Comparison of plant parts consumed to other chimpanzee populations

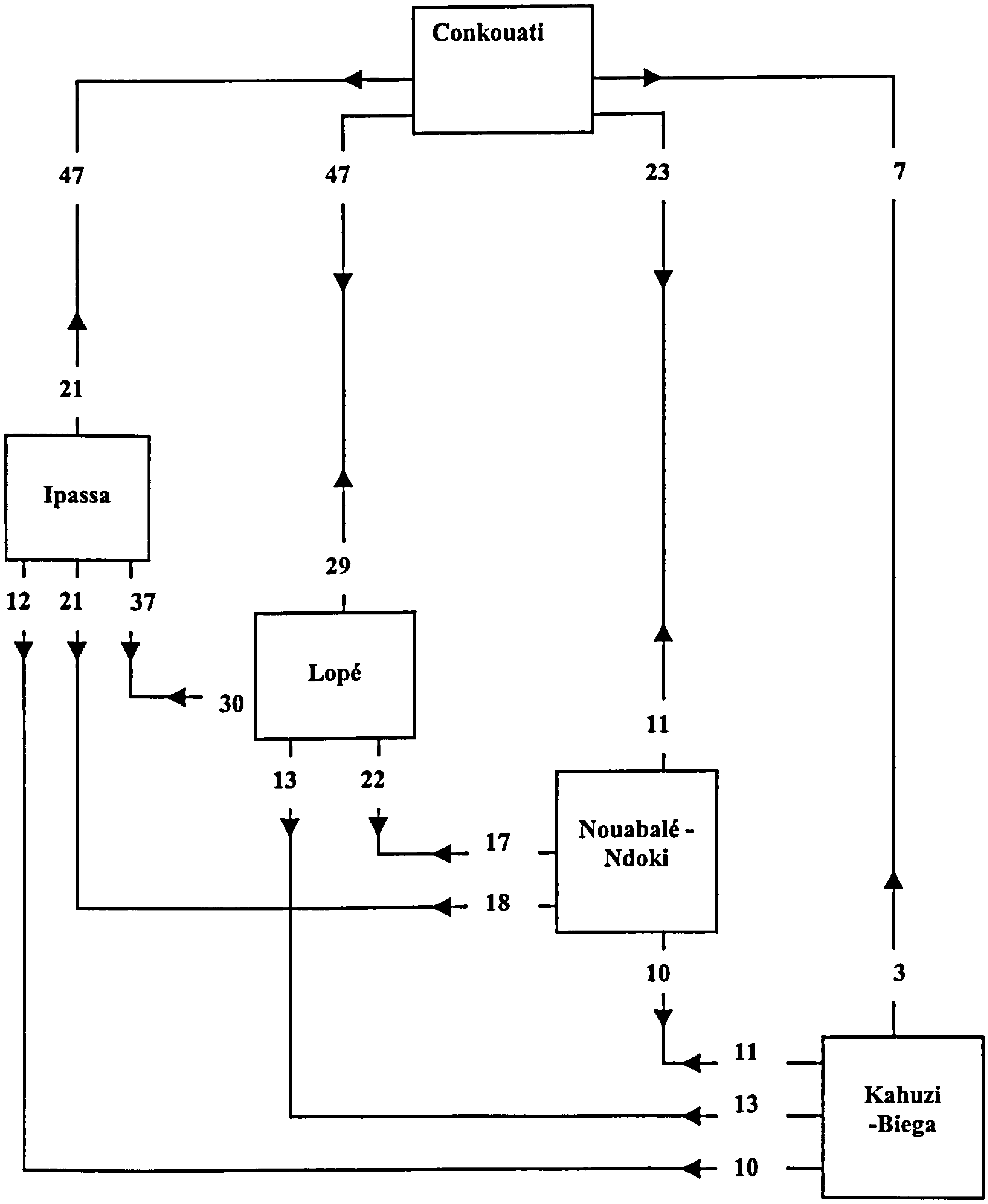
As mentioned earlier, overall the reintroduced chimpanzees consumed more plant parts (part consumed at least once) in comparison to the three studies of wild chimpanzees and the study of the Ipassa reintroduced chimpanzees (Table 8.2, p.243). Furthermore, comparisons of the number of plant parts consumed from shared feeding plant species revealed that in nearly all comparisons the reintroduced chimpanzees at Conkouati consumed more parts (Figure 8.7).

Figure 8.7 illustrates that both reintroduced populations consumed more plant parts of shared feeding species in comparison to the wild populations although the extent of this separation is more evident with the chimpanzees at Conkouati. For example, chimpanzees at Conkouati ate 47 parts of the same plant species in comparison to 29 at Lopé; 61.70% similarity of plant parts consumed. Chimpanzees at Ipassa ate 37 parts of the same plant species in comparison to 30 at Lopé (81.08%). A similar pattern was found for comparisons made between Conkouati and Nouabalé-Ndoki (47.83%) and Kahuzi-Biega (42.86%) and between wild populations and chimpanzees at Ipassa. The number of parts consumed by chimpanzees at Conkouati was more similar (although not to a great extent) to wild chimpanzees at Lopé in comparison to Nouabalé-Ndoki and Kahuzi-Biega. Comparisons between wild populations also revealed differences in two out of the three populations. However, the differences were comparatively small; at Lopé 22 parts of the same plant species were consumed in comparison to 17 at Nouabalé-Ndoki, and 10 at Nouabalé-Ndoki in comparison to 11 at Kahuzi-Biega.

An example of differences in parts consumed from the same plant species is the case of *Pseudospondias longfolia*; chimpanzees at Conkouati, Ipassa and Lopé consume its fruit, but chimpanzees at Conkouati have also been known to consume its leaves. Another example is *Irvingia gabonensis*; chimpanzees at Conkouati, Lopé and Nouabalé-Ndoki all consume the fruit, chimpanzees at Conkouati and Lopé have also been known to consume its seed, as do chimpanzees at Ipassa but not chimpanzees at

Nouabalé-Ndoki. Furthermore, the Conkouati chimpanzees have also been known to consume the stem pith, leaf and flower of *Irvingia gabonensis*. Refer to Appendix E for more examples.

Figure 8.7 Multi-comparisons of the number of plant parts consumed from shared feeding species between reintroduced and wild chimpanzees

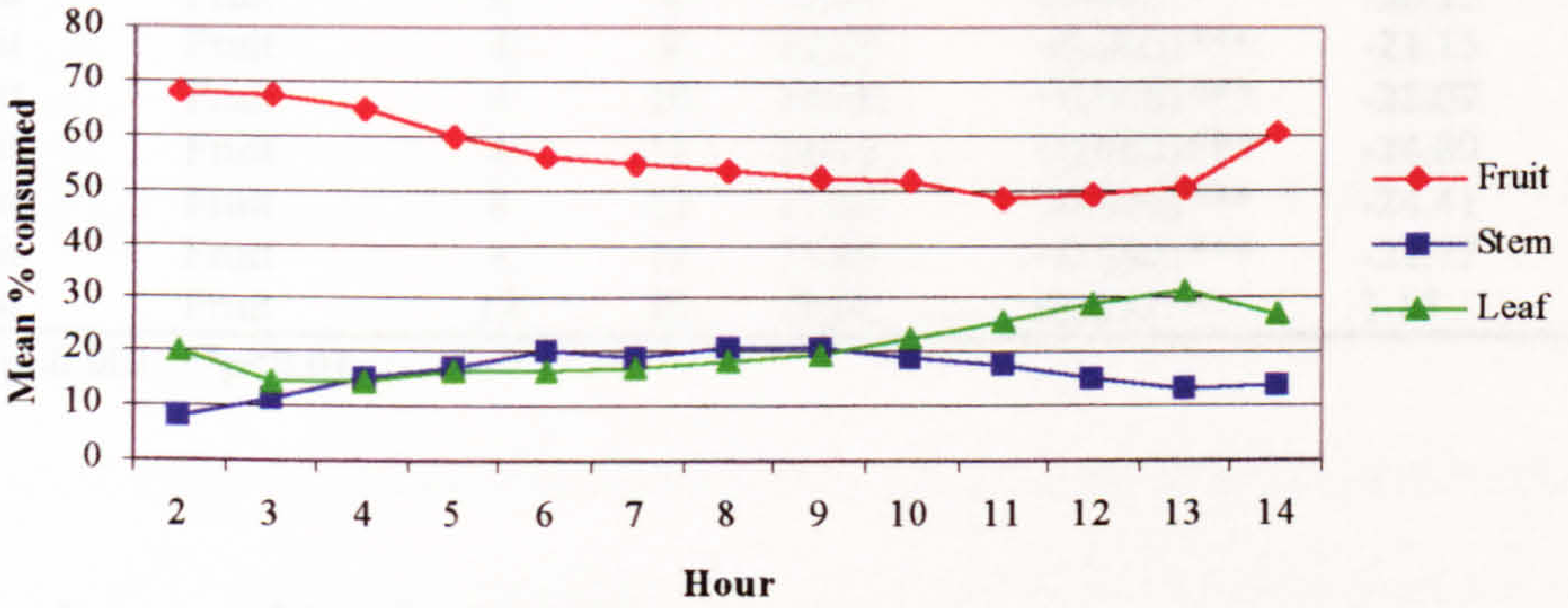


Key: The numbers placed closest to each site box represent the number of plant parts from the same plant species consumed by each chimpanzee population

8.4.2.6 Hourly variation in plant part consumption

To examine hourly temporal variation in levels of plant part consumption across the day, the mean amount of time per hour that the chimpanzees spent consuming fruit, stem pith and leaf were compared. Repeated measures ANOVA were performed on plant part and hour and significant main effects were found for plant part (*F* (2,28) = 204.56, p<0.001) and hour (*F* (12,168) = 4.64, p<0.001) and a significant interaction between plant part and hour (*F* (24,330) = 18.65, p<0.001) (Figure 8.8). As mentioned earlier due to the large number of post-hoc tests generated by the multivariate analyses, only results pertinent to questions asked are presented. (Refer to Table 6.3, p.134 for a reminder of time category that each hour represents).

Figure 8.8 Mean percentage time spent per hour consuming fruit, stem pith and leaf



Hourly fruit consumption

Clearly fruit consumption predominated throughout the day; its consumption was significantly higher in comparison to stem pith and leaf in every hour (Table 8.12). Fruit consumption was at its highest during hours 2 and 3; for example its consumption was significantly higher in hour 2 in comparison to hours 6 -13 and the same was true for hour 4 in comparison to hours 7 -13. This was followed by a gradual decline until hour 12 when the mean level increased; the mean level of fruit consumption was significantly higher in hour 14 in comparison to hour 13 (Figure 8.8, Table 8.12).

Table 8.12 Results of post-hoc tests performed on hour and consumption of fruit in comparison to stem pith and leaf

Plant part		Hour		Mean difference	Significance	95% confidence intervals for difference	
						Lower bound	Upper bound
Fruit	Stem pith	2	2	59.12	<0.0001***	-68.13	-50.10
Fruit	Leaf	2	2	45.44	<0.0001***	-54.81	-36.06
Fruit	Stem pith	5	5	42.89	<0.0001***	-51.67	-34.10
Fruit	Leaf	5	5	43.34	<0.0001***	-52.13	-34.55
Fruit	Stem pith	9	9	31.69	<0.0001***	-40.48	-22.91
Fruit	Leaf	9	9	32.50	<0.0001***	-41.29	-23.71
Fruit	Stem pith	12	12	33.99	<0.0001***	-42.77	-25.20
Fruit	Leaf	12	12	20.19	<0.0001***	-28.97	-11.40
Fruit	Fruit	2	6	12.16	<0.0001***	-20.95	-3.37
Fruit	Fruit	2	7	13.59	<0.0001***	-22.37	-4.80
Fruit	Fruit	2	8	14.98	<0.0001***	-23.77	-6.19
Fruit	Fruit	2	9	15.98	<0.0001***	-24.77	-7.19
Fruit	Fruit	2	10	16.89	<0.0001***	-25.68	-8.11
Fruit	Fruit	2	11	19.72	<0.0001***	-28.51	-10.93
Fruit	Fruit	2	12	19.23	<0.0001***	-28.02	-10.45
Fruit	Fruit	2	13	17.60	<0.0001***	-26.39	-8.81
Fruit	Fruit	4	7	9.97	0.0049**	-18.76	-1.19
Fruit	Fruit	4	8	11.37	0.0002**	-20.15	-2.58
Fruit	Fruit	4	9	12.37	<0.0001***	-21.15	-3.58
Fruit	Fruit	4	10	13.28	<0.0001***	-22.07	-4.49
Fruit	Fruit	4	11	16.11	<0.0001***	-24.89	-7.32
Fruit	Fruit	4	12	15.62	<0.0001***	-24.41	-6.83
Fruit	Fruit	4	13	13.99	<0.0001***	-22.77	-5.20
Fruit	Fruit	13	14	-9.94	0.0052**	1.15	18.73

***p<0.001, **p<0.01

Hourly stem pith consumption

Consumption of stem pith showed a steady increase from hour 2 until hour 8 (12h00-12h55) when a decrease was seen (Figure 8.8). Its consumption was significantly lower in hour 2 in comparison to hour 6 -10, but not significantly different in comparison to hours 11-14 (Table 8.13). Only in hour two was the consumption of stem pith significantly higher than leaf; in hours 2 -11, there were no significant differences; and from hour 12 -14 the amount of stem pith consumed was significantly lower in comparison to leaf (Table 8.13).

Table 8.13 Results of post-hoc tests performed on hour and consumption of stem pith in comparison to leaf

Plant part		Hour		Mean difference	Significance	95% confidence intervals for difference	
						Lower bound	Upper bound
Stem pith	Stem pith	2	6	-10.79	0.0015**	1.77	19.81
Stem pith	Stem pith	2	7	-9.96	0.0083**	0.95	18.98
Stem pith	Stem pith	2	8	-11.86	0.0002**	2.84	20.87
Stem pith	Stem pith	2	9	-11.44	0.0004**	2.43	20.46
Stem pith	Stem pith	2	10	-9.49	0.0208**	0.47	18.51
Stem pith	Stem pith	2	11	-8.51	0.1228	-0.51	17.53
Stem pith	Stem pith	2	12	-5.90	1.0000	-3.12	14.91
Stem pith	Stem pith	2	13	-3.91	1.0000	-5.11	12.93
Stem pith	Stem pith	2	14	-9.20	0.1607	-0.73	19.13
Stem pith	Leaf	2	2	-13.68	<0.0001***	4.31	23.06
Stem pith	Leaf	3	3	-2.61	1.0000	-6.18	11.39
Stem pith	Leaf	4	4	0.98	1.0000	-9.77	7.81
Stem pith	Leaf	5	5	0.45	1.0000	-9.24	8.33
Stem pith	Leaf	6	6	3.46	1.0000	-12.25	5.33
Stem pith	Leaf	7	7	2.16	1.0000	-10.95	6.63
Stem pith	Leaf	8	8	2.48	1.0000	-11.27	6.31
Stem pith	Leaf	9	9	0.81	1.0000	-9.59	7.98
Stem pith	Leaf	10	10	-4.25	1.0000	-4.54	13.03
Stem pith	Leaf	11	11	-7.88	0.2527	-0.91	16.67
Stem pith	Leaf	12	12	-13.80	<0.0001***	5.01	22.59
Stem pith	Leaf	13	13	-18.64	<0.0001***	9.85	27.43
Stem pith	Leaf	14	14	-12.30	0.0004**	2.59	22.02

***p<0.001, **p<0.01

Hourly leaf consumption

The overall pattern of leaf consumption was one of an initial high level that immediately decreased, and then from hour 2 showed a gradual increase across the course of the day. Leaf consumption in hour 3, 4 and 5 were significantly lower in comparison to hours 11 -14 (Table 8.14).

By pooling hourly means it is possible to compare the overall mean percentage time that chimpanzees spent consuming fruit, stem pith and leaf in the morning and afternoon (morning hours 2-7 and afternoon hours 8-14). Repeated measures ANOVA was performed on plant part and time of day consumed. A significant main effect of plant part (*F* (2,28) = 193.69, p<0.001), a non-significant main effect of time of day (*F* (1,14) = 0.01, p=0.922) and a significant interaction of plant part and time of day consumed (*F* (2,28) = 68.51, p<0.001) was found. Bonferroni post-hoc tests found that the amount of fruit consumed was significantly greater in the morning (before 12pm) in comparison to the afternoon (after 12pm) but the reverse was true for leaf consumption (Table 8.15, Figure 8.9). No significant difference was found in the amount of stem pith that was consumed in morning and the afternoon.

Table 8.14 Results of post-hoc tests performed on hour and consumption of leaf

Plant part		Hour		Mean difference	Significance	95% confidence intervals for difference	
						Lower bound	Upper bound
Leaf	Leaf	3	11	-11.34	0.0002**	2.55	20.13
Leaf	Leaf	3	12	-14.65	0.0083**	5.86	23.43
Leaf	Leaf	3	13	-17.50	<0.0001***	8.71	26.29
Leaf	Leaf	3	14	-16.45	<0.0001***	7.33	25.57
Leaf	Leaf	4	11	-11.31	0.0003**	2.52	20.09
Leaf	Leaf	4	12	-14.61	<0.0001***	5.83	23.40
Leaf	Leaf	4	13	-17.47	<0.0001***	8.68	26.25
Leaf	Leaf	4	14	16.42	<0.0001***	7.30	25.54
Leaf	Leaf	5	11	-9.25	0.0208*	0.46	18.03
Leaf	Leaf	5	12	-12.55	<0.0001***	3.77	21.34
Leaf	Leaf	5	13	-15.41	<0.0001***	6.62	24.19
Leaf	Leaf	5	14	-14.36	<0.0001***	5.24	23.48

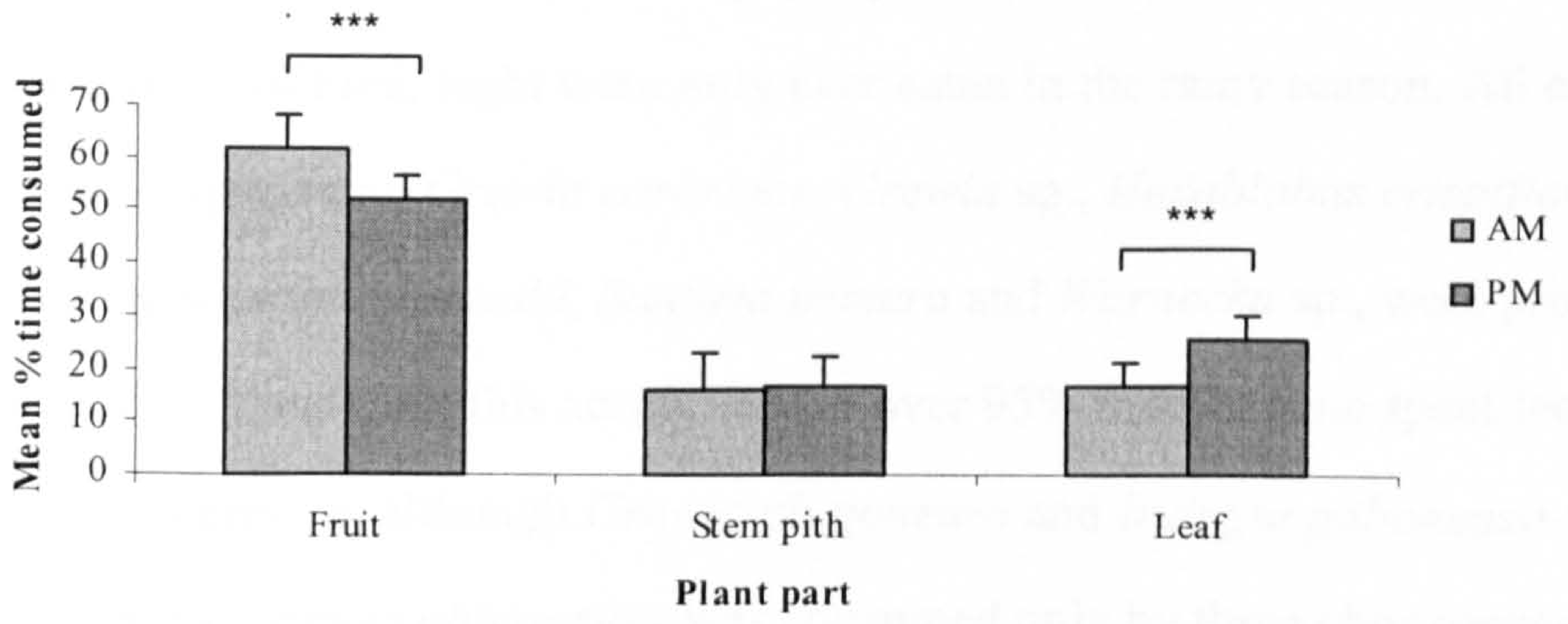
***p<0.001, **p<0.01, *p<0.05

Table 8.15 Results of post-hoc tests performed time of day (AM/PM) and consumption of plant part

Plant part	Mean difference	Significance	95% confidence intervals for difference	
			Lower bound	Upper bound
Fruit	9.56	p<0.0001***	-13.16	-5.96
Stem pith	-0.42	1.0000	-3.18	4.02
Leaf	-9.00	p<0.0001***	5.40	12.60

***p<0.0001

Figure 8.9 Mean percentage time spent consuming fruit, stem pith and leaf in the morning and afternoon



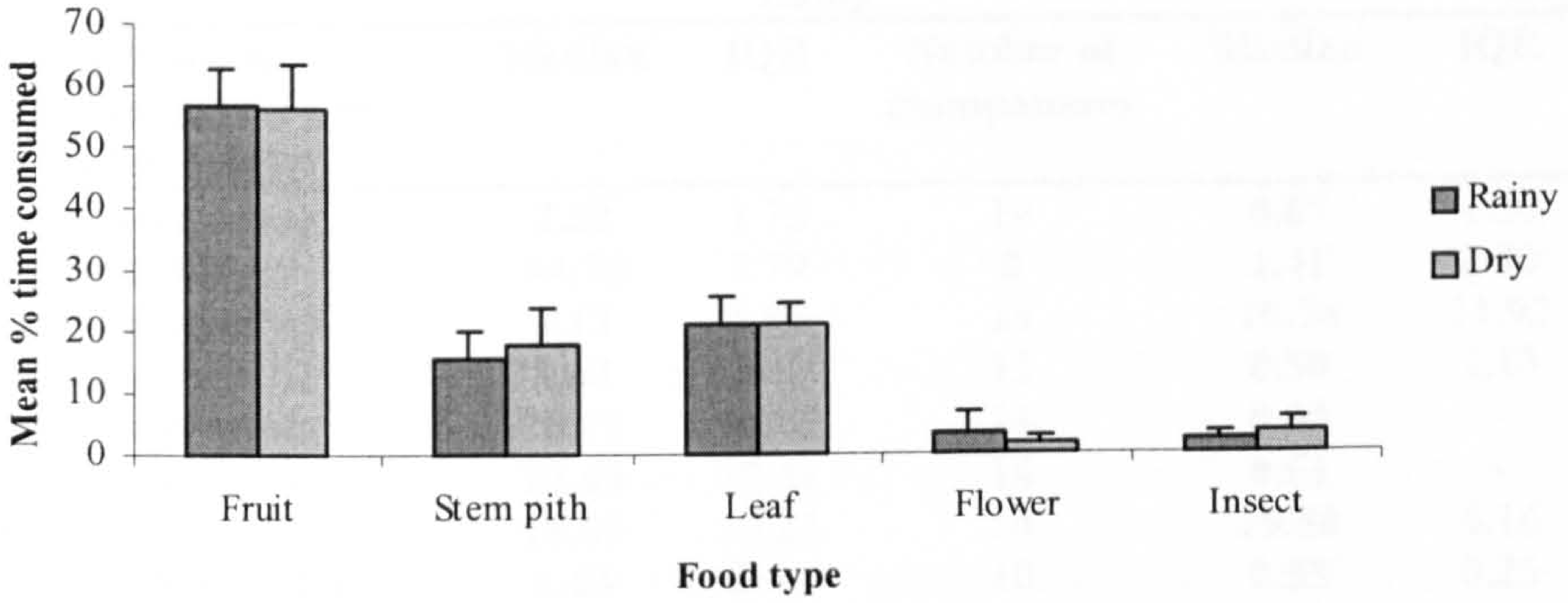
***p<0.0001

8.4.2.7 Seasonal and monthly variation in diet

8.4.2.7.1 Food type

The mean percentage time spent feeding on the major food types consumed; fruit, leaf, stem pith, flower and insects were compared between rainy and dry season. A repeated measures ANOVA performed on season and food type revealed no significant main effects (F (4,50) = 0.68, p=0.612); none of the food types were significantly consumed more or less in the rainy and dry season (Figure 8.10).

Figure 8.10 Mean percentage time spent consuming fruit, stem pith, leaf, flower and insects in the rainy and dry season (±SD)



8.4.2.7.3 Dietary variation in species consumed

By comparing the median percentage time that primary species were consumed (species consumed for 0.5% or more of time (refer back to Table 8.8, p.250) in the dry and rainy season it is possible to examine variation in species consumed. Of the 25 species (or genus, life form if not identified to species) listed in Table 8.8 that were consumed for 0.5% or more of time, eight were only ever eaten in the rainy season. All eight; *Dacroydes igananga, Grewia cororiace, Grewia* sp., *Hexablobus crispiflorus*, liana (no. 10), *Pacypodanthium staudii, Santiria trimera* and *Warnecka* sp., were primarily exploited for their fruit; this accounted for over 95% median time spent feeding in all cases. Furthermore, although *Grewia obigoneura* and *Irvingia gabonensis* were eaten in both seasons, *Grewia obigoneura* was consumed only by three chimpanzees in the dry season whereas all the chimpanzees consumed the fruit of this species in the rainy season. Likewise, only two chimpanzees consumed *Irvingia gabonensis* in the dry season but all chimpanzees consumed its fruit in the rainy season (Table 8.16). Again both these species were primarily exploited for its fruit (refer back to Table 8.8). Overall, more median time was spent consuming *Staudia gabonensis*, *Elaeis guinnensis* and *Vitex* sp. in the dry season. *Staudia gabonensis* and *Vitex* sp. were primarily exploited for its fruit and *Elaeis guinnensis* equally for fruit and stem pith (refer back to Table 8.8).

Table 8.16 Median time spent consuming plant species in the dry and rainy season

	Rainy			Dry		
Species (or genus, family, life form if not identified to species)	**Median**	**IQR**	**Number of chimpanzees**	**Median**	**IQR**	**Number of chimpanzees**
Aframomum (genus)	**2.22**	1.75	14	**0.67**	1.30	13
Dialium no. 47	**34.78**	5.79	6	**1.41**	2.90	6
Elaeis guinnensis	**8.12**	5.96	14	**10.74**	11.92	14
Ficus (genus)	**1.63**	3.00	13	**0.50**	2.13	12
Grewia obigoneura	**10.18**	26.70	14	**0.50**	-	2
Irvingia gabonensis	**28.69**	19.48	14	**0.53**	-	3
Liana (form)	**18.05**	10.23	14	**19.50**	4.16	14
Maccata (*Cola* genus)	**1.63**	2.92	10	**0.55**	0.25	8
Marantaceae (family)	**11.62**	5.87	14	**11.03**	6.91	14
Marantacholoa (genus)	**1.54**	1.36	9	**0.89**	1.14	8
Milletia comosa	**3.15**	3.39	14	**2.35**	1.25	14
Nauclea didderrichi	**3.85**	3.95	12	**1.72**	3.02	13
Nauclea (genus)	**8.26**	13.15	7	**7.77**	19.08	8
Non-identified tree	**1.28**	1.95	14	**0.56**	0.78	13
Scytopetalum klaineanum	**41.60**	-	3	**10.67**	-	3
Staudia gabonensis	**6.02**	6.03	14	**12.80**	20.70	14
Vitex (genus)	**10.51**	10.40	14	**28.79**	24.52	14

8.4.2.7.4 Richness, diversity and evenness of plant diet

The richness, diversity and evenness of the chimpanzee's diet were calculated for each consecutive calendar month of the post-release study period and displayed in Figures 8.11-8.13 for each chimpanzee (n=14).

Overall, the richness of the chimpanzee diet appeared relatively comparable, in particular the pattern of dietary richness between chimpanzees released in November

1996 (R1), January 1997 (R2), and November 1997 (R3) were similar in form (Figure 8.11). Chimpanzees released in January 1997 (R2) and November 1997 (R3) displayed a higher level of dietary richness upon release that subsequently decreased and then remained relatively constant. In contrast, chimpanzees released in November 1996 (R1) and February 1999 (R4) displayed an initial lower dietary richness upon release. All chimpanzees displayed a decrease in diet richness during and around the dry season months (June, July and August).

The pattern of diet diversity showed a similar pattern albeit it at a lower level to dietary richness (Figure 8.12). The pattern of dietary evenness likewise showed a similar pattern to dietary richness and diversity (Figure 8.13). Overall the mean degree of dietary evenness was 0.66 (±0.03) with a minimum of 0.47 and maximum 0.91. For chimpanzees released in November 1996 (R1) and January 1997 (R2), dietary evenness was lower during the months of May and July but higher in June (1997). Dietary evenness was slightly higher during the dry season period for chimpanzees released in November 1997 (R3, dry season 1998). Chimpanzees released in February 1999 (R4) showed a steady increase in dietary evenness until September. A peak in dietary evenness in January was also seen in the corresponding month for dietary richness and diversity.

Figure 8.11 Monthly variation in the dietary richness of plant food consumed for each reintroduced chimpanzee (C1-C16)

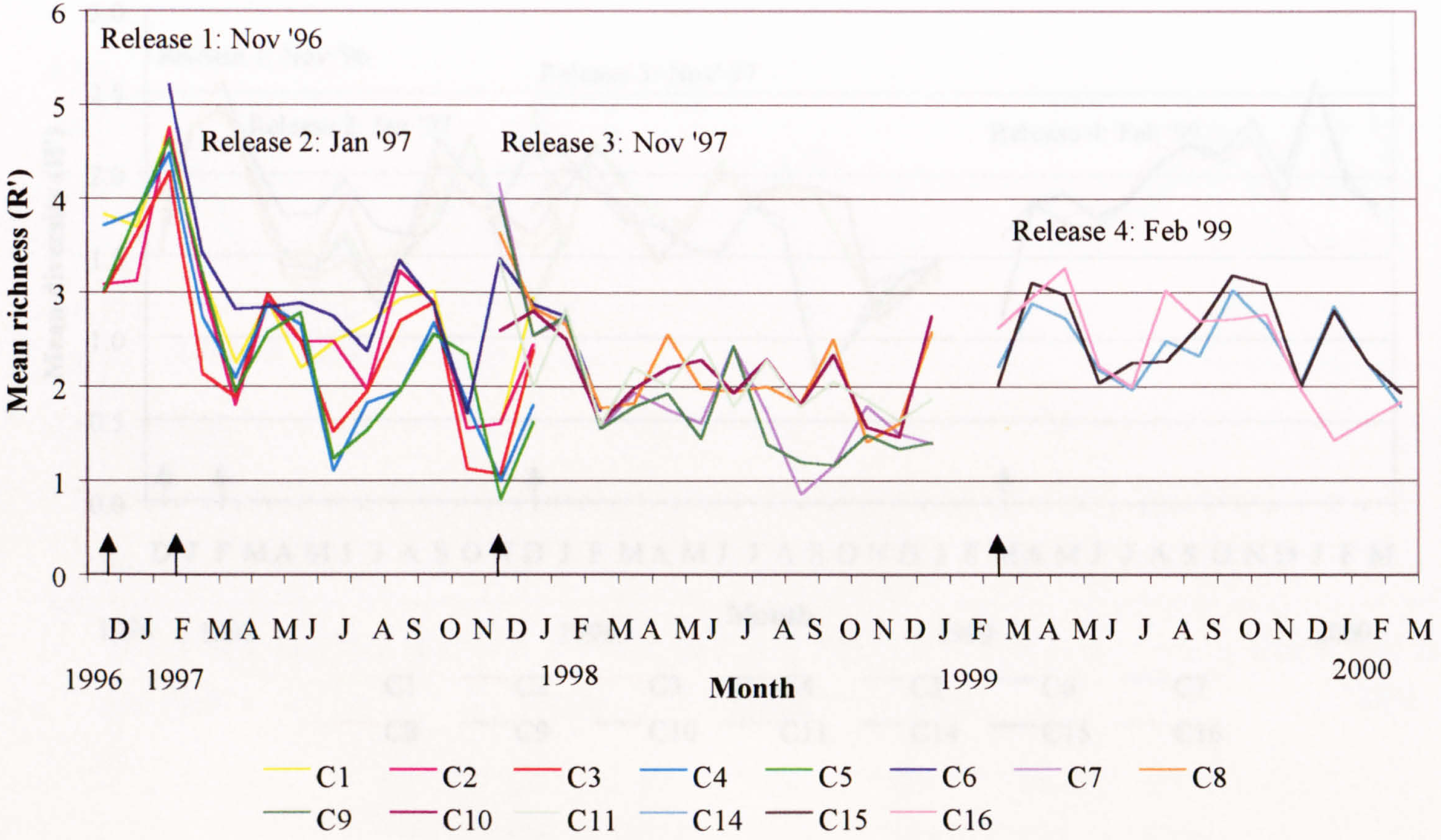


Figure 8.12 Monthly variation in the dietary diversity of plant food consumed for each reintroduced chimpanzee (C1-C16)

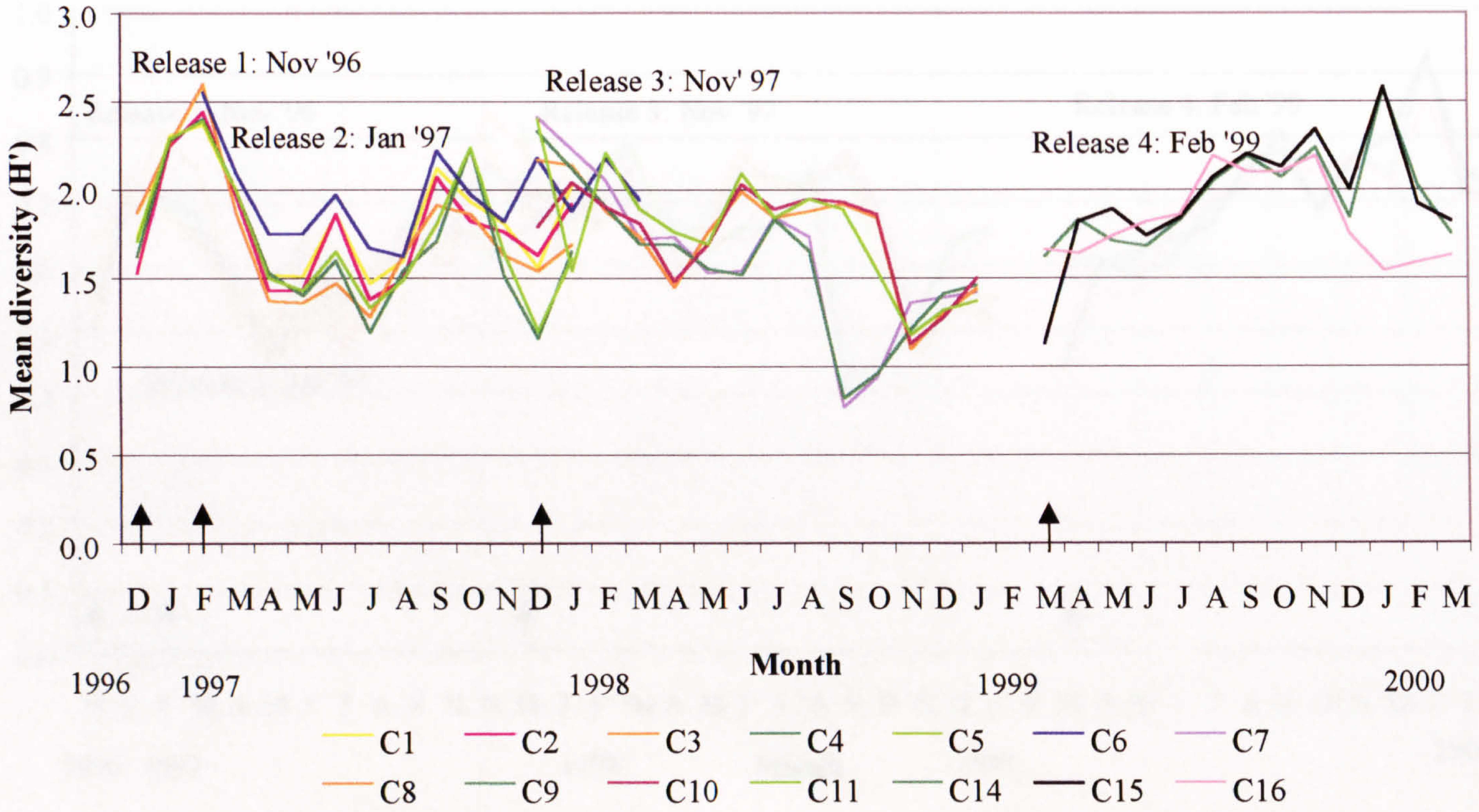
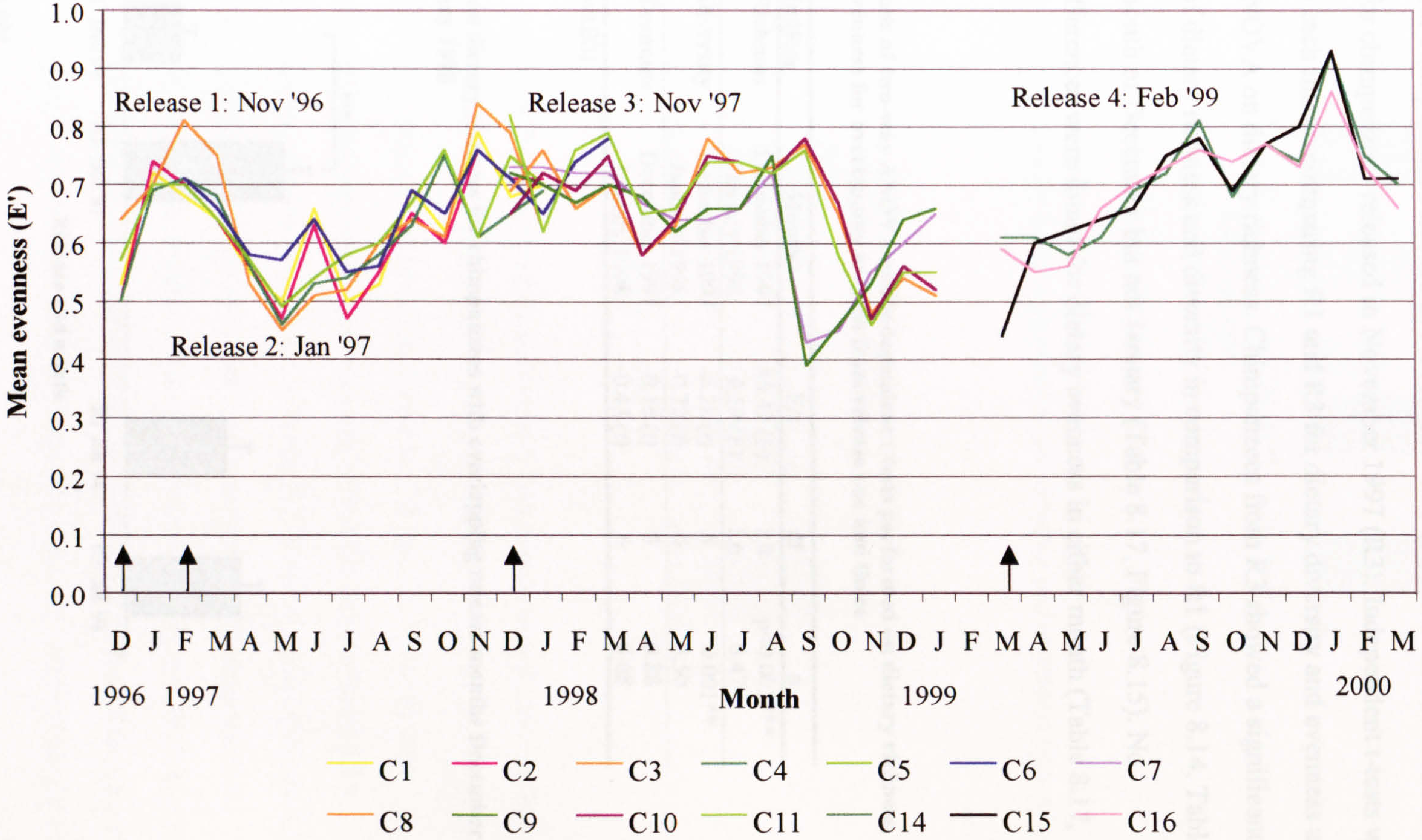


Figure 8.13 Monthly variation in the dietary evenness of plant food consumed for each reintroduced chimpanzee (C1-C16)



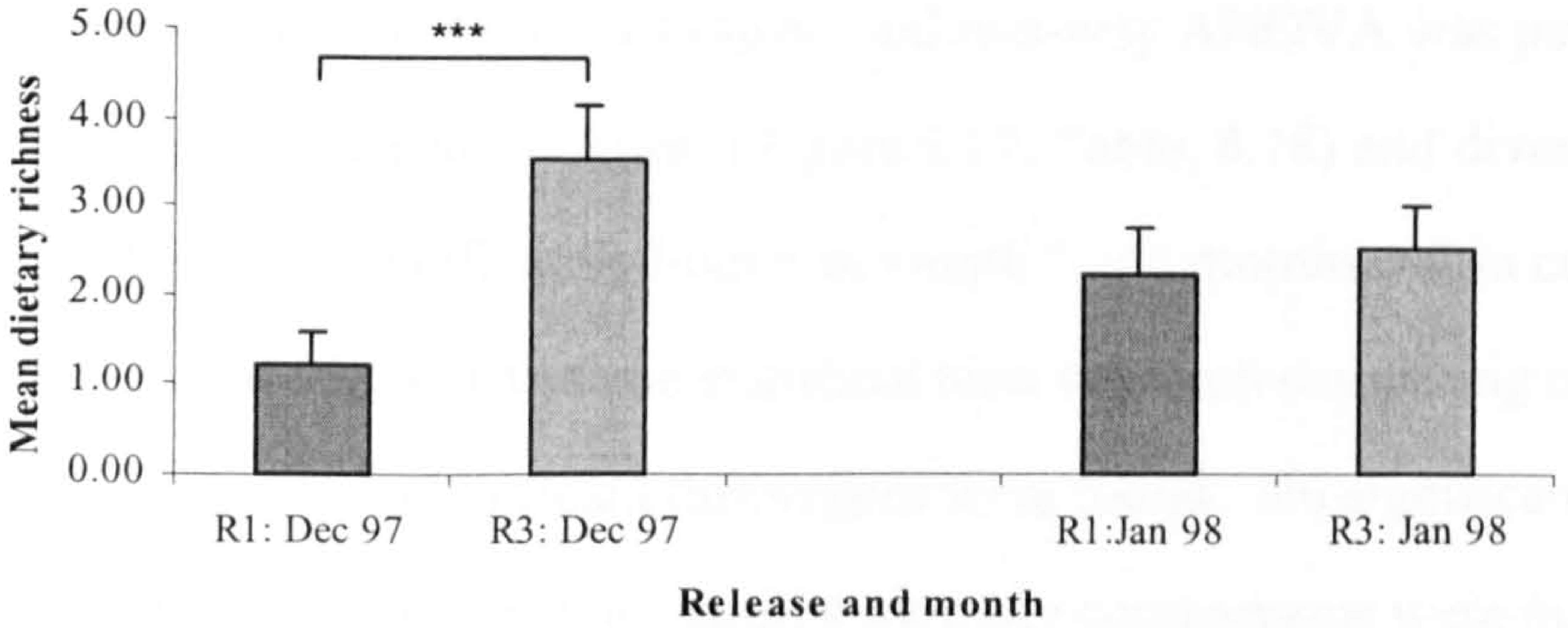
Figures 8.11-8.13 presents the opportunity to visually compare monthly overlap between chimpanzees that have already been released for some time and those just released. Months December 1997 and January 1998 correspond to the last two month study period for chimpanzees released in November 1996 (R1) and the first two months post-release for chimpanzees released in November 1997 (R3). Independent t-tests were performed on each month comparing R1 and R3 for dietary diversity and evenness and a two-way ANOVA on dietary richness. Chimpanzees from R3 showed a significantly higher level of dietary richness and diversity in comparison to R1 (Figure 8.14, Table 8.17) in the month of December but not January (Table 8.17, Figure 8.15). No significant differences were found for dietary evenness in either month (Table 8.17, Figure 8.16).

Table 8.17 Results of two-way ANOVA and independent t-tests performed on dietary richness, diversity and evenness for overlapping months from release one and three

Release	Indices	Months	F/t	df	p
R1 & R3	**Richness**	December 1997	46.42 (F)	1,8	p<0.001***
		January 1998	0.59 (F)	1,6	0.47
R1 & R3	**Diversity**	December 1997	-5.28 (t)	8	0.001**
		January 1998	-0.72 (t)	6	0.50
R1 & R3	**Evenness**	December 1997	-0.16 (t)	8	0.88
		January 1998	-0.43 (t)	6	0.68

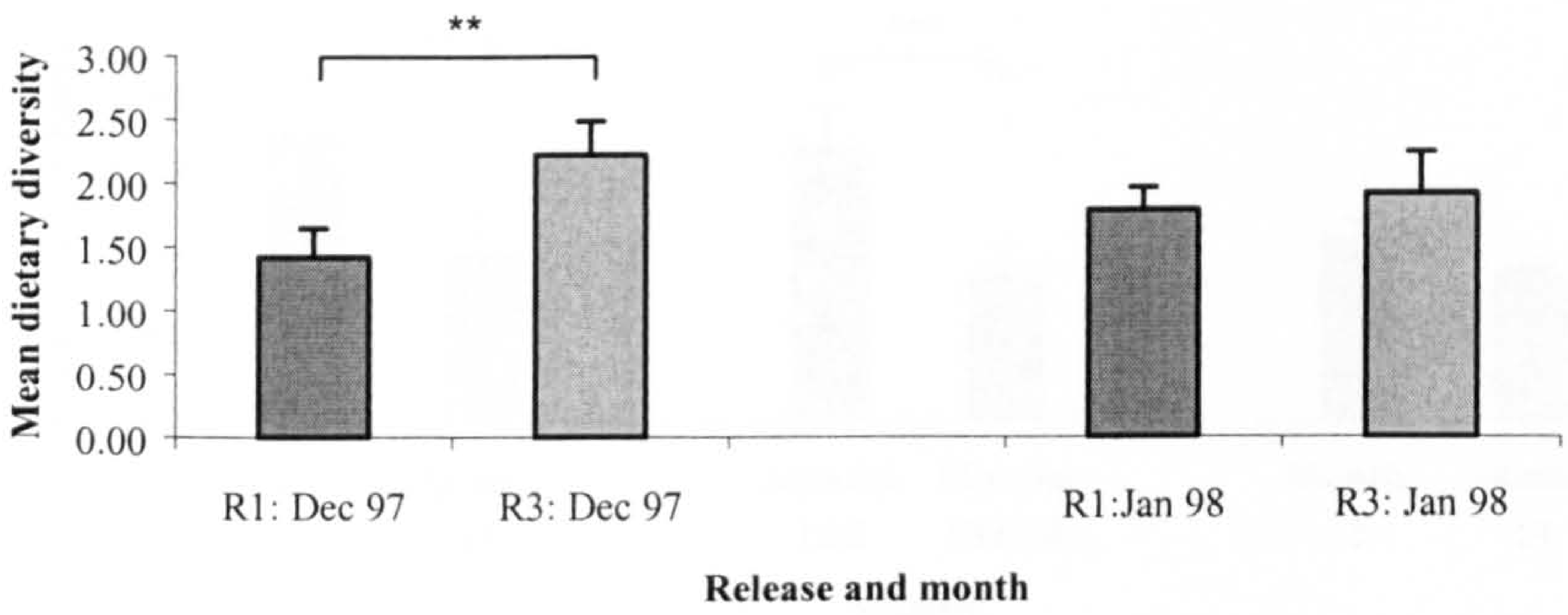
**p<0.01, ***p<0.001

Figure 8.14 Mean dietary richness for chimpanzees with overlapping release months December 1997 and January 1998



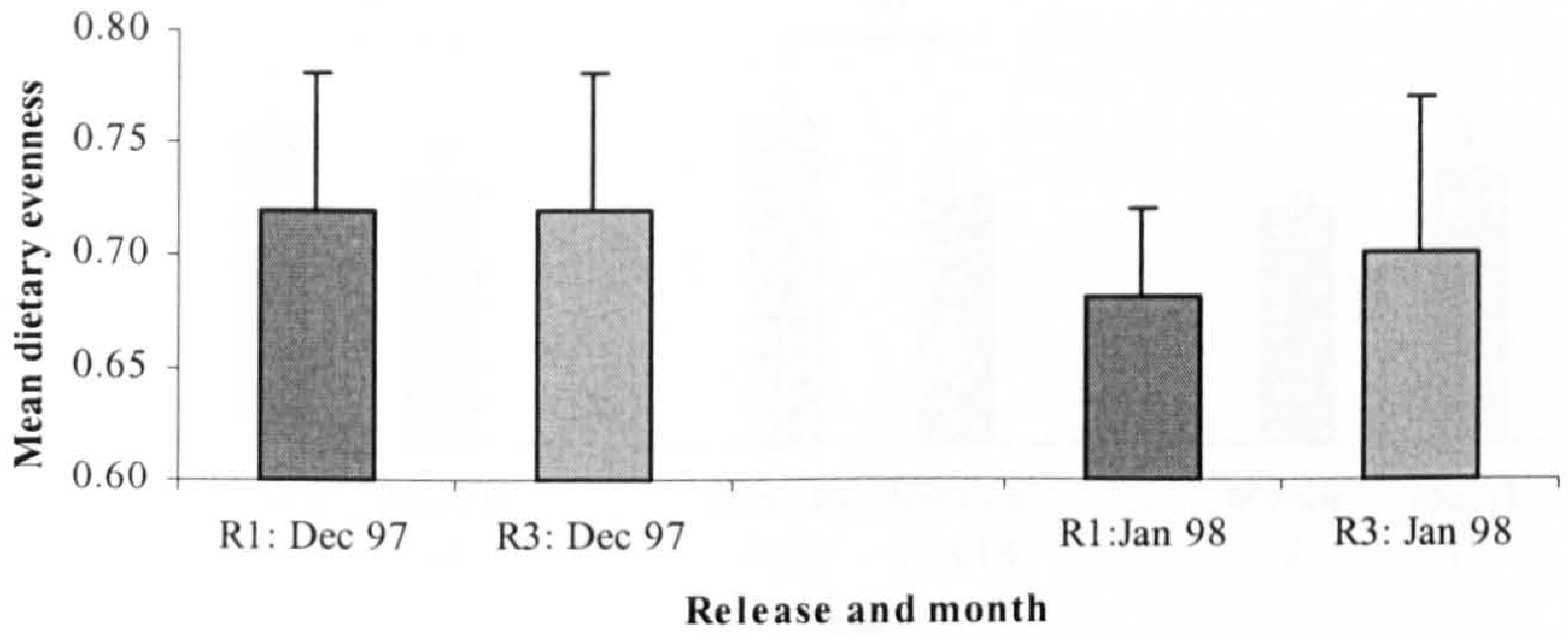
***p<0.001

Figure 8.15 Mean dietary diversity for chimpanzees with overlapping release months December 1997 and January 1998



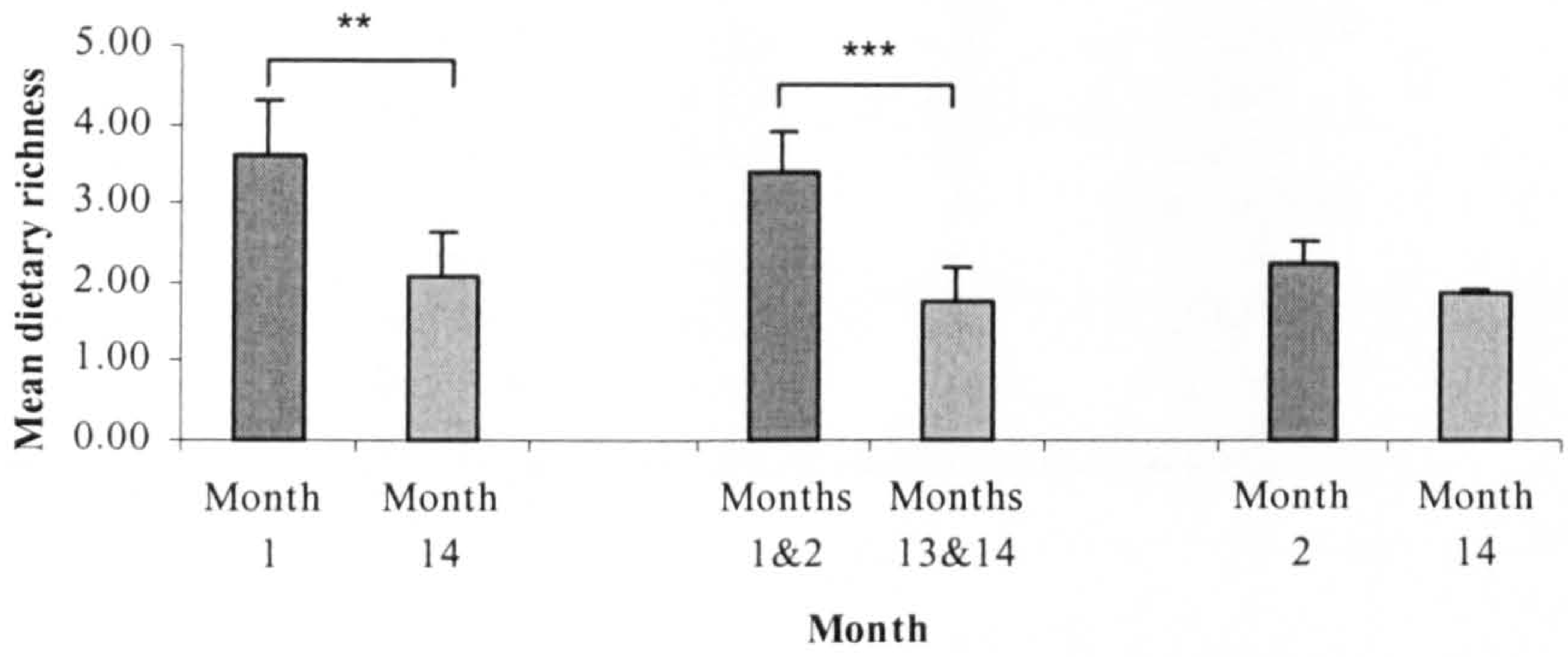
**p<0.01

Figure 8.16 Mean dietary evenness for chimpanzees with overlapping release months December 1997 and January 1998



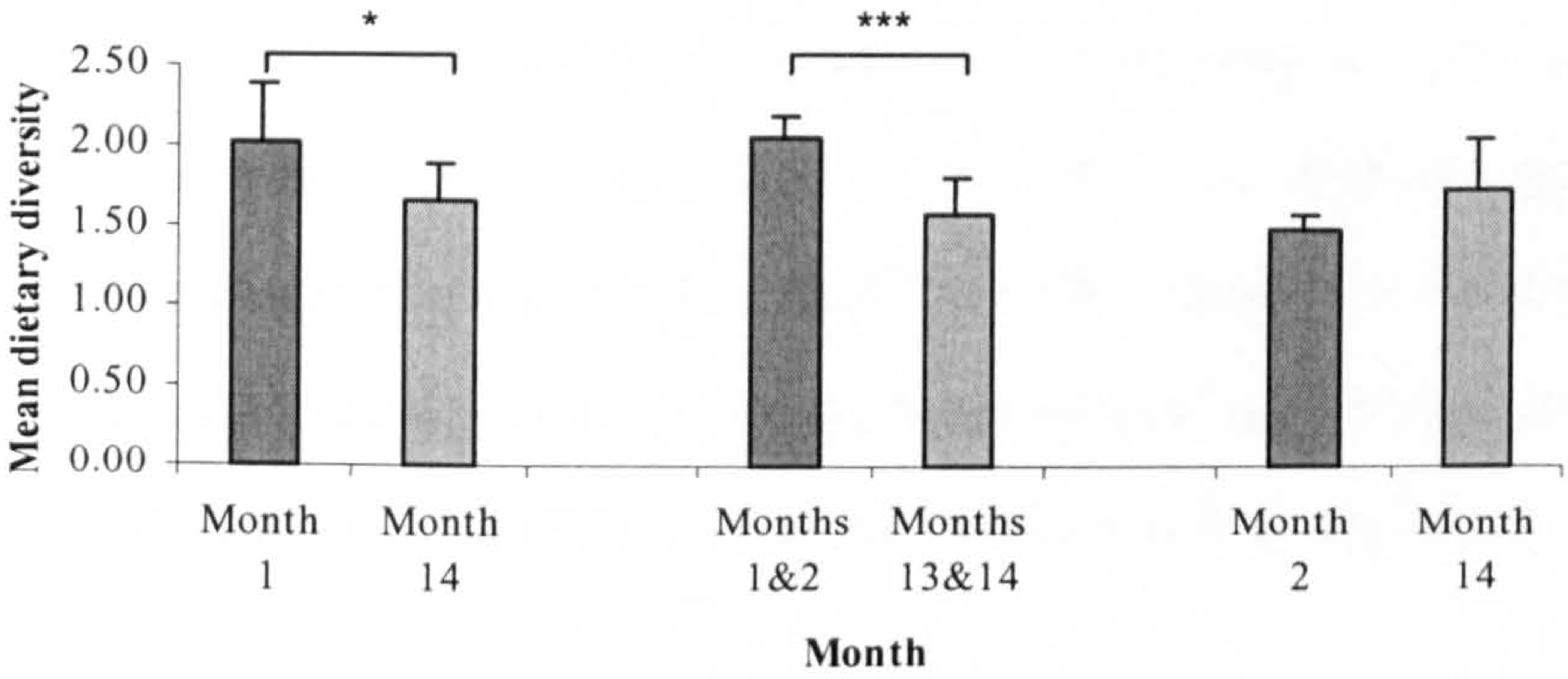
To examine any change in dietary richness, diversity and evenness post-release, the beginning and end of the study period were compared. Dietary diversity and evenness for months 1 and 14 (n chimpanzees=11) and months 1-2 and 13-14 (n=9) were compared using paired samples t-tests, and two-way ANOVA was performed for dietary richness. Dietary richness (Figure 8.17, Table, 8.18) and diversity (Figure 8.18, Table 8.18) were significantly higher in month 1 and months 1-2 in comparison to months 14 and 13-14. The same statistical tests were run comparing months 2 and 14 for R4 (n=3) but no significant differences were found. No significant differences were found in dietary evenness when similar monthly comparisons were made (Table 8.18, Figure 8.19).

Figure 8.17 Comparison of dietary richness at the beginning and end of the post-release study period



*p<0.05, ***p<0.001

Figure 8.18 Comparison of dietary diversity at the beginning and end of the post-release study period



*p<0.05, **p<0.01

Figure 8.19 Comparison of dietary evenness at the beginning and end of the post-release study period

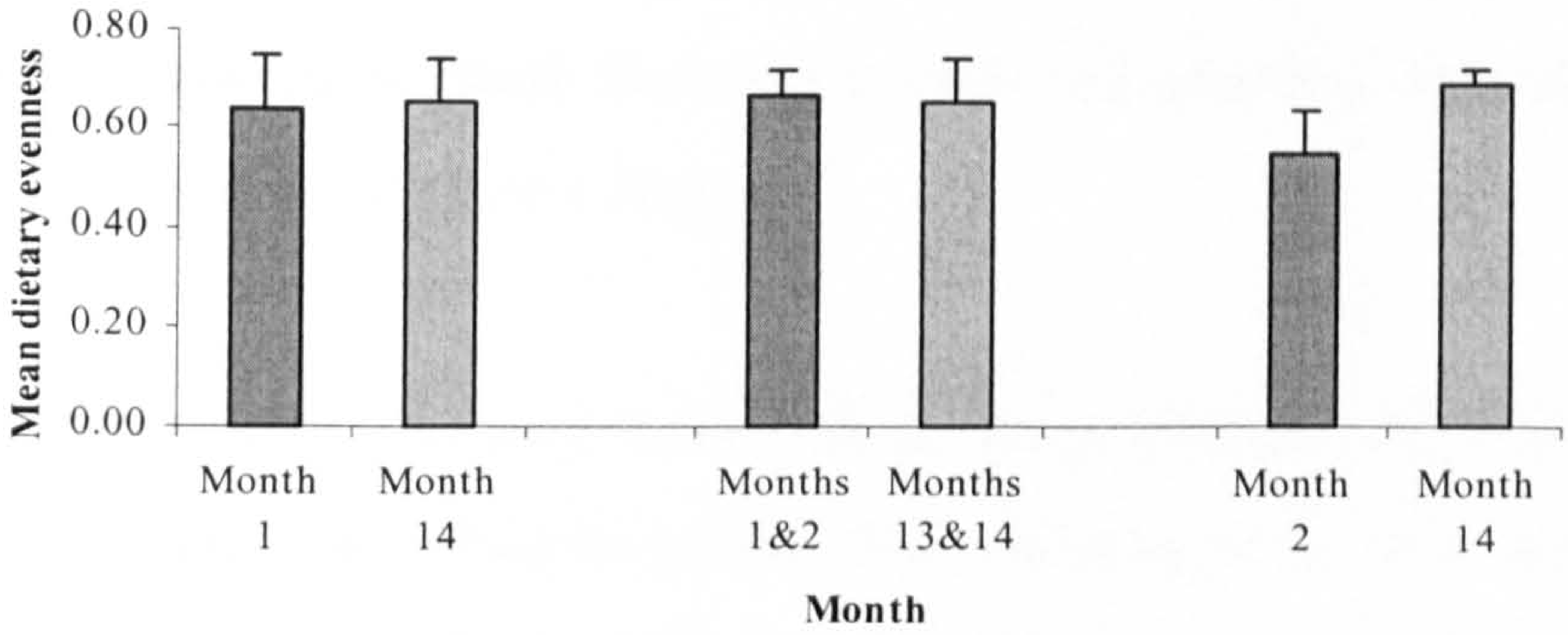


Table 8.18 Results of the paired t-tests performed on dietary diversity and months post-release

Indices	Months	F/t	df	p
Richness	1 and 14	20.92	1,10	0.001**
	1-2 and 13-14	57.88	1,8	p<0.001***
	2 and 14	4.62	1,2	0.165
Diversity	1 and 14	2.43	10	0.035*
	1-2 and 13-14	6.58	8	p<0.001***
	2 and 14	1.21	2	0.351
Evenness	1 and 14	-0.56	10	0.957
	1-2 and 13-14	0.27	8	0.794
	2 and 14	-2.25	2	0.153

*p<0.05, **p<0.01, ***p<0.001

8.4.2.8 Invertebrate and vertebrate prey consumed

Invertebrate prey

Results displayed on Table 8.3 (p.246) highlighted that all the chimpanzees at some point were observed consuming insect matter; that it accounted for a mean percentage of 2.35% (±1.47) time spent feeding and that its consumption did not significantly vary across the dry and rainy season (Figure 8.10, p.259). Invertebrate prey included ants (species or genera not identified) sometimes with nest (soil), caterpillar, centipede, grasshopper, larvae of insect and wasp, wasp, weaver ant *Oecophylla longinpoda* and termite *Macrotermes* sp. Honey from bees nests was also exploited.

The small sample size of insect feeding episodes (n=3790) prevent detailed statistical analyses. However, a Mann Whitney *U*-test did reveal that despite the median number of observations for females (113±499) feeding on insects being higher than males (82±183.50), it did not reach statistical significance (Mann-Whitney *U*-test, N_1=11, N_2=4, *U*=10.50, p=0.1333). The earliest episode of insect consumption was observed at 06h10 and the latest 19h00. However, insects were primarily consumed around midday, at a median time of 11h48 (±0.63).

The chimpanzees were seen to use tools (although infrequently) to extract insects (Plate 8.2, Appendix F describes the events). The chimpanzees had been previously shown how to crack the nut *Elaeis guinnensis* (palm nut) with a wooden baton by observers but not how to extract insects. Jeanette and Choupette could apparently successfully crack open the palm nut but never showed any inclination to repeat the behaviour independently on any species of nut unless provided with both tool and nut (M. Vacher-Vallas, former HELP reintroduction site manager, personal communication, 1999). The present study had originally included in its design attempts to teach chimpanzees released in 1999 to crack the nut *Coula edulis*. However, the nuts were not readily available in the forests and consequently both nut and baton had to be provided. Furthermore, locating a dry spot with suitable anvils in forests that were primarily inundated in nature was extremely difficult.

Plate 8.2 Choupette using a stick to extract termites from a rotten log on the ground (Source: S. Didier and J.M. Krief)

Vertebrate prey

Nine chimpanzees were seen to consume vertebrate prey, accounting for an overall mean of 0.07% (±0.07) time spent feeding. The only male observed consuming vertebrate prey was Koutou (n=9). The total number of observations (n=53) of vertebrate prey consumption consisted of eight separate episodes, six of which occurred in the rainy season. Five chimpanzees were only ever seen consuming vertebrate prey in the rainy season and four chimpanzees in both seasons. When a paired t-test was performed on the mean amount of time spent consuming vertebrate prey in the dry and rainy season for these four chimpanzees a non significant result was found (t=-0.96, df=3, p=0.407). Overall, the consumption of vertebrate prey was observed at a median time 11h50 (± 3.90); the earliest episode at 09h10 and the latest 15h20.

The chimpanzees both directly hunted prey and also found them opportunistically (i.e., consuming the remains of a dead animal) (refer to Appendix G for a description of vertebrate prey consumption and interaction). Vertebrate prey included the following: bird (non-identified species), bird eggs (non-identified species), flying squirrel (*Anomaluridae* family), owl (non-identified species), pangolin (probably *Phataginus tricuspis*) potto (*Periodicticus potto*) and tortoise (*Kinixys erosa*) (Plates 8.3-8.5).

Plate 8.3 Jeanette hitting a tortoise against a tree trunk to try and break the shell (Source: S. Didier and J.M. Krief)

Plate 8.4 Jeanette using a twig to poke at the body of the wounded tortoise (Source: S. Didier and J.M. Krief)

Plate 8.5 Jeanette attempting to get at the body of the tortoise with her teeth (Source: S. Didier and J.M. Krief)

8.4.2.9 Drinking

Chapter 6 highlighted that drinking accounted for an overall and daily mean 0.07% (n=188) of general activity (p.140). However, data on drinking behaviour were not reliably collected except for chimpanzees released in February 1999. All chimpanzees n=14) except Hinda were observed drinking at some point. From the data available, drinking bouts occurred at a median time of 12h05 (±0.32) the earliest bout was observed at 06h40 and the latest 17h30.

The chimpanzees were observed drinking from holes and depressions in tree trunks and branches directly with the lips (n=47). It was not always noted which method was employed to obtain the water from these holes and depressions but on one occasion a chimpanzee was observed scooping water by hand from a hole in a tree trunk (Plate 8.6 and 8.7) and on two occasions a leaf sponge was used. On one other occasion a chimpanzee was observed sucking water directly from a leaf. The chimpanzees were also observed to crouch down and drink water directly from rivers (n=14), swamps (n=25) and depressions in the ground made by elephant prints (n=9).

Plates 8.5 and 8.6 Choupette scooping water by hand from a crevice in a tree trunk (Source: S. Didier and J.M. Krief)

A paired t-test was performed on the amount of mean time that the chimpanzees spent drinking in the dry and rainy season. The chimpanzees were surprisingly found to spend significantly more mean time drinking in the rainy season (t= 3.40, df =7, p=0.011).

8.4.2.10 Coprophagy and Uriposia

Coprophagy

Overall, the reintroduced chimpanzees were observed to engage in coprophagy for a mean 0.89% (total n=2773) of their overall activity budget (Chapter 6, p.140). All the chimpanzees (n=15) were observed performing this behaviour at some point with individual differences. For example, Mekoutou was observed performing this behaviour the most frequently, accounting for a mean of 3.17% (n=628) of total activity budget whereas Agathe was observed performing this behaviour only for a mean of 0.33% (n=52). The chimpanzees ingested their own faeces immediately after defecating into their hand and occasionally the faeces of another chimpanzee. On some occasions the whole stool was eaten however, on other occasions seeds were removed and consumed. A paired t-test was performed on the mean time that chimpanzees performed coprophagy in the dry and rainy season. The chimpanzees performed this behaviour significantly more in the rainy season (t= 4.43, df=13, p=0.001).

Uriposia

Overall, the reintroduced chimpanzees were observed to engage in uriposia for a mean 0.03% (n=39) of their overall activity budget (Chapter 6, p.140). The chimpanzees were observed urinating directly onto their hand and then licking the urine from the hand and also licking urine from the ground. On one occasion a male was observed drinking from his own up-jetted stream of urine. Although ten chimpanzees were observed performing uriposia at some point, only three performed this behaviour in both the dry and rainy season. Four chimpanzees performed this behaviour only in the dry season and six in the rainy season. Due to the small number of chimpanzees that performed this behaviour in both seasons statistical analyses could not be performed.

8.5 Discussion

This section discusses the diet of the reintroduced chimpanzees in relation to study length, sex, pre-release island, diurnal hour, and environmental variables. Each sub-section compares the diet of the reintroduced chimpanzees to data on wild populations and other reintroduced populations where available and applicable.

8.5.1 Pre-release diet

Due to restricted access on all islands pre-release it was not possible to make a detailed inventory on available plant species and the amount of time spent consuming different species, food types and items. From ad lib observations it is possible to say that pre-release the chimpanzees were exposed to some plant species that were known to be edible and available post-release. It seems likely that the chimpanzees did consume plant species other than those that they were observed eating and some more regularly than others. This is suggested by their immediate adaptation from a supplementary diet to foraging and consuming sufficient food types and items to sustain themselves post-release. The overall finding that consumption of plant species varied between the chimpanzees on each pre-release island, between the reintroduced chimpanzees at Conkouati and wild chimpanzees, and between wild populations, highlights how diverse diet can be.

8.5.2 Post-release diet

8.5.2.1 Plant species consumed post-release

Inter-site comparisons are often confounded by incomplete knowledge of endemic flora species and the number of food items recorded can vary between habitat and duration of study. For example, after a seven-year survey Nishida (1974) listed 205 foods in the diet of chimpanzees of the Mahale Mountains, but following a further eight years the list had increased to 328 (Nishida and Uehara, 1983). Likewise, Wrangham (1977) found that the number of food types he recorded per month were related to observation time. After a five-year study at Mt. Asserik, Senegal, the diet of chimpanzees comprised only 43 plant species (McGrew et al., 1988). However, it was estimated from the food species eaten by other primate species that this list could include a maximum of 122 items (McGrew et al., 1988). Another confounding variable that may bias results is methodology of data collection, for example, indirect observations (e.g., faecal sampling) versus direct observations of chimpanzees feeding (McGrew et al., 1988). For example, plant parts such as flowers that are mostly soft tissue or parts that are ground to indistinguishable fragments (e.g., leaves) will be underrepresented (McGrew et al., 1988). The three studies on wild chimpanzees shown in Table 8.2 (p.243) used direct and indirect methods to assess plant species consumed, whilst at Ipassa chimpanzees were observed directly. The length of study and the plant lists in these studies do not show a linear relationship. In fact at Ipassa, the site with the shortest study length, identified the highest number of plant species consumed. The additional advantage of being able to observe a habituated group of chimpanzees at Ipassa (and the present study) may confer some bias. However, as wild chimpanzees at Lopé were seen consuming an almost comparable number of plant species (n=141) to chimpanzees at Ipassa, this difference may simply reflect the greater number of edible species available at both these sites in Gabon. In the present 14-month study employing direct observation of chimpanzees feeding, 62 plant species were identified upon which the reintroduced chimpanzees were seen to feed, a further 28 were identified to genus, and an additional 38 non-identified species were consumed where neither the genus nor family were distinguished. Furthermore, 0.48% of time was spent feeding on parts from plant species labelled 'not known'. Therefore the figure of 122 plant species consumed is conservative; it seems likely that more than one species within each genus (e.g., *Ficus* sp.) and family (e.g., *Marantaceae*) and life form (e.g., liana) were consumed and likewise may reflect a large number of edible plant species in the area. Dietary studies on wild populations in Conkouati and neighbouring areas would present an ideal comparison to the reintroduced chimpanzees.

However, as a guideline, it can be useful to compare diet between wild chimpanzee sites and in the present case to a group of reintroduced chimpanzees to provide an indicator of an expected number of species, parts etc., that one might expect to be consumed. The number of plant species upon which wild chimpanzees feed ranges from 48 at Kahuzi-Biega (Yumoto et al., 1994), 64 at Nouabalé-Ndoki (Moutsamboté et al., 1994) to 141 at Lopé (Tutin et al., 1994), 151 for the reintroduced chimpanzees at Ipassa (Hladik, 1977) and 122 at Conkouati. A greater number of edible species at Lopé, Ipassa and Conkouati in comparison to Kahuzi-Biega and Nouabalé-Ndoki is probably reflected in these figures. However, it does indicate that the reintroduced chimpanzees at Conkouati were able to locate and feed upon a comparable number of plant species to wild chimpanzees, in particular to chimpanzees at Lopé, an area considered similar in habitat and vegetation type to the Conkouati-Douli National Park. Therefore, the reintroduced chimpanzees, in common with wild communities had a broad diet. Moreover, they concentrated their feeding time on a small number of species. Over 80% of feeding time was accounted for by consumption of 13 plant species and a further 8 identified to genera, 1 to family and 2 to life form; such specialisation has also been observed in wild communities (Tutin and Fernandez, 1993; Wrangham et al., 1996; Newton-Fisher, 1999; Fawcett, 2000).

Comparability of the availability and consumption of plant species between sites can reveal much about diet; some plant species were available in all sites but were consumed at some and not others. Some species consumed by wild chimpanzees and available at Conkouati were not consumed. Likewise although some species were available at more than one wild chimpanzee site they were not always eaten. These figures may reflect variation in vegetation density and hence consumption, but ultimately illustrate there is not just 'one' diet suitable for chimpanzees but that a wide and varied array of species can provide the necessary nutrients to sustain chimpanzees surviving on the consumption of natural vegetation.

8.5.2.2 Plant parts consumed

Interestingly, the reintroduced chimpanzees were seen to consume 239 parts from the 122 plant species consumed, a substantially higher number than chimpanzees at Lopé, Ipassa, Nouabalé-Ndoki and Kahuzi-Biega. Despite the large number of plant parts sampled they were not regularly consumed; the majority of plants were exploited primarily for one part. In the wild infant chimpanzees learn which foods to eat through observing their mothers. Deprived of their mothers from a very young age, the reintroduced chimpanzees when confronted with potential plants from which to feed may sample more parts in an attempt to assess what is and is not edible, a skill that normally would be facilitated through observation. Furthermore, the chimpanzees would have been confronted with a large array of plant species not known to them and inexperience of these species may help to explain the sampling of their many parts. By comparing parts consumed from the same plant species it can be seen that variation exists between sites and not only between the reintroduced and wild communities. The reintroduced chimpanzees at Ipassa also consumed more plant parts of the same species consumed by all three wild communities lending some support to the earlier suggestion of increased sampling of plant parts by chimpanzees deprived of their mothers from a young age and inexperience of plant species. The overall pattern of dietary richness and diversity stabilising post-release may offer this argument support. Differences are also apparent although to a lesser extent between wild communities. This again highlights variation in diet diversity between communities.

In agreement with all studies on wild populations fruit dominated the diet of the reintroduced chimpanzees; it accounted for over 50% of their diet. Fruit consumption in wild communities has ranged from 45-79%. The Conkouati community devoted over 20% of their time to leaf consumption and 17% to stem pith consumption. Percentage of leaf and stem pith consumption varies between sites considerably; leaf consumption has ranged from 2.6-20% and 2-3% for stem pith, highlighting that the reintroduced chimpanzees consumed more stem pith than seen in all wild communities. This may be a consequence of species variation and density of herbaceous vegetation, low variation/density of fruiting species and/or a combination of nutritional and environmental determinants.

Females and males, and chimpanzees released from Yombe and Yvette Island all significantly consumed more fruit in comparison to leaf and stem pith but no differences were found between the sexes and islands in terms of time spent consuming plant parts. That no difference was found in the amount of time consuming fruit, leaf and stem pith consumption between pre-release islands suggests that all the chimpanzees were exposed to a variety of life forms, plant species and parts to consume. Studies on wild communities have found some difference in plant part consumption between females and males but this has tended to concentrate on ripe versus unripe fruit and young versus mature leaves, a distinction that was not made in the present study. It is possible that the high number of females to males and their age are influencing factors. During adolescence male chimpanzees in the wild would normally be spending increasing amounts of time associating with other males, and these associations as highlighted in the introduction are likely to have an influence on diet. Such associations are not readily available to the small number of adolescent male reintroduced chimpanzees. Wild females start to show regular sexual swellings, travel with adult males and occasionally make temporary transfers to neighbouring communities. The reintroduced females would need to seek a wild community in order to associate with fully mature adult males and therefore transfer would be increasingly likely. However, recently Choupette gave birth and Mekoutou, an adolescent male, has been identified as the father.

8.5.2.3 Hourly variation in food selection

Fruit consumption dominated every hour of the day. However, fruit consumption was at its highest during the early morning, whereas stem pith consumption was at its highest around the middle of the day and leaf at its peak consumption in the afternoon. This pattern of increased exploitation of plant products in the morning and plant parts in the afternoon is reflected in most wild communities. This indicates that the reintroduced chimpanzees, like their wild conspecifics, were successfully responding to energy and digestive influences, and differences in item quality.

8.5.2.4 Seasonal variation

Chapter 6 revealed that the chimpanzees spent significantly more time feeding and less time resting in the dry season. Less time spent resting was explained in terms of increased allocation of time to feeding during a season characterised by scarce resources. Studies on wild communities have revealed varying strategies to coping with periods of scarce resources. Reduction in food availability may result in increasing time spent foraging and feeding or feeding on a broader range of lower quality items. Terrestrial vegetation and leaves have been identified as main fallback foods for some communities during periods of food scarcity. However, the reintroduced chimpanzees did not significantly differ in their consumption of fruit, leaf and stem pith in the dry and rainy season. The chimpanzees were able to maintain a diet dominated by fruit in both seasons. Stem pith was consumed at a slightly higher mean level in the dry season (although not significantly). Leaf consumption also remained at approximately the same levels between the two seasons. This indicates that for the reintroduced chimpanzees these fibrous foods were more representative of keystone and not fallback foods. Wrangham et al. (1996) also suggested that THV may play a nutritional role beyond being a fallback food. That the reintroduced chimpanzees were able to maintain a diet dominated by fruit may suggest that the dry season in Conkouati is not as severe as in other regions such as Lopé where wild chimpanzees were seen to increase consumption of vegetative foods. However, although fruit consumption did decrease at Lopé during the dry season, the chimpanzees there were able to maintain a diet of some fruit by depending heavily on the continuously available *Elaeis guinnensis* (Tutin et al., 1991). *Elaeis guinnensis* was consumed regularly in both seasons by the reintroduced chimpanzees but at a slightly higher median level in the dry season. *Staudia gabonensis* and species from the genus *Vitex* were primarily exploited for their fruits and approximately twice as much time was spent consuming these fruits in the dry season. In contrast, *Scytopetalum klaineanum*, *Irvingia gabonensis*, *Grewia obigoneura* and *Dialium* no.47, species also primarily exploited for their fruit, were all consumed at much higher levels during the rainy season. That the reintroduced chimpanzees spent significantly longer periods of time feeding in the dry season and yet were able to maintain a diet of fruit implies that their feeding efficiency was reduced during this season; they were having to feed for longer to obtain equivalent amounts. Chapter 7 revealed that significantly more time was spent feeding at heights above 15m in the dry season; this may offer an explanation as to why the chimpanzees were feeding more in the dry season if the fruits were more widely dispersed.

It seems likely that patterns of food availability change from year to year resulting in important differences in diet (Hladik, 1977). However, monthly variation in dietary richness, diversity and evenness was relatively comparable between chimpanzees and release years; slight variations between years can probably be explained by productivity. Decreases in dietary richness, diversity and evenness were seen in and around the dry season months. This indicates that the proportion of each species consumed and time spent feeding on the species did fluctuate seasonally. As mentioned in the methods section of this chapter, caution must be taken when interpreting these results in particular for dietary richness. Comparison of the two-month overlap between chimpanzees released in1996 and 1997 revealed a significantly higher level of dietary richness and diversity for the chimpanzees newly released in comparison the chimpanzees that had already spent one year in the forest. One possible explanation is that as a consequence of initial guidance by observers to areas known to be high in fructification at that particular time, this may result in them ranging further and sampling more foods. Alternatively, perhaps they simply did not know what to eat and initially sampled more widely. When levels of dietary richness and diversity were compared at the beginning and end of the study period (for release one and three) the chimpanzees had a significantly lower level of richness and diversity in their diet by the end of the study period. This could be a consequence of the proposed initial wide sampling of plant species becoming gradually refined.

8.4.2.5 Invertebrate and vertebrate prey

Insect and mammal prey consumption by wild chimpanzees at Lopé constitutes a respective 6% and 2% of their overall diet (Tutin et al., 1991), at Budongo insects constitute 3% of diet (Newton-Fisher, 1999), termites 4% at Okorobiko-Matama (Sabater-Pi, 1979) and animal matter 4% at Ipassa (Hladik, 1977). In the present study insect consumption accounted for a mean 2.35% of overall diet and vertebrate prey 0.07%; lower levels than those found for wild communities. Due to the prevalence of females in the present study one may have expected insect consumption to be higher but no differences were found in rates of consumption between males and females. Unfortunately insects were not identified to specific species and this prevents possible discussion on comparisons of species consumed across sites. An earlier report following the immediate post-release period of chimpanzees released in 1996 identified five species of ants eaten and two species of termites (Paredes, 1997). The most frequently eaten was the weaver ant (*Oecophyla* sp.) and others ants consumed were from *Macromoscoides* sp., *Polyrhachis* sp., *Camponotus* sp. and *Crematogsater* sp. The two species of termites eaten were *Nasutitermes* sp. and *Procubitermes* sp. All the reintroduced chimpanzees consumed insects and there was no difference in rates of consumption across seasons. Interestingly, both invertebrate and vertebrate prey were consumed around approximately midday, similar to what has been found in wild communities, lending some support to the argument that exploitation of fauna is more likely to occur when energy levels are still high but basic satiation satisfied (Teleki, 1981).

The number of vertebrate species hunted at wild chimpanzees sites varies from 16 at Mahale (Uehera et al., 1992) to eight at Gombe (Goodall, 1986) and six at Tai (Boesch and Boesch, 1989). In the present study a minimum number of five species were consumed although on at least one occasion the animal (an owl) was found dead and opportunistically consumed. Numerous cases of scavenging or piracy have been recorded at Gombe (Morris and Goodall, 1977; Goodall, 1986) and Mahale (Hasegawa, Hiraiwa, Nishida and Takasaki, 1983; Muller, Mpongo, Stanford and Boehm, 1995; Uehera, 1997). However, instances of chimpanzees feeding on carcasses that they have not killed themselves or seen killed are rare (Hasegawa et al. 1983; Goodall, 1986). There are obvious potential dangers of feeding on carrion of unknown origins; the dead animal may have died of a disease that could be transmissible by consumption.

The overall low level of hunting may be a consequence of the high number of young females in the present study. Hladik (1973) used the same argument to explain low levels of hunting on large mammals. However, in the present study only one male

(Koutou) in comparison to eight females was seen consuming vertebrate prey and the particular hunt in question was initiated by a female (Sophie).

Tool use was observed to obtain insects on a small number of occasions resulting in both successful and failed attempts. The small number of cases observed may reflect a deprivation in learning this skill due to removal from their natal group during the first year of life. In the wild it is at approximately three years of age when skilled adult level activities with objects are first observed (Goodall, 1968). However, one female chimpanzee immediately and successfully started to crack nuts when released onto an island in Liberia, and this behaviour gradually spread throughout the group (Hannah and McGrew, 1991). This chimpanzee had been taken from the wild when she was aged approximately one year and had spent eight and a half years at the laboratory before being released (Hannah, 1989). Furthermore, tool use and type is known to vary between sites, and evidence of tool use by wild chimpanzees in the area has yet to be identified. However, if the limited tool use displayed by the reintroduced chimpanzees is representative of nearby wild communities, then this may represent a local tradition. Wild chimpanzees in the Ituri Forest (DRC), in common with the reintroduced chimpanzees, have been reported to use sticks to gorge out the contents of tortoise shells (J. Hart, personal communication, cited in McGrew, 1992).

8.5.2.6 Drinking behaviour

Observations of drinking behaviour are not commonly described in wild communities primarily due its infrequency that requires intensive follows of habituated groups. However, from the small amount of literature that exists it is possible to say that the reintroduced chimpanzees obtained water by similar methods (see introduction) employed by wild populations; from holes in tree trunks, leaf sponges, and drinking directly from rivers and swamps. The reintroduced chimpanzees also were seen to drink water from depressions made by elephant foot prints, this has not been described in any studies on wild chimpanzees. However, the reasons for its absence may be ecological rather than cultural (Whiten et al., 1999). Gombe, a site of long-term data collection on habituated groups of wild chimpanzees has no elephants. It seems likely that given the nature of tropical rain forests that where chimpanzees and elephants coexist, this behaviour does occur but perhaps has not been observed due to the small number of sites that have managed to habituate groups of wild chimpanzees.

In contrast to wild conspecifics the reintroduced chimpanzees spent significantly more time drinking in the rainy season. The Triangle is an area characterised by seasonally flooded forest types and it is likely that this behaviour may be more visible in the rainy season and bias results. Furthermore it was only during Release 4 that data on drinking behaviour were reliably collected.

8.5.2.7 Coprophagy and uriposia

Although incidences of these behaviours occurred infrequently, due to the debate that centres on why they do and do not occur, they are included. All the chimpanzees performed coprophagy although some more than others. An unpublished study conducted on the chimpanzees released in November 1996 and January 1997 examined coprophagic behaviour in detail during their first three months post-release (Didier, Roeder, Krief, Poullet and Jamart, unpublished manuscript). The authors found a positive correlation between coprophagy and *Dialium* sp. consumption. They argue that this behaviour does not reflect food deficiency, food scarcity, lack of fibre or boredom but an adaptation to increase protein intake; seeds of *Dialium* sp. are known to contain high levels of crude protein. Wild chimpanzees have also been observed indulging in this behaviour during the fruiting season of *Dialium* sp. at Lopé (Voisey, 1995) and numerous nutritional studies suggest that protein content is positively correlated with food selection (e.g., Matsumoto-Oda and Hayashi, 1999). In the present study coprophagic behaviour was significantly higher in the rainy season and it is interesting to note that the species *Dialium* no.47 was consumed primarily in the rainy season. Furthermore, over half of all uriposia incidences occurred in the rainy season. Lambert

(2000) recently described this behaviour in wild red tail monkeys and argued that it may serve to balance protein deficiencies as up to 50% of urine is composed of nitrogen rich urea. Perhaps the reintroduced chimpanzees in performing these behaviours were compensating for a diet that for whatever reason was lacking in sufficient levels of protein.

8.6 Conclusions

- Pre-release the chimpanzees were exposed to some edible vegetation that was available post-release.
- The post-release diet was comparable to diets observed in wild chimpanzees. Fruit dominated the diet, included 122 plant species (conservative number) and invertebrate and vertebrate prey. Over 70% of the diet could be accounted for by a small number of plant species; similar broad diets with a specialisation on a small number of species is also seen in wild chimpanzees. Some differences between the reintroduced and wild chimpanzees were apparent but this chapter has highlighted how diverse diet can be, and that it varies not only between reintroduced and wild chimpanzees but also between wild communities.
- A comparatively larger number of plant parts were consumed by the Conkouati chimpanzees in comparison to wild chimpanzees at three sites. The same was true for the reintroduced chimpanzees at Ipassa (although to a lesser extent). This wide range of sampling may reflect inexperience of what parts are and are not consumed and is supported by differences in dietary diversity between the first and last two months of overlapping release periods.
- Some studies on wild populations imply that biases may exist in the number of plant species identified as a consequence of length of study and methodology employed. However, in the present relatively short-term 14-month study, a large number of plant species were identified. The possibility to follow a group of habituated chimpanzees likely facilitates the identification of species consumed but probably

also reflects a greater number of edible species. The implication is that with time the number of plant species consumed will increase.

- The present data set is lacking in botanical detail (and species identification of invertebrate prey) and measures of species availability and density. Future releases should incorporate these measures in order to provide more comprehensive measures of dietary breadth and diversity. Studies of local wild chimpanzee diet would provide a more accurate comparison of dietary preference and breadth to the reintroduced chimpanzees at Conkouati than to wild populations at other sites.
- No significant differences in plant part consumption were found between females and males, and chimpanzees released from Yombe or Yvette Island.
- Hourly variation in plant part consumption indicates that although fruit consumption dominated every hour of the day, the reintroduced chimpanzees, like their wild conspecifics, tend to eat more fruit in the morning and leaf/stem pith in the afternoon. Furthermore, consumption of invertebrate and vertebrate also peaked around midday and a similar finding has been seen in wild communities.
- The chimpanzees managed to maintain a diet of fruit throughout the dry season; different species were exploited in the dry and rainy season. The consumption of fibrous vegetation; stem pith and leaf, also remained constant across the seasons implying that these parts are more representative of keystone and not fall back foods.
- The reintroduced chimpanzees were observed obtaining drinking water by similar methods employed by wild chimpanzees; from holes in tree trunks, leaf sponges and directly from rivers and swamps. Furthermore, a new behaviour was observed not previously described in chimpanzees; they drank water from depressions made by elephant prints.
- On a small number of occasions the chimpanzees were seen using tools to obtain insects and water. As all the chimpanzees are thought to originate from the Kouliou region in which the Conkouati-Douli National Park is based, this behaviour may

represent a local tradition in nearby wild communities and warrants further investigation.

- Coprophagy and uriposia were performed on a small number of occasions; coprophagy significantly more so in the rainy season. Its occurrence may be related to diet.
- The reintroduced chimpanzees were able to adapt nutritionally post-release; they responded to environmental changes, obtained a broad and diverse diet, and ultimately survived the change from a diet that was primarily supplemented to one that required the ability to forage independently. The ability to adapt behavioural strategies to changing social and ecological challenges likely results and reflects a combination of social group living (exposure to experienced individuals pre-arrival to the sanctuary and on the pre-release islands) and to a wide array of edible natural vegetation (pre- and post-release). Their long-term post-release survival is the best indicator of their dietary success.

Another behaviour necessary to survive in the natural environment is the ability to build nests and the following chapter will examine if the reintroduced chimpanzees successfully demonstrated this skill.

Chapter 9

Nesting behaviour

9.1 Introduction

A feature of chimpanzee behaviour in the wild is the fabrication of nests (also known as beds or platforms) as sleeping sites (Plate 9.1). Goodall (1962) described how a nest basically consists of a main branch or branches forming the foundation, over which smaller branches or 'crosspieces' are bent. The chimpanzee, standing on the foundation bends the crosspieces down over the foundation, holding them in place with her/his feet whilst secondary crosspieces are bent over in a similar manner. The chimpanzee finishes the nest by bending in the small leafy twigs that project from the larger branches, to provide extra support and comfort. Detached twigs are sometimes added for lining.

Plate 9.1 A chimpanzee at the HELP sanctuary resting in a day nest

Chimpanzee nests are normally made off the ground in vegetation (Nissen, 1931; Goodall, 1962; and Jones and Sabater Pi, 1971) although nests built on the ground have been documented (Izawa and Itani, 1966; Reynolds and Reynolds, 1965; Goodall, 1968; Matsuzawa and Yamakoshi, 1996; Maughan and Stanford, 2001). Normally a nest is constructed, immediately used, and then abandoned. All weaned individuals build a new nest every night, although occasionally old nests are re-used and in such cases old nest material is usually supplemented or reworked (Goodall, 1962). Re-use has been found to occur more frequently in drier habitats where nesting materials are limited (Hiraiwa-Hasegawa, 1989). A group may sleep in the same general area for two or three nights in succession (Rahm cited in Baldwin, Sabater Pi, McGrew and Tutin, 1981). Chimpanzee members converge at dusk and nest at night within groups, named 'nest parties'. A group may all nest in the same tree, or at least in close proximity. Although there seem to be preferred trees types, these do not necessarily seem to be the strongest or most suitable and occasionally nests are made using the intertwined branches of two or more small trees, and these are known as 'integrated' nests. The maximum number of trees used to make a single nest is four, although two is more common (Fruth and Hohmann, 1996).

Nests are occasionally made during the day when apes are resting (Baldwin, 1979) and these are more frequently made on the ground (Goodall, 1962) by female chimpanzees (Hiraiwa-Hasegawa, 1989). Recent evidence suggests that there is clear structural and functional distinction between day and night nests. Brownlow, Plumptre, Reynolds and Ward (2001) describe day nests as rest stops between daytime feeding episodes due to their predominance within feeding trees or nearby sites, and that they are weakly constructed or more frequently re-used nests in comparison to night nests. In addition to nests being built during the day for resting and to sleep in at night, nests are also built during social contexts such as play and agonistic encounters (Fruth and Hohmann, 1994) or during encounters with humans (Reynolds and Reynolds, 1965).

Studies with captive chimpanzees suggest that some kind of appropriate early experience may be necessary for the development of nest building behaviour (Bernstein 1962). In the wild there is a great deal of opportunity during infancy for the chimpanzee to learn nest making, facilitated by observation and practice. During the final year of suckling (2-3 years of age as defined by Goodall) infants often build their own night nests. However, they do not typically sleep in them until a new sibling is born but continue to sleep with their mother in her nest (Clark, 1977, cited in Anderson, 1984). Infant chimpanzees have been known to sleep with their mothers for up to five and a half years. During this time the young chimpanzee has nightly opportunities to watch her nest building, representing over 2000 possibilities to observe nest building (Baldwin et al., 1981). Chimpanzee infants make day nests ten times more frequently than do adults (Hiraiwa-Hasegawa, 1989), starting as young as eight months of age by building rudimentary nests in play (Goodall, 1962). Many skills and behaviours important in the life of the individual are developed and practised in playful activity long before they are ever used in adult life (Dolhinow and Bishop, 1972).

Comparison of nesting behaviour between sites and sub-species

Studies of single chimpanzee communities have described nest height, tree species used and sex differences (Brownlow et al., 2001). However, the potential for variability in nest building patterns between independent wild populations exists if, as studies suggest, the behaviour includes both innate and learned components (Bernstein, 1962; Lethmate, 1977). By comparing data between chimpanzee populations and subspecies it may be possible to identify links between environmental conditions and nest building. For example, Goodall (1968) reported a temporary fashion for building nests in palm trees among chimpanzees at Gombe which Wrangham (1975, cited in Fruth and Hohmann, 1994) argued reflected a seasonal variation in available materials. Kortlandt (1996) argued that nests made in palm trees occur only in areas where more comfortable sleeping opportunities were not available, but a recent survey by Ham (1997) found that chimpanzees in Guinea seemed to prefer nesting in oil palm trees even when other species of tree were available. Such comparisons may help to elucidate the importance of single factors such as hunting pressure on particular aspects of this behaviour (e.g., nest height), and to select those features that are most likely to represent local culture. McGrew (1985) argued that tradition may be a factor as palm trees are used at one site and not at others. It was with such discussion in mind that Fruth and Hohmann in two review papers (1994, 1996) compared nesting characteristics between the great apes, categorising the results in tables according to species, subspecies, country, and study site. Data used were largely derived from censuses designed to estimate population densities using nest numbers and age (Tutin and Fernandez, 1984). Despite the available field study data being fragmentary, and in the majority of cases collected for only short periods of times and from abandoned, anonymous nests of unknown age, differences were found. Fruth and Hohmann (1994) found that all species showed some subspecies differences in nest building behaviour. For example, chimpanzees at Gombe (*Pan troglodytes schweinfurthi*) and Bossou (*Pan troglodytes verus*) built nests in oil palms but others did not. Baldwin et al. (1981) also compared two populations of chimpanzees and found that Senegalese chimpanzee nests (*Pan troglodytes verus*) in contrast to the nests made by chimpanzees at Equatorial Guinea (*Pan troglodytes troglodytes),* were higher, more open, more clumped in trees, and often in larger groups. They attributed structural differences to environmental factors and found no evidence of cultural variation in nest building behaviour. Knowledge of behaviour within the vicinity of nesting sites and the factors influencing their construction has important implications for understanding the diversity of adaptive behaviour to the environment. Behaviour in and around nests takes up much of the lives of apes (Anderson, 2000) and may include eating, sex, socialising, giving birth and dying (Fruth and Hohmann, 1996; Yamagiwa, 1998). The following section will examine the main factors proposed to affect nest characteristics.

Environmental influences on nesting behaviour

a. Seasonal availability of food

As a general rule of thumb the nesting area chosen depends almost entirely on the seasonal availability of food, because chimpanzees nest close to the trees in which they happen to be feeding in just before dusk. Despite this, there are certain nesting sites where the presence of old nests, in varying stages of decay, show that a tree or group of trees has been used repeatedly (Goodall, 1962) perhaps indicating a preferred nesting site. It seems reasonable to assume given the amount of time chimpanzees spend at nesting sites (spending approximately half of their life or more in nests), that they are carefully chosen.

b. Tree species of nest building tree

Goodall (1962) found that almost any type of tree may be used for nesting, providing it was taller than 6m in height, fairly well foliaged, and had reasonably supple branches. However, there does seem to be some selectivity at work as some trees are more commonly used (Goodall, 1962; Baldwin et al. 1981; Sept, 1992). A recent study found that five tree species constituted over half of all trees in which nests were made and attributed this to the high density of foliage on branches, making them particularly suitable as nest substrate (Brownlow et al., 2001). It seems conceivable that trees may be selected, at least partly on how fibrous the branches are (Anderson, 2000).

Until recently evidence suggested that although feeding trees bearing ripe fruit were frequently used for day nests, chimpanzees rarely build their night nests within these in order to avoid a restless night in the midst of nocturnal frugivores (Goodall, 1962; Fruth and Hohmann, 1996). However, a recent study has revealed that at least one community of chimpanzees do make nests in fruiting trees used as food sources, and that this nest site choice may be influenced by scarcity of other frugivores and low density of fruit (Basabose and Yamagiwa, 2002).

Ground nests have been discovered at several study sites although the proportion of ground nest to tree nest has overall been small and may simply be a response to unsuitable trees in which to nest (Izawa and Itani, 1966; Reynolds and Reynolds, 1965) or made by sick individuals (Goodall, 1968). Matsuzawa and Yamakoshi (1996) found numerous ground nests at one site, and suggested that the high steep slopes that characterised the area did not provide good tree nesting material.

c. Protection from predators

Goodall (1962) reported that chimpanzees at Gombe seemed to prefer nest sites at forest edges, in trees overhanging gullies or streams, above well-defined routes and sparse undergrowth, with branches no lower than 3m from ground level and overlooking open stretches of country. Such locations may reduce the possibility of attack by a predator. At Mt. Asserik, Baldwin (1979) found that 33% of nests were built with branches occurring lower than 3m off the ground, but only 7% of the nests did not have an alternative escape route to the ground.

One explanation as to why adult male chimpanzees may nest closer to the ground is to offer protection to the group (to females, juveniles and infants above) against predation from ground predators such as leopards and lions. Adult baboons have been reported to do likewise (DeVore and Hall, 1965). A recent study of the Sonso community (Budongo) found that males nested significantly closer to the ground than females, but that both leopards and lions were rare and predation pressure low, although this may not have always been the case (Brownlow et al., 2001). Alternative explanations suggest that males are simply heavier (Brownlow et al., 2001) or that lower ranking chimpanzees or males with a female in oestrus may nest below a higher one to reduce mating competition (Maughan and Stanford, 2001).

d. Climate

During daylight hours chimpanzees frequently move to the base of a large tree to protect themselves from the rain (Nishida, 1980). Surprisingly, chimpanzees have been found to build their nests higher and with reduced canopy cover during the rainy season (Baldwin et al., 1981). However, it has been suggested that open nests may reduce discomfort from dripping vegetation, and provide better exposure to the warming early morning sun (Goodall, 1968; Baldwin et al., 1981). Ground nests in the high altitude areas may be a response to strong winds that would not only be uncomfortable but also dangerous if they cause branches to sway (Matsuzawa and Yamakoshi, 1996).

e. Nest parties

Congregation at sleeping sites may provide an opportunity for dissemination of information among members of nesting groups (Anderson, 1984). Baldwin et al. (1981) found no difference in the minimum distance between nests at two sites regardless of whether the nests had been made in the same trees or separately, and suggested that there may be an optimal distance that would allow easy communication between members of a nesting party. This distance would be one that maintains intra-group contact, but avoids encroachment or a threatening level of proximity. Nearest nest neighbour analyses may reflect inter-individual proximity during the day and social organisation (Fruth and Hohmann, 1994). Group patterns have only been analysed for the gorilla and have found that nest position is related to age and sex classes. However, recent evidence with chimpanzees does not support this suggestion (Brownlow et al., 2001). Nest group size has been attributed to the composition and size of parties formed during the day, which in turn can be attributed to environmental differences such as the distribution of food, water, and available cover (Baldwin et al.,1981).

The rehabilitation of nesting behaviour

The ability to obtain a suitable place to rest and sleep is listed as one of the skills necessary to successfully adapt to a natural environment following release from captivity (Box, 1991b). Captive environments vary in the extent to which they provide challenges, but generally they do not imitate the pressures confronting primates living in the wild, or reflect adaptive behaviour that has a 'real' consequence depending on whether an action is correctly performed. Rehabilitation projects face the challenge of trying to teach and equip animals with the necessary skills to survive in the wild. Brewer's (1978) approach to nest building was to place newly arrived chimpanzees onto elevated platforms providing them with fresh leaf bedding each evening, choosing heights greater than 7-8m. She argued that providing less experienced chimps with ready cut leafy branches stimulated nest building, although all the chimpanzees whether wild- or captive-born, performed rudimentary nest building patterns. All of the chimpanzees were able to make nests, although it is not known whether they made a new nest each evening. The method of providing freshly cut branches was similarly used with wild-born chimpanzees prior to release in Liberia and all the chimpanzees post-release built nests (Hannah and McGrew, 1991) and rehabilitant orang-utans (Borner and Stonehouse, 1979). Through watching the nest building techniques that Brewer or the other chimpanzees used, Brewer argued the newcomers gradually learnt how to construct nests. Rijksen (1978) also reported that some orang-utans that could not initially make a nest, soon learned how by practice and/or by watching others during play sessions. Carter (1981) spent several months making day nests with the chimpanzees on or near the ground, using the same construction technique to be used later for constructing elevated night nests. Carter had successfully managed to encourage the wild-born chimpanzees to nest independently for several weeks on the island, when two captive-born chimpanzees were introduced to the group. Carter had to resort to a variety of techniques to try and persuade the captive-born 'rehabilitees' to sleep off the ground away from their human guardians. The potential danger of this situation was highlighted when Carter once discovered one of the ground dwelling chimps with a high fever, swollen glands, and eyes swollen shut. The most likely cause was an encounter with a spitting cobra. The chimpanzee was unable to see for a week, which in the wild would have been life threatening. Carter succeeded in encouraging the two chimpanzees to nest in trees by mimicking the bite of an animal. A possible factor as to why the captive chimpanzees continued to remain on the ground at night was the psychological need of the chimpanzees to be near their human surrogate mothers following the move from their captive environment. As mentioned earlier young chimpanzees share a nest with their mothers for three to five years. In hindsight, Carter may have been better to construct elevated nests instead of ground nests from the start, immediately providing an example of correct nest building.

9.2 Aims

- To describe the characteristics and features of nests made by a group of reintroduced chimpanzees in comparison to published data on nests built by wild chimpanzees
- To examine any change in nesting behaviour over the course of the study

9.3 Methods

9.3.1 Study animals

Data were collected on 277 night nests. In all cases, the chimpanzees were seen to start the nest making process, although due to failing light sometimes the whole process was not observed. The majority of these nests (n=264) were made by chimpanzees released in February 1999 (David, Agathe, Sophie and Koutou), who are the focus for this data set. Valentine was released with her mother Sophie, she was aged one and half months at release. At this age infant chimpanzees still sleep with their mother and consequently no data were collected on Valentine.

David was responsible for 28 of the total number of nests, Agathe 78, Sophie 84, and Koutou 74. The reason for David making so few nests in comparison to the other chimpanzees is due to his disappearance as mentioned in Chapter 4. 161 nests were made before David's disappearance and 103 were made subsequently by the remaining three chimpanzees.

Previously reintroduced chimpanzees that occasionally joined up with this group made up the remaining 13 nests. These nests have been excluded from analyses, as their numbers do not represent a sufficient sample size for comparison, and could cloud interpretation due their makers' increased amount of time and experience in the forest. During the post-release period of chimpanzees released in 1996 (R1) and 1997 (R2 and R3), data were not specifically collected on nesting behaviour. However, occasionally details of nests built were noted on check-sheets during normal daily behavioural observations. Where applicable these details are described.

9.3.2 Pre-release nesting behaviour

No data were collected on nests pre-release as it was impossible to enter the island. Only a few nests could be seen from the periphery of the island, and it was not possible to collect any data reliably from such a long distance. Occasionally lone nests were spotted in the mangrove (Plate 9.2), clearly illustrating that nests were made, but to what extent and by whom it is difficult to say. Nests were regularly spotted in the mangrove area and high in trees on the adjacent Yvette Island. Systematic data were not collected on these nests as the chimpanzees on this island were not due for release in the foreseeable future (Release 7-9). Pepere Island is inhabited by three adult chimpanzees that have spent at least 20 years in poor captive conditions before arriving at the sanctuary (see Table 4.1, p.73). No nests have ever been observed on this island in any shape or form.

Plate 9.2 A nest located in the mangrove area of Yombe Island

9.3.3 Post-release nesting behaviour

Three main articles have attempted to compare characteristics of nests across wild chimpanzee populations (Baldwin et al., 1981; Fruth and Hohmann, 1994, 1996). The review papers by Fruth and Hohmann (1994, 1996) consist of compiled field study data taken from a variety of sources. They set out to identify and explain structural characteristics of nests and behaviour in the vicinity of nests, to try and relate these to ecological and environmental determinants, and evaluate possible cultural diversity. It was with these aims in mind that a check-sheet (see Appendix H) was designed to attempt to collect comparable data from the reintroduced group, to enable comparisons to be made with the data collected on wild chimpanzee populations at other sites. Table 9.1 details the information that was collected.

Data collection did not commence until approximately two months post-release due to a variety of logistical problems in initially locating and tracking the chimpanzees (see Figure 4.4, p.84). Once the data collection commenced, as far as possible, data were collected on a daily basis, on all four released chimpanzees. The data period spanned a period of 3.5 months (3/04/99-23/07/99) and nest data were collected on 86 days within this period. The chimpanzees were usually followed from approximately 06h00 until nests were built in the evening. If the group split during the day, it was normally only possible to continue to follow one splinter group and consequently collect nest data on those individuals only. It was usually possible to locate the other chimpanzee(s) from the group, but not to collect detailed nest data due to failing light. In my absence, a well-trained team of Congolese observers who had been following the chimpanzees on a daily basis collected the nest data. All knew the forest and the chimpanzees well, and were given full instructions on data collection and completion of the nest check-sheet. Inter-observer reliability was not assessed specifically for the estimation of nest or tree heights. However, refer to Chapter 5 (p.120) for inter-observer reliability scores calculated from height categories utilised for daily observations of behaviour that were all greater than 80%.

Table 9.1 Data collected on nesting behaviour check-sheet

Category	Description
Date/time	As soon as the chimpanzee began to make a nest, the date and the time at which the activity started was noted.
Chimpanzee	The name of the chimpanzee making the nest. The observers were all very familiar with the chimpanzees and could readily identify them from several metres away. Binoculars were occasionally used. On the rare occasions it was not possible to identify who was making the nest, data were not collected.
Location	Exact locations of nest trees were calculated using transect markings and compass bearings. Nest trees were marked with a tree tag, and each tree tag was allocated a number. This number was inscribed onto the aluminium tag to mark the nesting tree and entered onto the check-sheet against each corresponding nest.
Forest type	The forest types were categorised as either primary forest (PF), inundated forest (IF) or swamp forest (SF).
Weather	The weather at the time of data collection was categorised as either heavy rain, rain, cloudy, or sunny.
Water level	The level of water on the ground at the time of nest data collection was categorised as: 0 = none, 1 = below ankle level, 2 = below knee level, and 3 = above knee level.
Height of nest	The height of the nest was estimated to the nearest metre.
Height of tree	The height of the tree was estimated to the nearest metre.
Diameter of tree (cm)	The diameter of the tree where each nest was built was measured at breast height in centimetres using a tape measure. For these data, breast height was approximately 1.3m from the ground.
Nearest nest	The distance between each individual nest and their nearest nest was estimated in metres.
Nearest neighbour	The name of the closest nesting neighbour for each chimpanzee was noted.
Canopy cover	The degree of canopy cover above each nest was categorised as 1 = covered (layer of vegetation covering the nest), 2 = intermediate, 3 = open (clear view to the sky).
Number of nests per tree	The number of nests made in each tree was noted.
Type of nest	The number of distinguishable distinct trees used to make each nest was noted, in addition to whether the nest was freshly made or re-used.
Tree species	The name of tree species in which each nest was made was noted. If more than one tree species was used to make a nest, all species were named. If the species was not recognisable, a description of the tree was noted and where possible a sample of a leaf/fruit (some potential identifiable marker) was taken to facilitate later identification.
Pre-nest building behaviour	The distance from the last feeding site to nest site location were estimated in metres and last feeding bout prior to commencing nest building noted in minutes.
Nest and/or feeding tree	Whether the chimpanzee prior to building a nest also fed in the same tree.
Observer	The name of the observer was noted on each check-sheet.

9.3.4 Statistical analyses

Due to the small number of animals contributing nests to this data set (n=4) statistical tests should not be performed on group data. Analyses have been applied to individuals only unless otherwise stated as a means to illustrate relationships (or lack of) suggested by descriptive statistics. Data were judged to be normal and mean with standard deviation descriptive measures were used and parametric tests performed. Where data have been presented as a group figure, the mean score for each animal was calculated, summed together and divided by the number in the group. Where both a mean (±SD) and median (±IQR) have been quoted (Tables 9.22-9.27) this was to enable direct comparison to data collected on wild chimpanzee populations that have used variable descriptive statistics. The number of times each variable was collected (e.g., diameter at breast height, nearest neighbour distance etc.,) for each chimpanzee may not be constant. Any differences in n scores (or degrees of freedom) or where scores do not add up are a reflection of missing values.

Following comparisons of nest and tree heights for the reintroduced chimpanzees to various wild chimpanzee populations, it appeared that the estimated heights for both nest and tree height categories were substantially greater for the reintroduced chimpanzees than all the wild chimpanzee populations studied. Although there will be some variation between sites due to varying habitat and forest descriptions, the extent of the difference implied that the heights had been over-estimated by all observers. As a cross-reference, two unpublished survey reports on the area were consulted. Tutin (1994) reported the height of the inundated forest canopy to be approximately 20-25m, whilst Sita (1996) estimated 25-30m. The inundated forest is the forest type where the chimpanzees made the majority of their nests. The mean height of nest trees for the reintroduced group was 30.65m (±0.73) with a range of 10-50m. Although the mean height of tree for the group does fall into the range estimated for canopy height in one of the two surveys, it is at the higher end of the range, and the spread of scores is large. Consequently, it was decided to reduce the reported height of all the nests and trees by

15% to compensate for possible over-estimation and bring the maximum scores in line with the estimations made by Tutin (1994) and Sita (1996). It was decided to use 15% as this reduced the mean heights and range of scores in accordance with the higher range of heights observed in wild chimpanzees, without radically altering the nature of the data. The reintroduced chimpanzees did build their nests high, which was reflected by the large DBH scores that were accurately measured using a tape measure. The original estimates and those with a 15% reduction are both displayed for group data, but individual data are only displayed with the 15% reduction.

9.4 Results

9.4.1 Immediate post-release

During the first few days immediately post-release it was not possible to approach the chimpanzees as they were very wary of observers. After approximately one week we were able to get closer and began to follow them in the forest. It was at this point that we established that David, Agathe and Sophie were all building nests high in the trees and needed no encouragement to do so. Immediately post-release Koutou ran away from the group and release site, and could not be found (see Figure 4.4, p.84). When he was re-released approximately one month after the original release date he also immediately made nests high in the trees. All the nests made by the chimpanzees appeared complete in structure, and seemed comparable with nests made by wild chimpanzees in size and form (Plate 9.4).

Plate 9.4 A nest made by a chimpanzee post-release

9.4.2 Day nests

The 264 nests on which data were collected were all night nests. During the 3.5 month study period (specific to this chapter) seven day nests were made; three by Koutou, two by Agathe, and one each by Sophie and David. Unfortunately no comparatively detailed data were collected on the day nests and due to their small number no analyses have been performed. During the total 14 months that the chimpanzees were followed, 22 day nests were built, the females built 9 each, Koutou 3 and David 1. None of these nests were built on the ground. When resting during the day, this group spent 60% (±SD17.64) of their mean time resting above ground. Interestingly, if the males and females are compared, the females spent a mean 72% (±SD3.25) of time resting above ground whereas the males only spent 47% (±SD17.64) of mean time resting above the ground. When lying on the ground the chimpanzees would be very close together, frequently with limbs touching (personal observation).

It was noted that the chimpanzees released in 1996 (R1) and 1997 (R2 and R3) built 101 day nests during the 14 month study period. As stated previously these data were not specifically collected and the number may not reflect the total number of day nests made during this period. Ninety-two of these nests were made by females (n=9) and nine by males (n=2). The females made a mean 10.22 (±7.68) day nests and the males 4.50 (±3.54). Nine of the day nests were built on the ground, three by females and six by one male, Mekoutou. In the rainy season a mean number of 10 nests were made per month and in the dry season five. No standard deviations are shown due to small sample sizes.

9.4.3 Time of nest construction

The time when nest construction began ranged from 16h20 to 18h40. As mentioned earlier in Chapter 6 (p.133) sunset fell between 18h05-18h36 in the region, and at the latter part of this range during the dry season. The rainy season in the region extends from mid November to mid May and the dry season between mid April/beginning of

June, to October (see Chapter 3, p.61). The mean time to start nest construction was 17h47 (±0.04). The mean time nests were started demonstrates the order in which nests were made by the chimpanzees. On average Sophie made her nest first followed by David, Agathe and Koutou. However, there was very little variation between the chimpanzees (Table 9.2) and a one-way ANOVA found no significant differences ($F_{3,260} = 1.62$; p=0.184).

Table 9.2 Mean time (hours/minutes ±SD) that nest construction began for each chimpanzee

Chimpanzee	n	Mean time (hour/minute ±SD)
David	28	17.45 (±0.32)
Agathe	78	17.47 (±0.25)
Sophie	84	17.44 (±0.25)
Koutou	74	17.53 (±0.26)

9.4.4 Arising and leaving nests

In many cases the chimpanzees had already left the nests, although often not the nest tree, before the observers arrived early in the morning. However, it was noted that the chimpanzees habitually urinated and defecated after waking and moving to the edge of the nest or completely out of the nest. Even when not directly seen, this action could be heard, and evidence in the form of faeces below the nest confirmed this. Following defecation, the day usually began with a period of relative inactivity in the nest tree, but outside of the nest. This sometimes consisted of social contact in the form of grooming or mere proximity. Following this, the nest tree would be vacated and a period of feeding would commence either in a nearby tree or on the ground.

9.4.5 Structural characteristics of nests

9.4.5.1 Nest height

All of the night nests made by the reintroduced chimpanzees were off the ground in trees, and no ground nests were observed; the minimum height (-15%) at which nests were constructed at was 2.55m and the maximum was 42.50m. The mean height (-15%)

of nests in metres for the whole group was 21.95m (±0.71) (Table 9.3). The original non-adjusted data produced a mean nest height of 25.83m (±0.85). A one-way ANOVA indicated that there was no significant difference between the nest height of the individual chimpanzees ($F_{3,257} = 1.01$; p=0.388).

Table 9.3 Descriptive statistics of overall mean nest height (-15%)

Height of nest (m)	Chimp	n	Mean (±SD)	Minimum	Maximum
Overall	David	27	22.18 (±5.57)	10.20	34.00
	Agathe	78	21.31(±6.86)	2.55	42.40
	Sophie	83	22.86 (±5.87)	2.55	38.25
	Koutou	73	21.46 (±6.41)	2.55	34.00
Total		261	21.95 (±0.71)	4.46	37.69

Over the study period, the height of the nests increased overall for <u>all</u> the chimpanzees (Figure 9.1). Pearson's product moment correlation (two-tailed) of height of nest (-15%) against month post-release in which nest was made were significant in the case of Agathe and Koutou, but not for David or Sophie although the latter was also making her highest nests in the final month (Table 9.4).

Figure 9.1 Monthly mean nest height (±SD) for each chimpanzee (-15%)

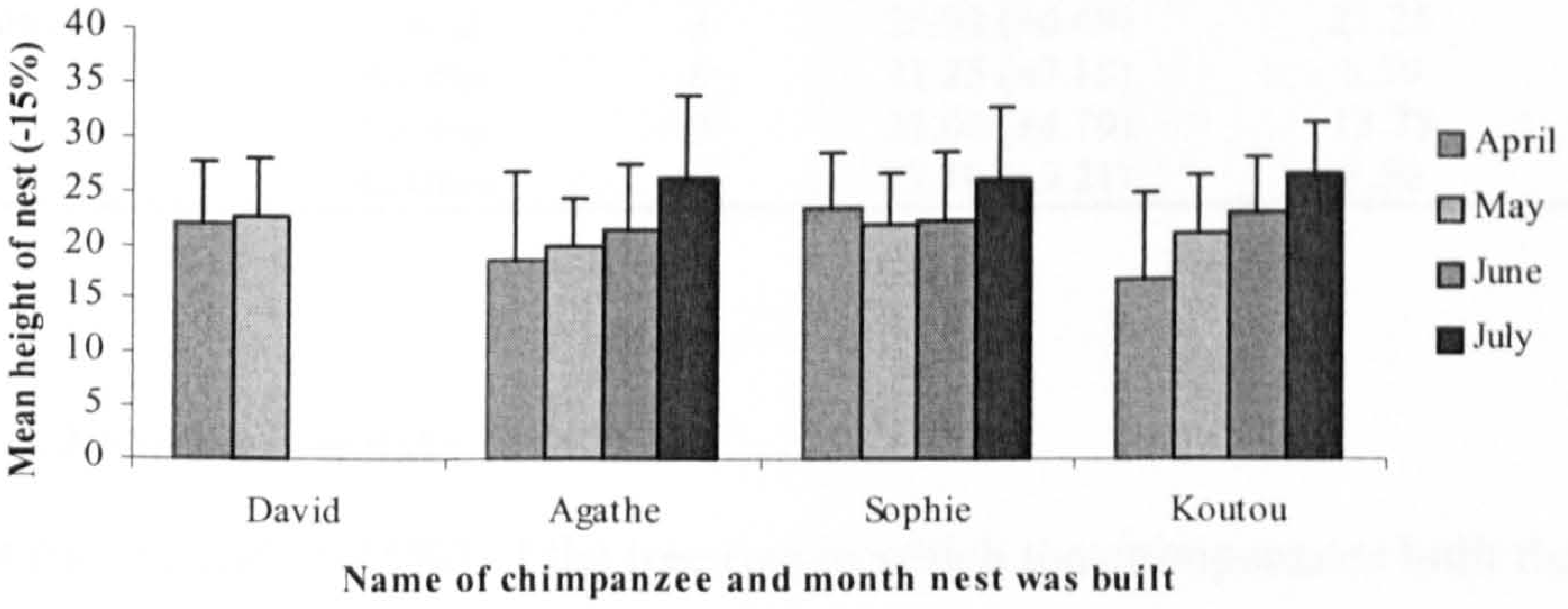


Table 9.4 Results of Pearson's correlation between height of nest (-15%) and month post-release

Chimpanzee	r	n	Significance
David	0.06	27	0.779
Agathe	0.34	78	0.002**
Sophie	0.12	83	0.272
Koutou	0.47	73	<0.001***

**p<0.01, ***p<0.001

One explanation for the gradual increment in nest height could be a result of changing environmental factors such as the habitat type in which the nests were made. However, the majority of nests (n = 236/264) were made within inundated forest. In April, 93.95% (n = 66) of nests were built in inundated forests but by July this figure had fallen slightly to 85.67% (n = 36). The decrease was small, and as trees in swampy forests are generally lower than trees in inundated forests, these figures cannot logically explain the increment. In the present study the mean tree height (-15%) in the inundated forest was 26.39m (±0.62) whereas in swampy forests, the mean was 22.83m (±2.76) (Table 9.5).

Table 9.5 Descriptive statistics of tree height within each forest type (-15%)

Forest	Chimp	n	Mean (±SD)	Minimum	Maximum
Inundated	David	24	26.60 (±5.33)	17.00	38.25
	Agathe	70	25.79 (±5.98)	12.75	42.50
	Sophie	74	27.17 (±4.97)	17.00	38.25
	Koutou	68	26.01 (±5.51)	17.00	38.25
	missing	3			
Swamp	David	3	26.92 (±6.49)	21.25	34.00
	Agathe	8	21.25 (±7.18)	8.50	29.75
	Sophie	9	21.06 (±4.79)	12.75	29.75
	Koutou	5	22.10 (±9.21)	8.50	29.75

9.4.5.2 Nest tree height

The mean height (-15%) of the tree (m) in which the chimpanzees built their nests was 26.05m (±0.62) (Table 8.6). The original non-adjusted data produced a mean of 30.65m (±0.73). A one-way ANOVA indicated that there was no significant difference between the nest tree height of the individual chimpanzees ($F_{3,257} = 0.73$; p=0.537).

Table 9.6 Descriptive statistics of overall mean nest tree height (-15%)

Height of nest tree (m)	Chimp	n	Mean (±SD)	Minimum	Maximum
Overall	David	27	26.63 (±5.32)	17.00	38.25
	Agathe	78	25.33 (±6.22)	8.50	42.50
	Sophie	83	26.50 (±5.28)	12.75	38.25
	Koutou	73	25.75 (±5.83)	8.50	38.25
Total		261	26.05 (±0.62)	11.69	39.31

Overall, there was an increment in nest tree height similar to nest height over the months (Figure 9.2) The nest tree height for David remained fairly constant for April and May. Agathe and Koutou again showed an increase in nest tree height across the months. Sophie mirrored the pattern shown in nest height by a decrease in nest tree height in May, but this trend continued in June before increasing in July. Pearson's correlation (two-tailed) of height of nest (-15%) against month in which nest was made reached significance in the case of Agathe and Koutou, but not for David or Sophie although Sophie was also making her nests in the highest trees in the final month (Table 9.7).

Figure 9.2 Monthly mean nest tree height (±SD) for each chimpanzee (-15%)

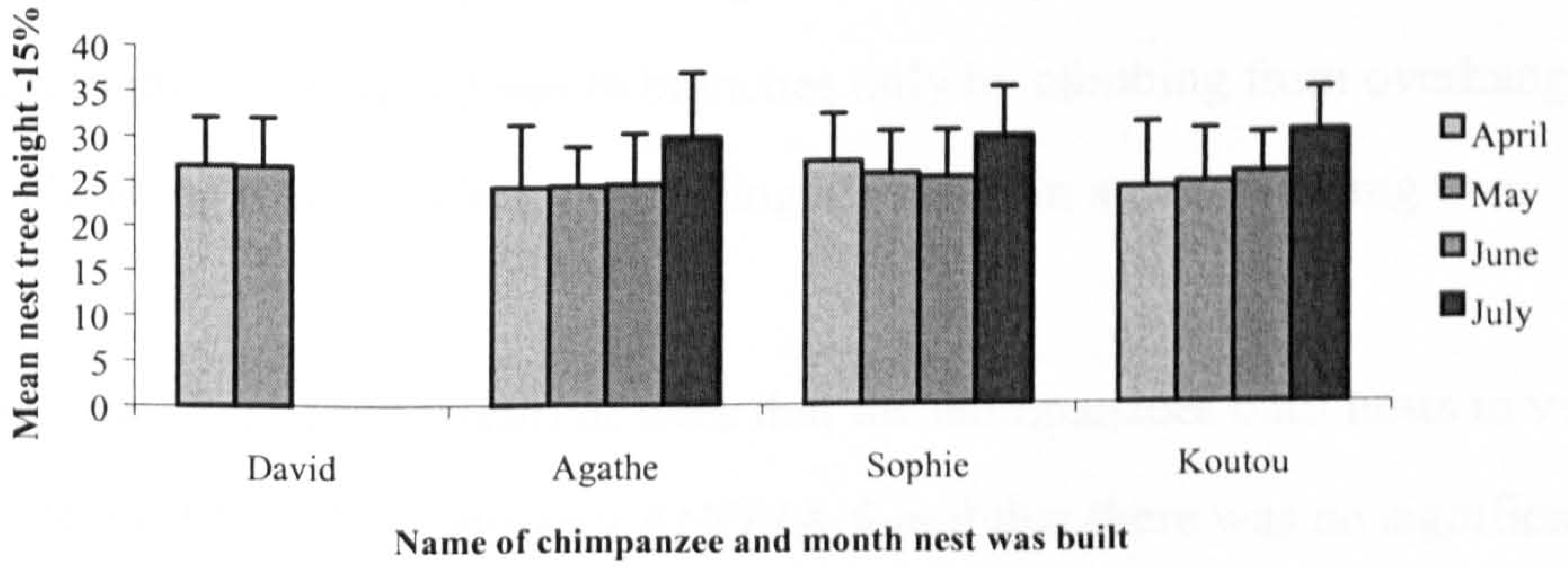


Table 9.7 Results of Pearson's correlation between height of nest tree (-15%) and month post-release

Chimpanzee	r	n	Significance
David	0.95	27	-0.012
Agathe	0.25	78	0.031*
Sophie	0.12	83	0.280
Koutou	0.32	73	0.006**

*p<0.05, **p<0.01

By calculating the height of the nest as a proportion of the height of the nest tree, it is possible to examine the proportional height of the nest to the tree in which it was built. The overall mean proportional height of nest was 0.83 (±0.01) (Table 9.8). A one-way ANOVA indicated that there was no significant difference in proportional nest to nest tree height between the chimpanzees ($F_{3,257} = 0.56$; $p=0.64$).

Table 9.8 Mean proportional height of nest to nest tree (m) for each chimpanzee (-15%)

Height of nest tree (m)	Chimp	n	Mean proportion (±SD)
	David	27	0.83 (±0.11)
	Agathe	78	0.83 (±0.13)
	Sophie	83	0.86 (±0.12)
	Koutou	73	0.84 (±0.16)
Total		261	0.83 (±0.01)

9.4.5.3 Diameter at breast height of nest tree (DBH)

Botanists use DBH to calculate growth rates of trees, and foresters to estimate timber volume. Primatologists use this measurement because it is a practical measure in the field, and gives an indication of tree structure, and consequently inferred behaviour. For example, a tree with a very small DBH is likely to be spindly and lacking in adequate support for nest building. A very large DBH may prevent a chimpanzee from climbing up the trunk, allowing access to branches only by climbing from overhanging neighbouring tree branches, or jumping across from a neighbouring tree.

The mean overall DBH (cm) of trees that the chimpanzees built nests in was 76.53cm (±4.38) (Table 9.9). A one-way ANOVA found that there was no significant difference in the DBH of nest tree between the chimpanzees ($F_{3,254} = 0.59$; $p=0.622$).

Table 9.9 Mean diameter at breast height of nest tree (cm) for each chimpanzee (±SD)

Chimp	n	Mean (±SD)	Minimum	Maximum
David	27	79.22 (±30.63)	37	150
Agathe	77	74.03 (±34.49)	18	150
Sophie	82	79.40 (±31.66)	17	150
Koutou	72	73.47 (±35.46)	18	150
Total	258	76.53 (±4.38)	22.50	150

Logically as nest and tree height increase so should the diameter at breast height of the nesting tree. In support of this the chimpanzees that built the highest nests in the taller trees also had the largest DBH scores (Table 9.3 and 9.6 for comparison). Pearson's correlation produced significant positive results for three out of four chimpanzees when DBH and nest height (-15%) were compared, and for all four chimpanzees when nest tree height (-15%) and DBH were compared (Table 9.10).

Table 9.10 Results of Pearson's correlations between height of nest and nest tree (-15%) and DBH

Analyses	Chimpanzee	r	n	Significance
Height of nest and DBH	David	0.66	27	<0.001***
	Agathe	0.29	77	0.01*
	Sophie	0.20	82	0.07
	Koutou	0.37	72	0.001**
Height of nest tree and DBH	David	0.70	27	<0.001***
	Agathe	0.34	77	0.002**
	Sophie	0.33	82	0.002**
	Koutou	0.55	72	<0.001***

*p<0.05, **p<0.01, ***p<0.001

9.4.5.4 Tree species

Table 9.11 lists the tree species used for nesting with the number (and percentage) of occasions each species was used. Twenty-one species of trees in which nests were built were identified, representing 62% (n=163/264) of all species in which nests were made. The remaining 38% of tree species remain unidentified. The most favoured tree species for nesting by the reintroduced group was *Panda oleosa,* used on 39 (15%) occasions followed by *Irvingia gabonensis* on 24 (9%) occasions. The sample size of identified species is too small to look for individual preferences, however, nests were made in *Elaeis guineensis,* more familiarly known as the oil palm tree on only three occasions, and each time they were made by the same female Agathe. These nests were made on the 2nd and 13th May, and 6th July. These dates were not significant except on 13th May Agathe spent the day on her own and made her nest alone. It was noted that nests were made within *Elaeis guineensis* on ten occasions by chimpanzees from R1: Jeanette (n=4), Choupette (n=4) and R3: Massabi (n=1), Mossendjo (n=1). All of these nests were night nests except one made by Choupette.

Table 9.11 List of tree species in which nests were made by the reintroduced chimpanzees

Scientific name	Family name	Local name	No. of times used to make nest	% of times used to make nest	Part eaten by reintroduced group	No. of times feeding tree used as a nesting tree
Acioa pallescens	Chrysobalanaceae	-	6	2.3	Leaves	0
Berlinia bracteosa	Cesalpinioideae	Ibiara	10	3.8	Leaves, sap	1
Elaeis guineensis	Arecaceae	Oil palm	3	1.1	Fruit, flowers, stem, leaves	2
Enantia chlorantha	Annonaceae	-	1	0.4	?	0
Ficus sp.	Moraceae	-	5	1.9	Fruit, sap	2
Grewia coriacea	Tiliaceae	-	2	0.8	Fruit, sap	1
Hexalobus crispiflorus	Annonaceae	Vadou	4	1.5	Fruit	0
Homalium sp.	Flacourtiaceae	-	1	0.4	?	0
Irvingia gabonensis	Irvinigiaceae	-	24	9.1	Fruit	1
Microberlinia sp.	Cesalpinioideae	-	4	1.5	Leaves	0
Nauclea didderichii	Rubiaceae	-	21	8	Fruit	1
Panda oleosa	Pandaceae	-	39	14.8	?	2
Pterygota beguaertii	Sterculiaceae	-	1	0.4	Fruit, leaves, sap	1
Pycnanthus angolensis	Myristicaceae	Ilomba	5	1.9	Fruit, sap	0
Santiria trimera	Burseraceae	-	5	1.9	Fruit	0
Scytopetalum sp.	Scytopetalaceae	-	10	3.8	Fruit, sap	7
Staudtia gabonensis	Myristicaceae	Niove	1	0.4	Fruit	0
Symphonia globulifera	Clusiaceae	-	1	0.4	?	0
Terminalia superba	Combretaceae	Limba	3	1.1	?	0
Vitex doniana	Verbenaceae	-	15	5.7	Fruit, leaves	5
Xylopia sp.	Annonaceae	-	2	0.8	?	0
Total identified species	**21**	**-**	**163**	**62**	**15**	**23**
Total unidentified species	**?**	**-**	**101**	**38**	**-**	**6**
OVERALL TOTAL	**?**	**-**	**264**	**100**	**15**	**29**

9.4.6 Nest features

9.4.6.1 Feeding behaviour in and around the nest tree

Sixty seven percent (n=15/21) of the identified tree species in which nests were built have some parts that are normally eaten by chimpanzees. However, in only 11% of cases (n=29/254) did the chimpanzees eat in a tree in which they also made their night nest later in the day. There was slight individual variation. The females made nests in feeding trees on average more than the males (Table 9.12).

Table 9.12 Number and percentage of nests made in feeding trees

Chimpanzee	n	%
David	2	8%
Agathe	11	14%
Sophie	9	11%
Koutou	7	10%
Total	29	11%

The 29 occasions in which nests were made in feeding trees spanned 18 separate days. In the majority of cases when a chimpanzee made a nest in a feeding tree it was the only one to do so on that particular day (61%, n=11 days). Of those remaining seven occasions (39%) when a nest was made in a feeding tree with other chimpanzees present, in 57% (n=4) of cases the same tree was used. When this did occur, in the majority of cases the tree species was either *Scytopetalum* sp. (n=7 nests) or *Vitex doniana* (n=5).

In 84% (n = 221/252) of cases, the chimpanzees made a nest near to the last feeding place of the day. The mean distance (m) from the last feeding place to nest site for the whole group was 14.48m (±1.59), with slight individual variation (Table 9.13). A one-way ANOVA found a non-significant difference between chimpanzees ($F_{3,200} = 0.34$; p=0.796).

Table 9.13 Mean distance (±SD) between the last feeding session of the day and site of nest

Chimpanzee	n	Mean distance (m)	SD
David	19	12.16	±14.21
Agathe	60	15.33	±14.30
Sophie	69	15.67	±13.97
Koutou	56	14.77	±12.75
Total	204	14.48	±1.97

The overall mean time (minutes) that elapsed between the last feeding session of the day and building a nest was 14.88 minutes (±0.98), with slight individual variation (Table 9.14) that did not reach statistical significance when a one-way ANOVA was performed ($F_{3,53} = 0.42$; p=0.739).

Table 9.14 Mean time (±SD) between the last feeding session of the day and starting to nest build

Chimpanzee	n	Mean time (minutes)	SD
David	4	12.75	±8.38
Agathe	19	13.84	±9.11
Sophie	20	17.15	±12.90
Koutou	14	15.79	±8.35
Total	57	14.88	±1.97

9.4.6.2 Integrated nests

The chimpanzees primarily made their nests using only one tree (n=248/261), single tree nests accounted for 95% of nests built. Integrated nests were made on 13 occasions, accounting for only 5% of nests. The maximum number of trees incorporated into a nest by the group was two. The two females made more integrated nests than the two males (Table 9.15). Due to the low number of integrated nests, it is not possible to determine if environmental variables such as forest type, tree species and height/DBH of nest tree were an influencing factor.

Table 9.15 Number and percentage of integrated nests

Chimpanzee	n	%
David	1	4%
Agathe	7	9%
Sophie	4	5%
Koutou	1	1%

9.4.6.3 Nest re-use

Chimpanzees have been known to re-use nests built previously, usually after relining them with fresh leaves and twigs for additional comfort. In the present study 6% of nests were re-used (n= 16/261). Each chimpanzee re-used a nest rather than make a fresh one on a similar number of occasions (Table 9.16). However, as data collected on nests made by David were so few in number due to his disappearance, the percentage of times he re-used nests appears high (Table 9.16). Nests were re-used on 11 separate days. On one day three chimpanzees re-used a nest and on another day, two chimpanzees re-used a nest. Of the remaining days, only one nest was re-used. Due to the low number of nests re-used, it is not possible to determine if environmental variables such as forest type and tree species were influencing factors.

Table 9.16 Number and percentage of nests re-used

Chimpanzee	n	%
David	3	11%
Agathe	4	5%
Sophie	4	5%
Koutou	5	7%

9.4 6.4 Nest parties

Ninety four percent (n = 245/264) of nests were made in a group. A nest group refers to clusters of nests built by different individuals in close proximity (within human visibility) on the same night. If a chimpanzee made its nest away and separate from the rest of the group at dusk, it was assumed that they nested alone. Until David disappeared, on every occasion he nested with the group, however, Agathe, Sophie and Koutou did occasionally make nests alone (Table 9.17).

Table 9.17 Number and percentage that each chimpanzee nested as part of a group or alone

	Nesting with group		Nesting alone	
	n	%	n	%
David	28	100%	0	0%
Agathe	70	90%	8	10%
Sophie	81	96%	3	4%
Koutou	66	89%	8	11%
Total	245	94%	19	6%

9.4.6.5 Nest spacing

The overall mean distance to the nearest nest was 7.92m (±0.39), with slight variation between the chimpanzees (Table 9.18) that did not reach statistical significance in a one-way AVOVA ($F_{3,232} = 0.70$; p=0.554). The mean distance to the nearest nest was greatest for David but lowest for Sophie.

Table 9.18 Mean distance (m) to nearest nest (±SD)

Chimpanzee	n	Mean nearest nest distance (m)	SD
David	26	8.81	±11.29
Agathe	68	7.49	±3.94
Sophie	80	7.08	±5.34
Koutou	62	8.28	±7.21
Total	236	7.92	±0.78

One ecological factor that may affect the distance between nests could be the number of nests made in a tree. For example, one would expect that the nearest nest neighbour distance would be smaller if four nests had been made in the same tree in comparison to the nests being made in four separate trees. A significant relationship between nest distance and number of nests per tree was found. As the number of nests per tree increased, the mean distance (m) between nearest nests decreased (Table 9.19).

Table 9.19 Results of Pearson's correlation performed on distance to nearest nest and number of nests in a tree

Chimpanzee	r	n	Significance
David	-0.44	26	0.025*
Agathe	-0.60	68	<0.001***
Sophie	-0.53	80	<0.001***
Koutou	-0.44	62	<0.001***

*p<0.05, ***p<0.001

The reintroduced chimpanzees made a mean of 1.89 (±0.04) nests per tree. Forty four percent of nests were in made in separate trees (n=107/242). As the number of nests made per tree increased, its frequency decreased, reflecting a limited number of suitable trees in the forest in which to build more than one nest (Table 9.20).

Table 9.20 Frequency and percentage of the number of nests in a tree

Chimpanzee	Number of nests in a tree	n	%
David	1	11	40.74%
Agathe	1	34	48.57%
Sophie	1	31	38.75%
Koutou	1	31	47.69%
Total	-	107	43.94%
David	2	9	33.33%
Agathe	2	20	28.57%
Sophie	2	32	40.00%
Koutou	2	17	26.15%
Total	-	78	32.01%
David	3	6	22.23%
Agathe	3	13	18.57%
Sophie	3	15	18.75%
Koutou	3	14	21.54%
Total	-	48	20.27%
David	4	1	3.70%
Agathe	4	3	4.29%
Sophie	4	2	2.50%
Koutou	4	3	4.62%
Total	-	9	3.78%

The decreasing frequency as the number of nests made per tree increases, may be habitat specific. Logically a tree with a wider girth is likely to be sturdier and able to adequately support more than one nest in comparison to a spindly tree with a smaller DBH. Pearson's correlation were performed on DBH of nest tree and number of nests made per tree for each chimpanzee. A significant positive correlation was found in three out of four chimpanzees; as the DBH of nest tree increased so did the number of nests made per tree (Table 9.21). The one non-significant result (David) may be due to the small sample size (n=27).

Table 9.21 Results of Pearson's correlation performed on diameter at breast height of nest tree and number of nests in a tree

Chimpanzee	r	n	Significance
David	0.26	27	0.183
Agathe	0.49	70	<0.001***
Sophie	0.43	79	<0.001***
Koutou	0.49	64	<0.001***

***p<0.001

9.4.7 Wild and reintroduced chimpanzee nests

Nest structural characteristics

Tables 9.22-9.24 display structural characteristics made by wild chimpanzee groups and the reintroduced group according to chimpanzee subspecies. The minimum-maximum range of mean nest height regardless of subspecies spans from 8.7m-23.2m with a median of 11.45m. The reintroduced chimpanzees made their nests on average at 21.95m (-15%) and only two wild populations of the thirteen with height data came close; 19m (Ugalla, Tanzania) and 23.2m (Tai, Ivory Coast) both were other subspecies. Mean DBH of nest tree for the reintroduced group was the highest in comparison to all wild populations. Data collected on wild populations ranged from 24.90cm-59.50cm.

Nest features

Tables 9.25-9.27 display features of nests made by wild chimpanzee groups and the reintroduced group according to chimpanzee subspecies. Wild populations used a maximum of four trees to make a nest but an overall median of two. The reintroduced chimpanzees used a maximum of two trees, and a median of one. Twenty-one identified tree species were used to build nests in by the reintroduced chimpanzees. The figures for wild populations range from 14-45 species.

Table 9.22 Structural characteristics of wild chimpanzee nests ; subspecies *Pan troglodytes schweinfurthi*

Country	Tanzania	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Uganda	Uganda	Uganda	DRC	DRC	DRC
Study site	Mahale	Gombe	Ugalla	Ugalla	Budongo	Budongo	Budongo	Ngogo	Kanyawara	Kanyawara	Kahuzi-Biega	Lake Kivu	Virunga
Reference	Nishida 1966-94* (unpub.)	Goodall 1968	Moore 1985-94* (unpub.)	Itani 1979	Reynolds& Reynolds 1965*	Reynolds& Reynolds 1965#	Brownlow et al 2001	Ghiglieri 1984	Ghiglieri 1984*	Ghiglieri 1984#	Basabose& Yamagiwa 2002	Rahm 1967	Sept 1992
Duration of study	?	?	?	7 days	170 days	170 days	26 mths	11 mths	3 mths	3 mths	12 mths	1 mth?	6 mths
Habitat	GWF	GWF	W	GWF	RF	RF	SDF	RF	RF	RF	PF/SF	RF	GWF
Height of nest (m)													
n	-	384	-	491	259	259	[a]601 (104)	372	63	148	[b]104 (94)	-	101
mean (±SD)	-	-	-	19	-	-	12.1 (15.4)	12.2	10.3	10.8	9.4 (9.8)	-	13.5 (±6.1)
median	-	-	-	-	-	-	-	-	-	-	-	-	-
min-max	10-20	0-25	10-20	5-40	3-45	0-31	0-32.5	2-35	5-23	5-23	-	0-25	-
DBH (cm)													
N	-	-	-	-	-	-	411 (101)	-	-	-	104 (94)	-	-
mean (±SD)	-	-	-	-	-	-	26.4 (43)	-	-	-	24.9 (35.3)	-	-
median	-	-	-	-	-	-	-	-	-	-	-	-	-
min-max	-	-	-	-	-	-	-	-	-	-	-	-	-

Notes:

Country: DRC = Democratic Republic of Congo

Habitat types: GWF mosaic of grassland-woodland and forest, PKF plantation forest, PF primary forest, RF rain forest. SDT semi-deciduous tropical forest, SF secondary forest, W woodland

DBH: diameter at breast height of nesting tree

- denotes no data, ? denotes not known

*where it was impossible to gain original publications the * symbol indicates information cited from the review papers of Fruth and Hohmann (1994 , 1996)

where the same reference has been presented twice, the symbol # indicates original reference, to distinguish from above where discrepancies have been found between the two sources

[a] Figures outside of brackets represent data on night nests and figures within brackets represent data on day nests

[b] Figures outside of brackets represents data on nests in primary forests and figures within brackets represents data on nests in secondary forests

Table 9.23 Structural characteristics of wild chimpanzee nests; subspecies *Pan troglodytes verus*

Country	Rep. of Guinea	Rep. of Guinea	Rep. of Guinea	Rep. of Guinea	Senegal	Senegal	Senegal	Liberia	Liberia	Ivory Coast	Ivory Coast	Mali	Mali	Sierra Leone
Study site	Area around Kindia	Fouta Djallon	Bossou	Fouta Djallon, Guinée Maritime, Forestière & Haute	Mount Asserik	Mount Asserik	Mount Asserik	Sapo	Sapo	Tai	Tai	South-west	Bafing area	Tenkere
Reference	Nissen 1931	De Bouron -onville 1967	Sugiyama 1975-94* (partly pub.)	Ham 1996-97 (unpub.)	McGrew 1976-79* (partly pub.)	Baldwin et al 1981	Baldwin 1979	Anderson et al 1983*	Anderson et al 1983#	Boesch 1978*	Fruth 1990*	Moore 1984* (partly pub.)	Pavy 1992* (unpub.)	Alp 1989-94* (unpub.)
Duration of study	78 days	100 days	?	18 mths	?	40 days	18 mths	2 mths	2 mths	77 days	?	?	?	?
Habitat type	SW	-	SF	AG/OF/ CHF/GF CDF/WS	SV	SW	F/W/G	SW	RF/SF	RF	RF	GWF	W/F	SV/WF
Height of nest (m)														
n	100	184	-	941	-	252	163	67	62	146	154	-	-	-
mean (±SD)	11.5	-	-	13.74 (±0.19)	-	-	11.3	-	13.2	-	23.2	-	-	-
median	-	-	-	-	-	11	-	12	12	-	20	-	-	-
min-max	4-31.5	2-24	10-20	0-35	10-20	-	2-40	6-20	5-35	3.5-15	5-45	<10	10-20	10-20
DBH (cm)														
n	-	-	-	569	-	249	-	-	-	-	-	-	-	-
mean (±SD)	-	-	-	56.96 (±8.19)	-	-	-	-	59.50	-	42	-	-	
median	-	-	-	-	-	121-140	-	52	52	-	33	-	-	-
min-max	-	-	-	-	-	-	-	6-25	41-60	-	6-168	-	-	-

Notes: Habitat types: AG agricultural forest, CDF closed dry forest, CHF closed humid forest, F forest, GF gallery forest, G grassland, GWF mosaic of grassland-woodland and forest, OF open forest, RF rain forest, SF secondary forest, SV savanna, SW savanna-woodland, W woodland, WF woodland forest, WS wooded forest

DBH: diameter at breast height of nesting tree, - denotes no data, ? denotes not known

*where it was impossible to gain original publications the * symbol indicates information cited from the review papers of Fruth and Hohmann (1994, 1996)

where the same reference has been presented twice, the symbol # indicates original reference, to distinguish from above where discrepancies have been found between the two sources

Table 9.24 Structural characteristics of wild and reintroduced chimpanzees; subspecies *Pan troglodytes troglodytes*

	Wild chimpanzee populations					Reintroduced chimpanzee group
Country	Cameroon	Equatorial Guinea	Equatorial Guinea	Gabon	Gabon	Republic of Congo
Study site	Dja Reserve	Rio Muni	Rio Muni	Lopé	Lopé	Conkouati
Reference	Williamson 1994* (unpub.)	Jones & Sabater 1971*	Jones & Sabater 1971#	Tutin & Fernandez 1983*	Wrogemann 1992*	Current data
Duration of study	?	2 mths	2 mths	?	16 mths	3.5 mths
Habitat type	LF	AF/PF/SF/SWF	AF/PF/SF/SWF	RF	RF	IF/PF/SWF
Height of nest (m)						
n	-	195	195	1741	523	261
mean (±SD)	-	-	-	8.7	11.7	21.95 (±0.36) (adjusted data -15%)
median	-	10	10	-	10	21.25
min-max	<10	-	-	2-32	2-45	2.5-42.50 (adjusted data -15%)
DBH (cm)						
n	-	187	79	-	-	258
mean (±SD)	-	-	-	-	34.6	76.53 (±1.61)
median	-	41-60	9-13	-	25	72.38
min-max	-	-	-	-	5-400	17-150

Notes: Habitat types: AF agricultural forest, IF inundated forest, LF lowland forest, PF primary forest, RF rain forest SF secondary forest, SWF swamp forest

DBH: diameter at breast height of nesting tree

- denotes no data ? denotes not known

*where it was impossible to gain original publications the * symbol indicates information cited from the review papers of Fruth and Hohmann (1994, 1996)

where the same reference has been presented twice, the symbol # indicates original reference, to distinguish from above where discrepancies have been found between the two sources

Table 9.25 Features of nests made by wild chimpanzees; subspecies *Pan troglogytes schweinfurthi*

Country		Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Uganda	DRC
Study site		Mahale	Gombe	Ugalla	Kanyawara	Ngogo	Kanyawara	Budongo	Kahuzi-Biega
Reference		Nishida 1966-94* (unpub.)	Goodall 1968	Moore 1985-94* (unpub.)	Wrangham 1987-94* (partly pub.)	Ghiglieri 1984	Ghiglieri 1984	Brownlow et al 2001	Basebose & Yamagiwa 2002
Duration of study		?	?	?	?	11 mths	3 mths	26 mths	12 mths
Habitat type		GWF	GWF	W	MRF	RF	RF	SDF	PF/SF
Nest features									
Nest :	n	384	-	-	-	451	148	-	310
Position of nest in crown:	Indication	-	bottom	no preference	-	-	-	-	-
Type of nest cover:	%	-	-	-	-	-	-	-	-
Uncovered (open)	%	-	-	-	-	-	-	-	-
Intermediate	%	-	-	-	-	-	-	-	-
Covered (closed)	%	-	-	-	-	-	-	-	-
Nests made per tree:	median	-	-	-	-	-	-	-	-
	mean	-	-	-	-	-	-	-	[b]1.5 (104) 1.7 (94)
Trees used to make nest:	maximum	2	-	2	-	-	-	-	-
	median	-	-	-	-	-	-	-	-
Integrated nests:	%	<5%	-	-	-	-	-	-	-
Nest tree and feeding tree:	dn = day nest nn = night nest	dn/nn	dn	dn/nn	dn/nn	-	-	-	[b]24.7 (28) 29.6 (42)
Tree species:	n	-	-	-	-	21	14	-	28
Nest re-used:	Indication	yes	20x	yes	-	-	-	[a]9.6% (16.3%)	-
Nearest neighbour distance:	median	-	-	-	-	-	-	-	-
	mean	-	-	-	-	-	-	-	-

Notes: Habitat types: GWF mosaic of grassland-woodland and forest, MRF montane rain forest, RF rain forest, SDF semi-deciduous tropical forest, W woodland

- denotes no data ? denotes not known

*where it was impossible to gain original publications the * symbol indicates information cited from the review papers of Fruth and Hohmann (1994, 1996)

[a] First figure represents outside of brackets represents to the percentage of night nests re-used and the second in brackets to the percentage of day nests re-used

[b] First figure outside of brackets represents the percentage of nests made within feeding trees in primary forest and the second figure outside of brackets in secondary forest. Figure in brackets represent corresponding sample size. All data refer to night nests

Table 9.26 Features of nests made by wild chimpanzees; subspecies *Pan troglodytes verus*

Country		Rep. of Guinea	Rep. of Guinea	Senegal	Senegal	Senegal	Liberia	Ivory Coast	Mali	Mali	Sierra Leone
Study site		Bossou	Fouta Djallon, Guinée Martime, Forestière & Haute	Mount Asserik	Mount Asserik	Mount Asserik	Sapo	Tai	South-west	Bafing area	Tenkere
Reference		Sugiyama 1975-94* (partly pub.)	Ham 1996-97 (unpub.)	McGrew 1976-79* (partly pub.)	Baldwin 1979	Baldwin et al 1981	Anderson et al 1983	Boesch 1979-94* (unpub.)	Moore 1984* (partly pub.)	Pavy 1992* (unpub.)	Alp 1989-94* (unpub.)
Duration of study		?	18 mths	?	18 mths	40 mths	2 mths	?	?	?	?
Habitat type		SF	AG/OF/CHF/GF/CDF/WS	SV	F/W/G	SW	RF/SF	RF	GWF	W/F	SV/WF
Nest features:	Measure										
Nest:	n	-	918	-	163	252	252	-	-	-	-
Position of nest in crown:	indication	top/bottom	-	top	top	-	-	-	-	middle	top
Type of cover:											
Uncovered (open)	%	-	-	-	-	75	21	-	-	-	-
Intermediate	%	-	-	-	-	-	-	-	-	-	-
Covered (closed)	%	-	-	-	-	25	79	-	-	-	-
Nests made per tree:	median	-	-	-	-	2	-	-	-	-	-
	mean	-	1.55 (±0.04)	-	-	-	-	-	-	-	-
Number of trees used to make nest:	maximum	3	-	4	-	-	-	-	-	-	2
	median	-	-	-	-	2	-	-	-	-	-
Integrated nests:	%	5-10%	-	5-10%	-	-	-	-	<5%	-	<5%
Nest tree and feeding tree:	dn = day nest nn = night nest	dn/nn	-	dn/nn	-	-	-	-	-	dn/nn	dn/nn
Tree species used:	n	-	-	-	23	-	-	-	-	-	-
Nest re-used:	indication	yes	-	yes	-	-	-	yes	-	yes	yes
Nearest neighbour distance (m):	median	-	-	-	-	4	4	-	-	-	-
	mean	-	-	-	-	-	-	-	-	-	-

Notes: Habitat type: SF secondary forest, AG agricultural forest, CDF closed dry forest CHF closed humid forest, F forest, G grassland, GF gallery forest, GWF mosaic of grassland-woodland forest, OF open forest, RF rain forest, SV savanna, SW savanna-woodland, W woodland, WF woodland forest, WS wooded forest, - denotes no data ? denotes not known

* where it was impossible to gain original publications the * symbol indicates information cited from the review papers of Fruth and Hohmann (1994, 1996)

Table 9.27 Features of nests made by wild and reintroduced chimpanzees; subspecies *Pan troglodytes troglodytes*

		Wild chimpanzee populations				**Reintroduced chimpanzee group**	
Country		Cameroon	Equatorial Guinea	Equatorial Guinea	Gabon	Republic of Congo	
Study site		Dja Reserve	Rio Muni	Rio Muni	Lopé	Conkouati	
Reference		Williamson 1994 (unpub.)	Jones & Sabater* 1971	Jones & Sabater# 1971	Wrogemann 1992*	Current data	
Duration of study		?	2 mths	2 mths	16 mths	3.5 mths	
Habitat type		LF	PF/SF/AF	PF/SF/ SWF/AF	RF	IF/SWF/PF	
Nest Features:	**Measure**						
Nest :	n	-	195	-	523	see below against each feature	
Position of nest in crown:	indication	bottom	-	Bottom	middle	-	
Type of nest cover:							
Uncovered (open)	%	-	17	10.1	38.2	42	(n=109/261)
Intermediate	%	-	-	-	-	42	(n=111/261)
Covered (closed)	%	-	83	89.9	61.8	16	(n=41/261)
Nests made per tree:	median (±IQR)	-	1	-	-	2 (±1.00)	(n=242)
	mean (±SD)	-	-	-	-	2 (±0.02)	(n=242)
Trees used to make nest:	maximum	3	-		2	2	(n=261)
	median (±IQR)	-	1	-	-	1 (±0.00)	(n=261)
Integrated nests:	%	30-50			8.4	5	(n=13/261)
Nest tree and feeding tree:	dn = day nest						
	nn = night nest	-	-	-	dn/nn	nn	(n=29/264)
Tree species:	n	-	-	-	45	21	(n=163/264)
Nest re-used:	indication	-	-	-	yes	6%	(n=16/261)
Nearest neighbour distance:	median (±IQR)	-	4	3-4 (n=82)	6	5.75 (±5.00)	(n=236)
(m)	mean (±SD)	-	-	-	-	7.92 (±0.39)	(n=236)

Notes: Habitat type: AF agricultural forest, LF lowland forest, PF primary forest, RF rain forest, SF secondary forest, SWF swamp forest

- denotes no data ? denotes not known

* where it was impossible to gain original publications the* symbol indicates information cited from the review papers of Fruth and Hohmann (1994, 1996)

where the same reference has been presented twice the symbol # indicates original reference to distinguish from above where discrepancies have been found between the two sources

Ten studies of wild chimpanzee groups collected data on whether nests were re-used; eight simply reported that it did occur, one that it occurred once, and one study presented a percentage of 9.6% for night nests and 16.3% for day nests. The reintroduced group re-used night nests on 6% of occasions, slight lower than found for the one study that collected comparable data. Six studies on wild chimpanzee groups reported data on nearest nest distances. The median distance between wild chimpanzee nests ranged from 3-6m; the median distance found for the reintroduced group of 5.75m fell within this range although to the higher end of the scale.

Nine studies reported that day and night nests had been built in feeding trees although the amount of times this occurred was only specified in one study and accounted for approximately one quarter of all nests made. In the present study 11% of night nests were built in trees where feeding had also occurred. Due to the paucity of data collected and reported on wild chimpanzee groups, and lack of conformity in data presentation, precluding reportage, further comparisons will be addressed in the discussion.

9.5 Discussion

The following sections discuss the characteristics and features of nests made by the reintroduced and wild chimpanzees.

9.5.1 Time of nest construction

The reintroduced chimpanzees built night nests post-release, high in trees, without human encouragement. Although data collection did not commence until two months post-release, due to the presence of some nests pre-release and anecdotal observations of nest building immediately post-release, it is assumed that the chimpanzees were also building fully functional nests throughout this initial post-release period. They made their nests at the same time as wild chimpanzees (prior to dusk) and performed the same behaviours upon leaving the nest in the morning as wild chimpanzees (personal observation). There was little variation in the time at which nests were made between the chimpanzees. It is noteworthy that Koutou generally made his nests last. Koutou often remained on the periphery of the group and had a strong attachment to people. On several occasions close to dusk, Koutou remained on the ground, and would sit close to the observers in preference to selecting a tree as a nest site. Occasionally Koutou would not make a nest but wait for the observers to retreat, follow them, and make a nest close to camp.

Very few studies have published data on day nests. Nissen (1931) who worked during the dry season, never observed chimpanzees construct day nests. Goodall (1962), during a season of long rains observed the construction of day nests. She found that within a group of eight chimpanzees only one would make a day nest, whilst the others would merely lie along branches. In the present study all the analysed data refer to night nests as only a small number of day nests were made. There could be two possible explanations as to why day nests were infrequently made in the present study. Firstly the data were collected towards the end of the rainy season and a new dry season, rather than the midst of a rainy season as in Goodall's (1962) study. Interestingly, the eleven chimpanzees not included in the main body of analyses primarily built their day nests in the rainy season. Alternatively, due to a limited number of suitable nesting trees on the pre-release island, the possibility of making day nests may have been restricted. However, this did not prevent the aforementioned chimpanzees from building day nests. Two of these chimpanzees (Jeanette and Choupette) were responsible for making 16 of the day nests and they were also released from Yombe Island. If day nests do serve different functions and can be characterised as rest stops between feeding episodes (Brownlow et al., 2001) then as a consequence of supplementary food provision pre-release such rest stops may not have been necessary or routinely performed by the reintroduced chimpanzees. This factor may have exerted some influence on the prevalence of day nests post-release.

9.5.2 Structural characteristics of nests

9.5.2.1 Nest height, tree height and DBH

The height of nests made by wild chimpanzees varies according to study site (Tables 9.22-9.24). The mean height of nest ranges from 8.7m – 23.2m with the median score of this range falling at 11.45m. Overall, no obvious difference between the subspecies is apparent, although at each study site the sample size and forest description vary which complicates comparison. The mean nest height for the reintroduced group was approximately 22m (-15%) with very little individual variation. The only wild population whose mean nest height came close (23m) is that in the Tai forest (Fruth, 1990 cited in Fruth, 1994). The adjusted score (-15%) accounts for any possible over-estimation of nest height but it was still high. There are many possible explanations as to why the nests of the reintroduced chimpanzees were higher than those made by wild chimpanzees. It may be attributable to forest type and tree height. However, forest description varies according to site (which may reflect a difference in description rather than type), and no data have been collected on the height of nest tree for wild populations, and hence it is not possible to make the comparison. However, as height of nest tree has a linear relationship with DBH, it should be possible to compare DBH to gain an indicator of comparative tree size. Unfortunately from 30 study sites displayed in Tables 9.22-24, only four present DBH. The mean DBH (cm) of nest tree for the wild chimpanzee groups ranges from 35cm-60cm. The mean DBH for the reintroduced group is approximately 76cm, providing an indicator that the trees were larger, possibly explaining why the nests were higher. The reintroduced chimpanzees built their nests at the mean proportional tree height of 0.84 (±0.01) with slight individual variation (Table 9.8). Baldwin (1979) found that wild Senegalese chimpanzees built their nests at 0.8 of the height of the nest tree. The similarity in proportional height that nests were built suggests that tree height may explain the high nests for the reintroduced chimpanzees, although there may be other factors involved.

The relocation from a relatively 'safe' to a new and potentially 'hostile' environment may have caused the chimpanzees to build high nests. This could be attributed to negative encounters they experienced with the previously released groups, or possible (but unknown) contact with hostile wild groups and/or perceived predator presence, whether real or not. The chimpanzees may have been actively seeking taller trees in which to make high nests as an adaptive response to their new situation. It is worth noting that many of the nests must have been made in emergents because the mean canopy height (Tutin, 1994; Sita, 1996) was lower than the tree heights. Alternatively, the pre-release environment with its restricted range of nesting possibilities could have prevented the chimpanzees from climbing to such heights, and the recorded heights merely reflect an extension of height use and exploration. Whoever built their nest first, for example David could have started this behaviour and the others simply followed suit.

These explanations may also provide an answer as to why the height of the nests increased over the study period for the reintroduced group. This trend only gained statistical significance for Agathe and Koutou, but the trend was visible for all chimpanzees. However, if the increase in nest height was due to 'threat', we might have expected more of a sharp increase rather than a gradual one. Alternatively, the gradual increment seen in nest height could be a consequence of late afternoon feeding activity within particular areas dictated by seasonal availability of certain foods. Nests were made close to the last feeding place before dusk and their height could simply be a consequence of tree height within the feeding area. An increment was seen in nest tree height across the study period although not exactly the same pattern was seen for nest height. There are no ecological data to confirm or refute this argument except that the majority of nests were built in the same forest type; inundated forest. Supportive observations for particular explanations are lacking, and there may be many reasons for the high nests and the increase in nest height seen. One would expect where there has been an over-estimation of heights, it should over time correct itself. However, that the nest height increased rather than decreased over time supports the finding that the chimpanzees were building their nests high, and it was not just a factor of over-estimation of heights.

No nests made by the reintroduced group were located at ground level. Ground nests may be a consequence of environmental conditions such as steep sloping areas lacking suitable trees (Matsuzawa and Yamakoshi, 1996). Therefore it is possible that in the present study nests were made off the ground as a response to the seasonally inundated and swamp nature of the forest in which they built their nests. If this group extends its range, it will be interesting to see if ground nests occur in drier primary forests. Interestingly, Mekoutou (not included in these specific analyses) was responsible for making the majority of day nests and the majority of these were made on the ground (five out of six). Mekoutou was extremely attached to people and would frequently stay on the ground and remain close to observers rather than climb in the trees like other members of the group (personal observation).

9.5.2.2 Tree species

The number of different tree species within which wild chimpanzees made their nests varies from 14-45, however only 4 out of the 20 listed studies collected these data. Clearly the number of species identified may be a function of length of study period and how good the identification is. However, the present study of 3.5 months identified more tree species in comparison to some studies that were 11-18 months in duration (Tables 9.25-9.27) and this is with 38% of nest tree species remaining unidentified. The reintroduced chimpanzees made nests in 21 identified tree species. This preference is likely to be habitat specific but cannot be tested unless the density of each species is estimated, and this has not been achieved in any of the studies including the present one. However, within each broad habitat type, chimpanzees seem to favour a small number of tree species, and these preferences have been found not always to relate to their frequency in the type of vegetation. Baldwin (1979) found that the most popular species in woodland was also the most popular in grassland. This was surprising because although this species was the second most common found in woodland, in grassland it did not even occur on the transect. An ideal tree for nesting is presumably one that has many soft leaves attached to thin pliable twigs. Neither the trunk nor branches should be spiny. Branches should be pliable so that they can be bent in to form the base of the nest.

The most favoured tree species for nesting by the reintroduced group was *Panda oleosa*, followed by *Irvingia gabonensis*. Both of these trees fit the criteria for suitable nesting trees, although as *Irvingia* is generally a large tree in comparison to *Panda*, and taking into account the high nests the reintroduced chimpanzees made, *Irvingia* would seem a more obvious choice.

On three occasions nests were made in *Elaeis guineensis* (more familiarly known as the oil palm tree) by the same female; Agathe. This species was also used to make nests on ten occasions by four previously reintroduced chimpanzees. The use of this particular tree is worth noting because of the debate it has generated in its use, or more precisely its selective use (Nissen 1931; Schaller cited in Goodall, 1962; Goodall,1962; DeBournonville, 1967; Gippoliti and Dell'Omo, 1995; Kortlandt, 1996; Ham, 1997). Of the present study group, Agathe was the only chimpanzee to make a nest in the crown of a palm, despite all the chimpanzees having originated from the same area and same island. Interestingly, eight nests made in *Elaeis guinnensis* by two of the previously reintroduced chimpanzees were also released from Yombe Island. With such a small data set it is impossible to state whether Agathe also developed a fashion for making nests in oil palms. A long-term study may illustrate other factors involved and may even show the spread of this behaviour.

9.5.3 Nest features

9.5.3.1 Feeding behaviour in and around the nesting tree

Goodall (1962) found that when chimpanzees are feeding at dusk they will nearly always leave the feeding tree and make a nest in a non-feeding tree nearby. As mentioned previously the reintroduced chimpanzees made their nests within a mean distance of 14.48m (±0.98) from the last feeding site of the day. How often wild chimpanzees nest in feeding trees is unclear. Goodall (1962) and Fruth and Hohmann (1996) argue that despite the close proximity between nest site and last feeding place, wild chimpanzees rarely make their nests in a tree that they have just fed in, however, recent studies refute this (Basabone and Yamagiwa, 2002). At the Lopé Reserve wild chimpanzees also often make their nests in fruit-bearing trees, especially in trees with highly preferred fruits such as *Dialium* sp., (C.E.G. Tutin, personal communication, 2000). The data collected for wild chimpanzee populations are limited, but at nine study sites it was mentioned that day and night nests were made in feeding trees. The extent of this was only detailed in one study and accounted for approximately a quarter of all nests made (Basabose and Yamagiwa, 2002) but the remaining studies just mentioned that it did occur. The present study found that 67% of nests were made in trees that contained potential edible parts (it is not known whether these trees contained ripe fruit or not). Furthermore, 11% of nests were made in a tree that the reintroduced group had immediately fed in before making their nests. Basabose and Yamagiwa (2002) attribute the high number of nests made in feeding trees to a scarcity of frugivores and low density of fruit food. The precise number of frugivores and fruit density are not known in the present study, but is worthy of future investigation in the light of their results. It has been suggested that primates do not sleep in fruiting trees to avoid a restless night in the midst of nocturnal frugivores (Fruth and Hohmann, 1996). Evidence of wild chimpanzees making day nests more frequently in comparison to night nests in feeding trees supports this argument (Fruth and Hohmann, 1994), but what of diurnal frugivores? Building nests within feeding trees may help to keep competitors at bay (Basabose and Yamigawa, 2002). It is possible however, that there are some food trees which simply do not make comfortable nesting sites due to the seasonal lack of suitable leaves (Goodall, 1968). However, data at each site on potential frugivores, fruit density and feeding habits need to be collected to substantiate either argument.

One possible but as yet neglected explanation could be that it is not ecologically advantageous to make night nests in trees that are 'potential' feeding trees, an action which could involve the destruction of branches, canopy and fruit. Nests constructed in feeding trees at the Lopé Reserve were found to cause some damage to both the tree and its fruit (M.E. Rogers, personal communication, 2000). The reason why this would be less destructive for day nests is that normally they are less substantial than night nests. However, as the extent of nest building in feeding trees seems to vary across sites, it is more likely to be a consequence of differences in food availability, resource competition, or cultural differences.

9.5.3.2 Integrated nests

The maximum number of trees (foliage from) incorporated into a nest by wild chimpanzees is four (McGrew, 1976-79, Table 9.26). In five out of the eight available data sets for this category (Tables 9.25-9.27), the maximum number of trees used was two, and this occurred in 5-10% of all cases.

The percentage of integrated nests varies widely; at Conkouati 5% of nests constructed by the reintroduced chimpanzees were integrated nests, using a maximum of two trees. At Mahale (Tanzania) less than 5% of nests were constructed using more than one tree whilst in the Dja Reserve (Cameroon) this increased to 30-50%. The variation between populations has led Fruth and Hohmann (1996) to suggest that cultural diversity may have a role to play. However, this variation may simply be habitat-specific. The relatively low percentage of integrated night nests in this present study may simply be due to singular suitable nesting trees being abundant. An alternative explanation may involve their pre-release environment; the chimpanzees have spent the first few years of their life on a restricted island environment (an estimated 50 hectares for 14 chimpanzees). It is possible that due to limited tree numbers on the island the chimpanzees were restricted or unable to build integrated nests (a large proportion of the island consists of mangrove areas).

9.5.3.3 Nest re-use

The data on how often re-use occurs in wild populations are scarce and not detailed. At nine study sites (Tables 9.25-9.27) researchers stated that they had seen re-use but only one specified to what extent. Gombe chimpanzees usually made new nests each evening though they occasionally built them in the same tree on consecutive evenings (Goodall, 1968). Over a span of four years, Goodall (1968) noted re-use 20 times, and Nissen (1931) four times over a period of three months. Nissen suggested that fresh foliage gave more warmth and comfort, and reduced the risk of predation due to the change in location and a less noisy nest. It has been suggested that re-use is simply a question of habitat and availability of suitable nesting material. The drier the habitat the more often re-use occurs as in drier habitats trees are scarcer, semi-deciduous, and show a much lower rate of regeneration than in wetter habitats, making nest materials more limited (Fruth and Hohmann, 1996).

The present group re-used nests on 16 occasions (6% of nests) over a period of 3.5 months. This relatively high number in comparison to Goodall (1968) and Nissen (1931) could be habitat specific. However, the chimpanzees spent the majority of their time in seasonally inundated forest where according to Fruth and Hohmann (1996) re-use would be less likely to occur due to the wetter environment. It may be better explained by previous restrictions exerted on nesting behaviour due to limited tree availability on the island, with re-use potentially being the norm due to necessity. High levels of re-use may be maladaptive if they increase predation or increase the possibility of parasitic infestation. However, it has been suggested that wild chimpanzees may re-use nests more frequently than previously thought. Kortlandt (1962, cited in Reynolds and Reynolds, 1965) suspected that chimpanzees in Guinea quite often did not build new nests each night, as the number of nests were insufficient to account for the number of chimpanzees that habitually slept in the area he studied. The re-use of nests by wild chimpanzees may also be determined by cultural factors but so far the data are not sufficiently detailed to develop this argument. Detailed data from habituated groups of chimpanzees will facilitate data collection in many areas presently lacking sufficient comparative detail.

9.5.3.4 Nest parties

The wild chimpanzee normally builds her/his nest within a group. Fruth and Hohmann (1996) suggest that nest parties may reflect differences in social organisation with wild chimpanzees generally choosing to rest in small groups. In 94% of cases the reintroduced chimpanzees nested together as a group. Koutou nested alone on eight occasions and this may have been due to Koutou's attachment to people (personal observation). Occasionally he followed observers at the end of the day rather than stay with the group. Sometimes he would enter the base-camp and then nest nearby. Agathe nested alone on eight occasions. On approximately half of these occasions she had left the main group during the day following aggressive attacks from previously reintroduced chimpanzees after they joined the group. On six occasions the present group (Agathe was present on all of these occasions) nested with previously released chimpanzees (Mekoutou, Rosette and Bougnoule), indicating their ability to integrate successfully with other unknown chimpanzees.

Formation of sleeping groups is common across wild chimpanzee populations, although size of group seems to vary. At Lopé, single nests accounted for more than 53% of all nest groups of chimpanzees (Wrogemann 1992, cited in Fruth and Hohmann, 1994). Goodall (1965) reported that Gombe chimpanzees usually nested within groups of 2-6, the largest group was 17. Izawa and Itani (1966) reported groups of 1-5 for Mahale, with the largest being 9. At Mount Asserik, Baldwin et al. (1981) found a seasonal difference in nest group size, with larger groups being formed in the wet season. The authors explained this by groups ranging wider in the wet season, perhaps in less familiar areas, and as a consequence moving in larger parties affording greater protection. They also suggested that a larger group would have a greater chance of any one individual in the party having knowledge of nearby exploitable food sources. A recent study found that nest group size was positively correlated with the availability of preferred ripe fruits (Basabose and Yamagiwa, 2002). In the present study the size of the group was artificially imposed upon the chimpanzees by humans therefore it is not possible to discuss group size in detail.

9.5.3.5 Nest spacing

In Senegal and Equatorial Guinea, Baldwin et al. (1981) found no difference in the minimum distance between nests at both sites regardless of whether chimpanzees nested in single trees or with other nests in the same tree. They argued that there might be an optimal distance between nests, which would facilitate communication but avoid threatening levels of proximity. However, in the present study the number of nests per tree was significantly negatively related to distance to the nearest nest, for example, as the number of nests made per tree increased, the nearest nest distance decreased. However, that the reintroduced group made nests at a comparable nearest nest distance to data presented on wild populations may partially support a theory of optimal inter-spacing between chimpanzee nests (Baldwin, 1979). Alternatively, nest spacing could be determined by environmental variables. It is beyond the scope of the majority of studies to test for this. However, the present study found a positive correlation between DBH of nest tree and number of nests made in a tree (for three out of four chimpanzees); as the size of the tree increased so did the number of nests made within it. This logically suggests that the number of nests made within a tree may be dependent on tree size and hence forest type. The one non-significant correlation (David) may have been a consequence of small nest sample size in comparison to the other chimpanzees.

A lack of standardised forest descriptions used in fieldwork complicates cross-comparison.

9.5.4 Nest building behaviour in captivity and the wild

Studies of wild (Goodall, 1968; Baldwin et al., 1981) captive (Bernstein, 1969) and rehabilitated chimpanzees (Ron and McGrew, 1988; Marsden née Brewer, 1998) suggest that nest building is primarily learnt. Chimpanzees learn how to build nests by watching one another (particularly the mother with wild chimpanzees) and practising with suitable materials. Studies with rehabilitated chimpanzees have found that less experienced individuals learn from watching more experienced chimpanzees (Ron and McGrew, 1986, Marsden née Brewer, 1998). Furthermore, Bernstein (1969) argues that nest building must be learnt early in life and emphasised the importance of early experience. This is supported by the findings that wild chimpanzees as young as eight months old make rudimentary nest building movements in play (Goodall, 1968) and that captive-born adult chimpanzees fail to build nests despite being placed with more experienced chimpanzees (Bernstein, 1969). Maclean (1997) and Russon (2001) argue that ecological and social experiences must not occur too early as they cannot be assimilated, but likewise should not be offered too late as behaviours become resistant to change. These studies are of obvious importance to reintroduction projects and suggest that from an appropriate age, apes should be provided with suitable training environments and social settings to facilitate the development of such behaviours. However, traditional forms of captivity do not generally offer the necessary incentive or suitable materials for chimpanzees to build functional nests. Evidence suggests that both adult humans (Peterson, Smith, Kokman, Ivnik and Tangalos, 1992) and rhesus macaques (Rapp and Amarel, 1989; Arnsten and Goldman-Rakic, 1990) can learn new motor tasks but take longer to do it than younger individuals. Furthermore, the amount of time needed to acquire skills is generally underestimated (Russon, 2002). The nest building movements exhibited by young wild chimpanzees and captive chimpanzees that show individual components of nest building but not in the correct order, suggest that a desire to elevate and/or insulate the body above the ground may also be involved in the development of this behaviour. The reintroduced chimpanzees in the present study built nests from an early age on the pre-release islands (A. Jamart, founder of HELP, personal communication, 1999). They lived in a pre-release environment that provided them with the natural materials and conditions offering the necessary incentive to build fully functional nests. It seems likely that a combination of social and asocial learning facilitated the development of nest building skills that as highlighted throughout this chapter, resulted in the reintroduced chimpanzees building nests comparable to those built by wild conspecifics.

9.6 Conclusions

- The chimpanzees made functional night nests post-release (needing no encouragement to do so) and this suggests that they had been successfully building nests on the islands pre-release.
- The reintroduced chimpanzees made nests at approximately the same time of day as wild chimpanzees and performed the same behaviour upon vacating the nest.
- Very few day nests were made and this may be related to seasonal influence and the pre-release island. Its prevalence in wild chimpanzees is thought to be low, but is poorly documented.
- The mean height of nests built fell within the range found for wild chimpanzees but on average nests were higher. This may a consequence of taller trees, reflected by large DBH measures. The increment in nest height may be explained by fear, adaptation to a new environment, exploration of height use, and/or seasonal availability of food.
- The reintroduced chimpanzees like their wild conspecifics seem to favour certain tree species for nesting in. Preference of species and its frequency in vegetation warrants investigation.
- The reintroduced chimpanzees made their nests near to their last feeding place of the day and some nests were made within trees in which they had just fed. There is a

paucity of data from field sites but previously it was thought that nesting in food sources was rare in wild chimpanzees but recent evidence suggests it can be common, and may be related to fruit abundance and levels of competition for fruit.

- A lower number of integrated nests and more frequent re-use in comparison to some wild populations (there is a paucity of published data) may be attributable to the pre-release environment.
- The reintroduced chimpanzees primarily made nests within groups and the distance between nests was comparable to that found in wild populations. Distance may be influenced by environmental variables and perhaps reflect a theory of optimal inter-spacing between nests.
- Young chimpanzees whether captive- or wild-born perform rudimentary nest building patterns. A desire to insulate the body from the ground combined with maturation and learning (social and asocial) may explain the ability of the chimpanzees to successfully build nests comparable to those of their wild conspecifics.
- The reintroduced chimpanzees are easily habituated and this offers great potential for researchers to collect detailed information on nest building characteristics and influencing factors. This is a neglected area of research primarily due to the difficulty of collecting data on wild populations.

Chapter 10

Concluding discussion

10.1 Guidelines for reintroduction

The latest IUCN guidelines (2002) are detailed in their recommendations for the planning and implementation of primate reintroduction projects. They recommend that each reintroduction project should develop a set of instructions and protocol that applies specifically to its species, region, etc. The latest edition of the Reintroduction Specialist Group newsletter (Soorae, 2002) is devoted to case studies of primate reintroduction. Each case study describes the methods employed, results, and lessons learnt to guide future primate reintroduction projects. The HELP case study in the newsletter is a précis of this thesis; it describes the complex process of reintroducing chimpanzees to the natural environment, the results, and provides specific recommendations to guide future reintroduction projects to optimise chances of success. To summarise, firstly a suitable release site must be found that takes into account seasonal abundance and variety of food resources, impacts on native fauna and flora, presence and ranging patterns of conspecifics, human habitation and protection. The chimpanzees must possess the necessary skills (and/or be able to adapt and learn new skills) to enable them to survive in the natural environment. They must be provided with a suitable pre-release environment, post-release support and monitoring. The use of radio telemetry and post-release support are central to survival. This supports earlier work by Hannah and McGrew (1991) who likewise emphasised the importance of radio collars when releasing chimpanzees, and recent . research with golden lion tamarins highlighting that post-release support can enhance survival (Beck et al., in press). Capture, transportation and release should be designed to be as stress free as possible. Physiological parameters and psychological well-being should be considered at every stage of the reintroduction process. This is why, as suggested by the IUCN guidelines (2002), that a reintroduction should be a multidisciplinary approach involving a team of people including not only veterinarians but also primatologists that have an in-depth knowledge of species-specific behaviours and needs. So far the recommendations outlined are general and could refer to almost any primate species; all of these points are mentioned in some format within the new guidelines. However, different species in varying settings are likely to demand different considerations, and there are some points specific to apes that need to be emphasised.

During the feasibility and preparation phase of any reintroduction, the criteria of success should be defined. Definition of a successful ape reintroduction must take into account slow breeding rates and small numbers released. Apes require different considerations to other primates due to their slow rate of maturation and long period of dependency in comparison to other primate species (Taylor Parker and McKinney, 1999). This lengthy period of development during which skills are acquired and refined requires a 'soft' approach to reintroduction that should include long exposure to the pre-release environment (with conspecifics), and long-term post-release support in some form. The duration of both will depend upon the background and life history of the study animals. Merging the pre-release and post-release site will remove the stress of transfer and ensure that a suitable training environment is secured. Post-release support may need to be intensive and take the form of provisioning if deemed necessary, guidance to feeding sites, or simply the presence of known human observers to act as reassurance. Central to great ape reintroduction is the human-ape relationship; there should be trust but not excessive dependency. Trust is important as familiar observers can facilitate the acclimatisation phase. However, excessive dependency can be detrimental to the adaptation process and there should be no confusion of species identity; apes should not view humans as conspecifics. It seems likely that the majority of apes reintroduced in the future will originate from in-situ sanctuaries. Orphaned apes normally arrive to sanctuaries when they are infants; this necessitates that humans take on the role of surrogate mother. Therefore it is imperative that in-situ sanctuaries contemplating reintroduction, encourage apes to interact with one another as soon as possible, to gradually wean them from human dependency and influence.

The new guidelines (2002) recommend that release stock should be transported in the morning or evening to avoid the main heat of daytime temperatures. However, there is no recommendation of what time to release. With primate species that do not range far, this may be less of an issue, but apes, particularly chimpanzees who can travel for long distances, should be released in the morning to allow them time to explore and adapt to the new environment. Practically it is far easier to follow an animal during day light hours and releasing close to darkness could prove fatal. The guidelines also recommend that stock should be released at least one kilometre from wild populations. However, due to the xenophobic nature of chimpanzees and aggressive inter-community interactions, this distance should be as great as the release site habitat allows. The results of this study support the earlier findings of Marsden (née Brewer, 1998) and Hannah and McGrew (1991) who advised that ideally a release site should be devoid of wild conspecifics (see p.343-346, for further discussion).

10.2 The aims and objectives of a reintroduction

The new guidelines define the principal aim of any primate reintroduction as the establishment of a viable, self-sustaining population in the wild to an area from which it has been extirpated or become extinct. The HELP chimpanzee reintroduction was not therefore a reintroduction in the true sense, but could be better described as an attempt to supplement or reinforce an existing wild population. However, due to the threats facing wild chimpanzees and other wildlife in the area, it was decided that the reintroduction as part of a wider conservation initiative, called the Integrated Conservation Development Project that was being implemented by the IUCN, could make a significant contribution to conservation in the area (see Chapter 4, p.69). The overall objectives of a reintroduction should include enhancing the long-term survival of a species, maintaining and/or restoring natural biodiversity, providing long-term economic benefits to the local and/or national economy, and promoting conservation awareness. On reflection has the chimpanzee reintroduction programme met the principal aim and objectives?

10.2.1 Principal aim

- **Establishment of a viable, self-sustaining population**

Post-release behavioural analyses have revealed that the reintroduced chimpanzees are proving, in many respects, to be viable and self-sustaining, which satisfies the principal aim of reintroduction. Using the behaviour of wild chimpanzees as a guideline, the reintroduced chimpanzees are viable in the sense that they seem capable of living normally. Activity budgets were dominated by feeding, resting and moving reflecting the overall patterns observed in wild populations. A broad diet with specialisation on a small number of plant species was observed and fruit dominated the diet. The reintroduced chimpanzees adapted to environmental change; in the dry season more time was spent feeding and the chimpanzees managed to maintain a diet dominated by fruit by exploiting different species. The consumption of stem pith remained constant across seasons implying that this plant part was more keystone than fallback. Changes in activity levels over the post-release study period corresponded approximately with the onset of dry and rainy season and that no other distinctive pattern emerged implies that overall the chimpanzees were able to immediately adapt. Feeding and resting showed peaks of performance through the day and likewise although fruit consumption dominated throughout the day, the chimpanzees ate more fruit in the morning and more stem pith and leaf in the afternoon. The chimpanzees utilised both terrestrial and arboreal zones; they spent more time feeding and resting at heights above 15m than below, but more time moving on the ground than above ground level. All the reintroduced chimpanzees made nests high in trees and they were similar in structure to those made by wild conspecifics. Some variations in the budget, diet and nests built were found between the wild and reintroduced chimpanzees but also between wild populations. Populations separated geographically and ecologically can be expected to vary in dietary habits and technological skills. As a consequence of the reintroduced chimpanzees demonstrating successful behavioural and ecological adaptation, a minimum 55% (possible 70%) of the study group (Release 1-4, n=20) survived to the end of the 14 month post-release study period. If all chimpanzees reintroduced to date are included (n=37) a minimum 73% (possible 92%) have survived as of March 2002.

10.2.2 Objectives

- **Enhancing the long-term survival of a species**

Central to long-term viability of species survival is successful reproduction. The first post-release birth occurred in 2001 and nursing females (including those remaining on the islands) are displaying the necessary skills for successful mothering. Furthermore, the positive interaction between some reintroduced females and wild conspecifics suggests that females may successfully migrate and reproduce. If migration or integration into a wild population is not feasible (as with the chimpanzees in the Brewer, 1978 study) the best hope for the reintroduced chimpanzees may be to form an independent group. The effective size of a population is based on the number of breeders, their sex ratio, and the relative numbers of offspring they produce during their lifetime (Ballou and Foose, 1996). The extent and rate of loss of genetic diversity in turn depends upon the size of the population. Preserving genetic diversity is thought to maximise the chances that a population will adapt to varying environmental conditions in the future (Ryder and Fleischer, 1996). The question of how much genetic diversity is required to retain long-term fitness and evolutionary potential is of fierce debate within conservation biology (see Franklin and Frankham, 1998 for an example of opposing views). However, in long-lived species such as apes, numbers as low as 40 may be sufficient to ensure population survival over periods such as two hundred years (Cowlishaw and Dunbar, 2000). Hair sample analyses from the reintroduced chimpanzees found that genetic diversity was high and that no individuals were related (Goossens et al., in press). Furthermore, heterozygosity is apparently unaffected when the initial chimpanzee group size is greater than 20 individuals (Williams-Blangero and Dyke, 1992); presently there are 27 individuals surviving post-release. However, it must be noted that these 27 individuals do not remain together as a permanent group and resulting group fractions (if permanent) may limit and potentially prevent reproduction unless migration occurs. Furthermore, once all reintroduced males are returned to the island sanctuary, reproduction will totally rely upon female migration. If the reintroduced female chimpanzees remain isolated from the wild community, then the long-term survival of the species will not be enhanced.

- **Maintaining and/or restoring natural biodiversity**

At least 27 wild-born chimpanzees that originated primarily from the region have been reintroduced and the first post-release birth occurred in 2001. This is an area that had a low density of wild chimpanzees due to hunting, and the reintroduction has served to augment numbers of chimpanzees in the area. Since the project began in 1996 there have been no signs of poaching or deforestation in the Triangle due to the regular presence of project staff. Overall, this part of the reserve is in better condition now than it was in 1996; there have been no negative effects on food plants or sympatric fauna; ape numbers have not declined and the area is seen as an important feeding site for elephants (Maisels and Ononononga, 2000). A detailed survey examining the specific impact that the reintroduced chimpanzees may be having on flora and fauna in the area is needed. However, overall, it does seem as if the reintroduction has successfully maintained (not restored) natural biodiversity. The long-term monitoring of the reintroduced chimpanzees will provide the opportunity to evaluate if this situation continues.

- **Provision of long-term economic benefits to the local and/or national economy**

The economic benefits accrued by HELP extend only to a local level. The benefits include employment, training and locally bought produce. These local economic benefits will only remain viable in the long-term whilst the project maintains a presence in the area.

- **Promotion of conservation awareness**

Due to limited means and restrictive communication networks within the Congo, there has been very little education or public awareness programmes to promote conservation values even in the local population. However, this is due to change at least at a local level and certainly the continued publication of results in scientific literature and popular press will promote conservation concerns for chimpanzees both national and internationally, and highlight the importance of the region for biodiversity.

10.2.3 A welfare perspective

The IUCN/SSC Reintroduction Specialist Group provides guidance to those planning to reintroduce or translocate animals mainly for conservation purposes. Consequently the definition, aim, and objectives of a reintroduction, and the guidelines themselves, do not specifically address projects that release animals long habituated to captivity and released primarily for welfare purposes. However, as highlighted in *Chapter 1 (see p.6), motives* may be inter-linked. Release projects primarily designed to improve welfare may also contribute to wider conservation issues and projects designed primarily for conservation may enhance welfare. Increasing numbers of orphaned primates and sanctuaries throughout the world will ultimately lead to more release projects that include welfare as an objective. It is therefore regrettable that the new guidelines have chosen not to address releases that include welfare as an objective, and to develop guidelines that incorporate issues that may arise as a direct consequence.

The HELP project seems to have met the principal aim of a reintroduction, and all the objectives to some extent, as defined by the new guidelines. However, the reintroduction included both conservation and welfare within its objectives. By using the HELP project as a case study we can highlight what additional factors the issue of welfare introduces. From a welfare perspective, the release could be perceived as a success because 27 chimpanzees (possibly 34) have regained their liberty. However, although the notion of returning animals to the wild has romantic connotations, in reality, life in the natural environment is not, without risks. Three chimpanzees have died and the status of seven remains unknown as a consequence of being released into an environment less predictable than the semi-captive pre-release island. There have been numerous aggressive interactions between the reintroduced and wild chimpanzees. One and possibly two male chimpanzees died as a result of wounds inflicted by wild conspecifics, and consequently HELP has recently decided to return all reintroduced males to the relative safety of the island sanctuary. This strategy is only required due to the presence of wild conspecifics. If chimpanzees are released into an area devoid of wild chimpanzees, then males can also be released, as both males and females, seem able to successfully adapt ecologically. Releasing only female chimpanzees has consequences beyond the issue of reproduction. The removal of the released males in the present project, or female only release projects, may compromise the welfare of female chimpanzees if deprived from protection afforded by the males. Furthermore, female only release projects will produce a surplus of male chimpanzees that will be forced to form unnatural group compositions in captivity and be potentially difficult to accommodate. In the present project, due to the small number of males involved, and the large islands onto which they will be transferred, their welfare should not be adversely affected. Recently, two male chimpanzees (Koutou and Chinois) and a female (Perlette) were attacked by wild conspecifics but surprisingly it was the female that fared worse; she had to be anaesthetised to be administered sutures (HELP-INFO, April 2002). It is not known if the reintroduced chimpanzees are responding inappropriately and aggravating the interaction, or if the aggressive encounters are simply cases of inter-community attacks as seen between wild communities. However, as both sexes are subject to such attacks, coupled with the potential adverse affects on welfare for both sexes if only females are released, together strongly suggests that chimpanzees should only be released into areas devoid of wild chimpanzees. The new guidelines (2002) state that the survival prospects for released primates should at least approximate those of wild animals of the same sex and age. If we consider only the cases of known fatalities then the three deaths may be representative of mortality rates seen in the wild (see Chapter 4, p.88). However, if we assume that all status unknown cases (that consist primarily of females) are also fatalities, then this rate would be high. Clearly, if welfare is a principal objective, then it is important to reduce risks, and to set mortality rates against those accepted in captivity.

10.3 Chimpanzees as candidates for reintroduction

Given the overall successful behavioural and ecological adaptation of the reintroduced chimpanzees, and ultimately their survival, it might be suggested that chimpanzees make good candidates for reintroduction. Ex-laboratory and zoo chimpanzees that were released onto Rubondo Island in Tanzania received no pre-release training, no period to acclimatise, and very little post-release support and provisioning. However, despite this, some survived, and over a period of 30 years have successfully reproduced, and produced a viable population (Moscovice and Huffman, 2001). Likewise, chimpanzees released onto islands in Gabon, The Gambia, Liberia and mainland forest in Senegal have shown adaptive responses that include the consumption of wild foods, nest building, nut cracking, ant dipping and predatory behaviour. These adaptive responses have emerged, despite some chimpanzees having spent long periods of time in captivity without the opportunity to perform such behaviours. It must be stressed, however, that although the survival and successful adaptation of some chimpanzees in these studies may contradict the need to adhere to guidelines, the recommendations outlined will optimise the chances of successful adaptation and survival with minimal losses.

We can look to studies in the wild and captivity to both support and refute the suggestion that chimpanzees make good candidates for reintroduction. Studies on wild chimpanzees indicate that among African apes, the chimpanzee appears the most ecologically adaptable due to its broad geographical range, and utilisation of widely differing habitats (White and Tutin, 2001). The well-documented manufacture and use of tools by chimpanzees to combat practical problems, particularly to access food items, reflects behavioural and cognitive flexibility and adaptations to particular ecological niches (McGrew, 1992). Furthermore, the fission-fusion society, and female migration that characterise chimpanzee life also suggests that chimpanzees, especially females, are socially as well as ecologically adaptable. Consequently one might expect that chimpanzees would easily adapt to habitat change. However, studies in both east (Skorupa, 1986) and west Africa (Tutin and Fernandez, 1984; White and Tutin, 2001) have shown that chimpanzee densities decline following logging, and that recovery of density is a slow process that can take 15-25 years (White and Tutin, 2001). White and Tutin (2001) attributed the marked and long-term decrease in chimpanzee density to social factors, as the level of logging damage in their study was low, and chimpanzee food trees were not selectively extracted. The noise and disturbance that occurs as a result of logging, may displace entire chimpanzee communities into the home range of other communities, forcing inter-community encounters that are often characterised by aggression and mortality. In contrast, Plumptre and Reynolds (1994) found no evidence of negative effects of logging on chimpanzees at Budongo in Uganda. However, White and Tutin (2001) suggest that the smaller logging concessions in the area would probably not force the chimpanzees to move out of their home range, only to a different part of their own territory. Taken together, these studies suggest that although wild chimpanzees can adapt ecologically to changing physical environments, they may be socially less flexible. Interestingly, it is the xenophobic nature of wild chimpanzee society that has prevented the successful reintroduction of chimpanzees in the past (Marsden née Brewer, 1998) and also in the present project. Mortality and aggression have characterised encounters between released chimpanzees and wild conspecifics (Marsden née Brewer, 1998), and between chimpanzees released onto different islands when water levels were low (Hannah, 1989). Furthermore, released chimpanzees have even directed aggression towards human strangers (Brewer, 1978).

In captivity, chimpanzees live in a variety of unnatural social arrangements, and generally do well. Chimpanzees are the most common ape in captivity and can be found in zoos, circuses, sanctuaries, laboratories, and private homes. Chimpanzees have reproduced better in captivity than other apes, and the captive population is now considered self-sustaining (Wolfle and April, 1994). Furthermore, mortality rates in captive chimpanzees are lower in comparison to gorillas and bonobos (see p.40). Brent (2001) suggests that it is the resilience and adaptability of chimpanzees that explain their success in captivity. There have been numerous empirical studies dating back to the early 20th century that have highlighted influencing factors as to why chimpanzees may be so adaptable. Historically, captive chimpanzees have been subjects of a wide range of problem-solving experiments (Kohler, 1925; Crawford, 1937; Yerkes, 1943). In subsequent decades, studies on artificial language acquisition and comprehension dominated the literature (Fouts, 1972; Gardner, Gardner and Cantfort, 1989; Rumbaugh, 1977; Savage-Rumbaugh, 1986; Savage-Rumbaugh, Romski, Hopkins and Sevcik, 1989). More recently chimpanzees have been the subjects of empirical studies focusing on imitation (Custance and Bard, 1994; Custance, Whiten and Bard, 1995; Whiten, Custance, Gomez, Teixidor and Bard, 1996); tool use and innovative behaviours in captivity and the wild (Menzel, 1972, 1973; Kummer and Goodall, 1985; Hannah and McGrew, 1991; Boesch, 1995; Matsuzawa, 1997, cited in Boysen and Kuhlmeier, 2001); causality (Limongelli, Boysen and Visalberghi, 1995); gestural communication (Leavens, Hopkins, and Bard, 1996); self recognition (Povinelli, 1987), and numerical skills (Matsuzawa, 1985). The picture that has emerged is an ape with adept motor and cognitive skills, capable of innovative behaviours, observational learning capabilities, self-awareness and an enormous capacity to learn (Boysen and Kuhlmeier, 2001).

Innovation is an important component of behavioural flexibility; it is vital to the survival of species with opportunistic lifestyles, and potentially critically important to species forced to adjust to changed or impoverished environments (Box, 1991b; Lee, 1991; Reader and Laland, 2001). Innovative behaviours may occur both in social and ecological contexts, in some cases with technical assistance. Examples in captivity include Sultan, the chimpanzee who stacked boxes in order to reach a desired food item (Kohler, 1925), and the use of apparatus and structures by chimpanzees to escape from a large laboratory field enclosure (Menzel, 1973; McGrew, Tutin and Midgett, 1975). One female at Arnhem Zoo facilitated reconciliation between two males by sitting between them so that they both groomed her, and then she moved away leaving the males grooming each other (DeWaal, 1982). In the wild, ecological and technical innovations include various forms of tool use to extract food items, i.e., the use of sticks to extricate larva from a tree hole and mushrooms that grow inside termite mounds (Boesch, 1995). Interestingly although research has highlighted more instances of female tool use (e.g., McGrew, 1979), there have been more recorded observations of innovation in male chimpanzees, particularly in social contexts (Reader and Laland, 2001). Social innovations have included individual male chimpanzees rising earlier than the rest of the group to gain access to females (Tutin, 1989), and to gain the alpha position in the group by performing unexpected arboreal displays and causing confusion (Bygott, 1974; Riss and Goodall, 1977). One reason that previous research has emphasised females as more suitable candidates for reintroduction is due to female migration and prevalent tool use, highlighting behavioural flexibility (Hannah and McGrew, 1991). However, male chimpanzees have been observed performing more innovative behaviours in social contexts than females (Reader and Laland, 2001), and there are no more reported instances of innovative behaviour by females in foraging contexts than males. This suggests that males also show behavioural flexibility and therefore may be considered suitable candidates for reintroduction, except into areas inhabited by wild chimpanzees.

Innovative behaviours have also been observed in released chimpanzees. A female chimpanzee released onto an island in Liberia immediately started to crack nuts on the first day of release (Hannah and McGrew, 1991). Over the following weeks most of the group members showed the same technique. In the present study, a female chimpanzee used a stick to poke at the body of a tortoise in an attempt to extricate it from its shell. This behaviour, however, was not observed again. Not every innovative behaviour is disseminated within a group; diffusion may depend upon the adaptive value of the behaviour and the status of the inventor (Boesch, 1995). Using a stick to facilitate access to the body of the tortoise may be adaptive behaviour, however, if this prey is encountered infrequently, then there simply may be little opportunity to practice. There is strong indirect evidence of wild chimpanzees eating tortoises in Lopé (C. Tutin, personal communication, 2002) and for chimpanzees in the Ituri Forest (DRC) to use hammers to smash their shell (Hart, cited in McGrew, 1992). The capacity for innovative behaviours means that chimpanzees can respond to ecological and social problems in different ways, which can then be learnt and spread to other members.

Problem solving tasks have primarily focused on tool-use and have highlighted the learning abilities of chimpanzees. Some studies have exposed naive chimpanzees to both human (Nagell, Olguin and Tomasello, 1993) and chimpanzee demonstrators (Tomasello, Davis-Dasilva, Camak, and Bard, 1987) employing rake-like tools to reach desired food items. Similarly, a human experimenter demonstrated how to open a multi-mechanism transparent box containing fruit to chimpanzees (Whiten, Custance, Gomez, Teixidor and Bard, 1996). In both these studies, the chimpanzees were able to perform the task following the demonstration. Overall, what these studies suggest is that apes are very intelligent, creative in using tools, and have a highly developed understanding of environmental change (Tomasello, 1996). However, the precise learning processes involved remain poorly understood and continue to be fiercely debated (Laland, Richerson and Boyd, 1996; Tomasello, Kruger and Ratner, 1993; Byrne, 1995; Call and Tomasello, 1996; Taylor Parker, 1996; Tomasello, 1996). Regardless of the processes involved in learning (of which there are probably many, with individual variation), the propensity of chimpanzees to learn has been exploited in captivity. Training, using positive operant conditioning techniques, have been employed to facilitate co-operation in husbandry, veterinary and research procedures (Laule and Whittaker, 2001). Release projects have also exploited chimpanzees' learning abilities, to facilitate skill development and transmission to optimise adaptation, through the provision of suitable materials and demonstrators (Brewer, 1978; Hannah and McGrew, 1991). For example, chimpanzees later introduced to islands in Liberia benefited from travelling with chimpanzees that already knew their way around and what to eat (Hannah and McGrew, 1991). All great apes show positive social learning effects (Custance et al., 2002), which is not surprising if we consider for example, that in the wild, infant chimpanzees learn what to eat primarily through observation of their mothers and other members of the group (Goodall, 1968). The role of mothers in the acquisition of tool use has also recently been demonstrated in captivity (Hirata and Celli, 2002).

There is no simple answer to the question of whether chimpanzees make especially good candidates for reintroduction. Ecologically, chimpanzees, both wild and released, males and females, appear to be adaptable to some degree of environmental change. However, whilst their ability to learn from known conspecifics can be exploited to facilitate skill transmission in release programmes, interaction with 'strangers' has proven overall to be detrimental to survival. There is also likely to be great individual variation as a consequence of, for example, temperament and prior history (Hannah and McGrew, 1991).

10.4 Apes, sanctuaries and reintroduction

Although saving habitats should be the first priority, as this is the most effective and economical way to safeguard biodiversity, most conservation problems are too complex and variable to yield to one simple solution, and are likely to benefit from a mixture of tactics. Conservation management strategies follow fashions; the favoured protected area management has been displaced by sustainable utilisation and community conservation (Cowlishaw and Dunbar, 2000). Recent research highlighting that more than one-fifth of primates sold for meat in the markets of Cameroon are infected with the Simian Immuno-deficiency Virus (ancestor of HIV) are being used by conservationists to deter consumption of bushmeat. Formal links between the conservation community and logging companies are beginning to emerge (Tutin, 2001). The importance of law enforcement in conservation is just beginning to be recognised and this will necessitate the use and development of sanctuaries. Furthermore, as we continue to learn more about apes, it seems likely that conservationists will also turn to ethical issues and ape rights (Butynski, 2001). These approaches need not be in competition with one another (McGrew, 1983a; Tutin, 2001) as the preservation and protection of primate biodiversity will ultimately rely on a more eclectic approach.

The complex causal factors responsible for the decline in African ape numbers outlined in Chapter 1 are accelerating, whilst population numbers are sharply declining (Nellemann, and Newton, 2002). As a direct consequence, the number of orphaned apes in need of refuge continues to increase, as does the number of sanctuaries needed to accommodate them. The orphaned apes are the visible victims of this complex crisis and in the long-term it is the attitudes and actions of the people who share their habitat that will decide their fate. Sanctuaries not only address the welfare issues of displaced apes, but they also play an important role in facilitating law enforcement, and their activities are inextricably interlinked to conservation issues. In-situ sanctuaries are ideally placed to promote conservation education and to potentially supply 'flagship' species for future reintroduction programmes.

10.5 Final comments

As a consequence of increasing threats to primates, reintroduction projects are likely to increase in number due to the precarious status of many species in the wild. The results of this thesis overwhelmingly suggest that reintroduction may offer a long-term solution for some chimpanzees. However, it must be stressed that the situation at Conkouati is in many ways unique and may not be directly comparable to captive chimpanzees in most African sanctuaries where release onto islands or into areas of enclosed forest habitat may be the most appropriate solution. Physical and emotional contact was gradually reduced and kept to a minimum (although perhaps the level of contact in some cases was too minimal). The chimpanzees lived within groups, on islands of natural vegetation, for several years before being released. Finding an appropriate release site is difficult and it was the high female/male sex ratio that facilitated the release into an area where wild conspecifics ranged, however, as mentioned earlier, an area devoid of wild chimpanzees is recommended.

It is clear that published results from projects with already reintroduced (or introduced) populations can be important not only for future releases of the same species but also assist in the development of new projects considering reintroduction with other species. The methodology of the present reintroduction project was guided by the documented results from chimpanzee (Hladik, 1974; Brewer, 1978; Carter, 1981, 1988; Hannah and McGrew, 1991) and monkey (Beck et al., 1994; Kleiman et al., 1994) rehabilitation and reintroduction programmes.

The HELP case study provides an example of experience and recommendations that will benefit other projects if and when they deem factors to be sufficiently favourable to attempt reintroduction of chimpanzees. The latest development of the IUCN Guidelines for Nonhuman Primate Re-introductions (2002) and accompanying special edition newsletter (Soorae, 2002) will facilitate this form of wildlife management to become an increasingly important tool to address the crises confronting many primate species throughout the world. Stanley-Price (1989) argued that the future of reintroduction as a tool to manage wildlife depends upon careful planning, generalising the results from successful projects to reduce costs and then documenting results and experiences. By broadening the very limited knowledge about chimpanzee reintroduction, it is hoped that this study will contribute towards a better understanding of the issues involved and the possibilities that this form of wildlife management offers.

References

Adang, O. M. J. (1984). Teasing in young chimpanzees. Behaviour, 88, 98-122.

Alford, P.L., Bloomsmith, M.A., Keeling, M.E., & Beck, T.F. (1995). Wounding aggression during the formation of and maintenance of captive, multi-male chimpanzee groups. Zoo Biology, 14, 347-359.

Akers, J. S., & Schildkraut, D. S. (1985). Regurgitation, reingestion and coprophagy in captive gorillas. Zoo Biology, 4, 99-109.

Albrecht, H., & Dunnett, S. C. (1971). Chimpanzees in western Africa. Munich: Piper.

Anderson, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. Advances in the Study of Behaviour, 14, 165-229.

Anderson, J. R. (2000). Sleep-related behavioural adaptations in free-ranging anthropoid primates. Sleep Medicine Reviews, 4(2), 129-148.

Anderson, J. R., Williamson, E. A., & Carter, J. (1983). Chimpanzees of Sapo Forest, Liberia: density, nests, tools and meat-eating. Primates, 24(4), 594-601.

Ape Alliance. (1998). The African bushmeat trade - a recipe for extinction. London: Ape Alliance.

Arnsten, A., & Goldman-Rakic, P. (1990). Analysis of alpha-2 adrenergic agonist effects on the delayed non-matching-to-sample performance of aged rhesus macaques. Neurobiology of Aging, 11, 583-590.

Attwater, M., Blake, S., Hudson, H., & Kopf, H. O. (1991). Gorilla protection project proposal document. Unpublished report.

Baldwin, P. J. (1979). The natural history of the chimpanzee (*Pan troglodytes verus*) at Mt. Asserik, Senegal. Unpublished doctoral dissertation, University of Stirling, Stirling, Scotland.

Baldwin, P. J., Sabater Pi, J., McGrew, W. C., & Tutin, C. E. G. (1981). Comparisons of nests made by different populations of chimpanzees (*Pan troglodytes*). Primates, 22(4), 474-486.

Ballou, J. D., & Foose, T. J. (1996). Demographic and genetic management of captive populations. In D. G. Kleiman, M. E. Allen, K. V. Thompson, & S. Lumpkin (Eds.), Wild mammals in captivity (pp. 263-283). Chicago: The University of Chicago Press.

Bard, K. A., & Gardner, K. H. (1996). Influences on development in infant chimpanzees: enculturation, temperament, and cognition. In A. E. Russon, K. A. Bard, & S. Taylor Parker (Eds.), Reaching into thought - the minds of the great apes (pp. 235-256). Cambridge: Cambridge University Press.

Basabose, A. K., & Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. International Journal of Primatology, 23(2), 263-282.

Bayne, K. (1989). Resolving issues of psychological well-being and management of laboratory nonhuman primates. In E. F. Segal (Ed.), Housing, care and psychological well-being of captive and laboratory primates (pp. 27-88). San Diego, California: Noyes Publications.

Beck, B. B., Castro, M. I., Stoinski, T. S., & Ballou, J. (in press). The effects of pre-release environments on survivorship in reintroduced golden lion tamarins . In D. G. Kleiman, & A. Rylands (Eds.), The lion tamarins of Brazil: twenty-five years of research and conservation. Washington: Smithsonian Institution Press.

Beck, B. B., Kleiman, D. G., & Dietz, J. M. (1991). Losses and reproduction in the reintroduced golden lion tamarins *Leontopithecus rosalia*. Dodo, Journal of the Jersey Wildlife Preservation Trust, 27, 50-61.

Beck, B. B., Rapaport, L. G., Stanley-Price, M. R., & Wilson, A. C. (1994). Reintroduction of captive-born animals. In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), Creative conservation: interactive management of wild and captive animals (pp. 265-286). London: Chapman & Hall.

Beck, B. B., & Russon, A. Reintroduction of African great apes. Unpublished manuscript.

Begon, M., Harper, J. L., & Townsend, C. R. (1990). Ecology: individuals, populations and communities. Oxford: Blackwell Scientific Publications.

Berkson, G., Mason, W., & Saxon, S. (1963). Situation and stimulus effects on stereotyped behaviour of chimpanzees. Journal of Comparative and Physiological Psychology, 56, 786-792.

Bernstein, I. S. (1962). Response to nesting materials of wild-born and captive-born chimpanzees. Animal Behaviour, 10, 1-6.

Bernstein, I. S. (1969). A comparison of nesting patterns among the three great apes. In G. H. Bourne (Ed.), The Chimpanzee. Volume 1: anatomy, behaviour and diseases of chimpanzees (pp. 393-402). Basel: Karger.

Bernstein, I.S. (1991). Social housing of monkeys and apes: group formations. Laboratory Animal Science, 41, 329-333.

Biggins, D., Godbey, J., Hanebury, L., Marinari, P., Matchett, R., & Vargas, A. (1998). Survival of black-footed ferrets. The Journal of Wildlife Management, 62, 643-653.

Bloomsmith, M. A., Alford, P. L., & Pazol, K. A. (1991). Juvenile chimpanzee behavioural development in four social settings. American Journal of Primatology, 24, 90.

Bloomsmith, M. A., Finlay, T. W., Mershalski, J. J., & Maple, T. L. (1990). Rigid plastic balls as enrichment devices for captive chimpanzees. Laboratory Animal Science, 40(3), 319-322.

Bloomstrand, K. R., Riddle, K. A., & Maple, T. L. (1986). Successful feeding enrichment for captive chimpanzees. Zoo Biology, 5, 293-300.

Boesch, C. (1995). Innovation in wild chimpanzees (*Pan troglodytes*). International Journal of Primatology, 16(1): 1-15.

Boesch, C., & Boesch, H. (1981). Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. Journal of Human Evolution, 10, 585-593.

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. Journal of Human Evolution, 13, 415-440.

Boesch, C., & Boesch, H. (1989). Hunting behaviour of wild chimpanzees in the Tai National Park. American Journal of Physical Anthropology, 78, 547-573.

Boesch, C., & Boesch-Achermann, H. (2000). The chimpanzees of the Tai Forest - behavioural ecology and evolution. New York: Oxford University Press.

Borner, M. (1985). The rehabilitated chimpanzees of Rubondo Island. Oryx, 19, 151-154.

Borner, M., & Stonehouse, B. (1979). Orang-utan orphans of the forest. London: W.H. Allen & Co. Ltd.

Box, H. O. (1991a). Responsiveness to environmental change: interrelationships among parameters. In H. O. Box (Ed.), Primate responses to environmental change (pp. 57-74). London: Chapman & Hall.

Box, H. O. (1991b). Training for life after release: simian primates as examples. In J.H.W. Gipps (Ed.), Beyond captive breeding: re-introducing endangered mammals to the wild (pp. 111-123). Oxford: Clarendon Press.

Boysen, S. T., & Kuhlmeier, V. (2001). Conceptual capacities of chimpanzees. In B. B. Beck, T. S. Stoinski, M. Hutchins, T. L. Maple, B. Norton, A. Rowan, E. F. Stevens, & A. Arluke. (Eds.), Great apes & humans, the ethics of coexistence (215-229. Washington: Smithsonian Institution Press.

Brent, L. (2001). A brief history of captive chimpanzees in the United States. In L. Brent (Ed.), The care and management of captive chimpanzees (pp. 1-15). San Antonio, Texas: The American Society of Primatologists.

Brent, L., Lea, D. R., & Eichberg, J. W. (1989). Evaluation of two environmental devices for singly caged chimpanzees (*Pan troglodytes*). American Journal of Primatology Supplement, 1, 65-70.

Brent, L., Kessel, A.L., & Barrera, H. (1997). Evaluation of introduction procedures in captive chimpanzees. Zoo Biology, 16, 335-342.

Brewer, S. (1978). The forest dwellers. London: Collins.

Britt, A., Welch, C., & Katz, A. (1999). Re-stocking of *Varecia variegata vartiegata*: the first six months. Primate Eye, 67, 36-39.

Brownlow, A. R., Plumptre, A. J., Reynolds, V., & Ward, R. (2001). Sources of variation in the nesting behaviour of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. American Journal of Primatology,_55, 49-55.

Bryant, C. E., Rupniak, N. M. J., & Iversen, S. D. (1988). Effects of different environmental enrichment devices on cage stereotypies and autoaggression in captive cynomolgus monkeys. Journal of Medical Primatology, 17, 257-269.

Butynski, T. M. (1997). African primate conservation - the species and the IUCN/SSC Primate Specialist Group Network. Primate Conservation, 17, 87-100.

Butynski, T. M. (2001). Africa's great apes. In B.B. Beck, T. S. Stoinski, M. Hutchins, T. L. Maple, B. Norton, A. Rowan, E. F. Stevens, & A. Arluke (Eds.), Great apes and humans, the ethics of coexistence (pp. 3-56). Washington: Smithsonian Press.

Bygott, J. D. (1974). Agonisitic behaviour and social relationships among adult male chimpanzees. Unpublished doctoral dissertation, University of Cambridge, Cambridge, England.

Byrne, R. (1995). The thinking ape: evolutionary origins of intelligence. Oxford: Oxford University Press.

Call, J., & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In A. E. Russon, K. A. Bard, & S. Taylor Parker (Eds.), Reaching into the though: the minds of the great apes (pp.371-403). Cambridge: Cambridge University Press.

Carter, J. (1981). The Journey to Freedom. Smithsonian, 12, 90-101.

Catrer, J. (1988). Freed from keepers and cages, chimps come of age in Baboon Island. Smithsonian, June, 36-49.

Carter, J. (in prep). Captive chimpanzees in West Africa: experiences and prospects for viability in chimpanzee rehabilitation. In R. Kormos (Ed.), Status survey and recommendations for the conservation of the West African chimpanzee. Washington DC: Conservation International.

Castro, M. I. (1990). A comparative study of anti-predator behaviour in the three species of lion tamarins (*Leontopithecus*) in captivity. Unpublished masters thesis, University of Maryland, Maryland, USA.

Chamove, A. S., Anderson, J. R., Morgan-Jones, S. C., & Jones, S. P. (1982). Hygiene, feeding and behavioural enhancement in eight primate species. International Journal for the Study of Animal Behaviour, 3, 308-318.

Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: comparisons with other *mammals in relation to diet. Journal of* Morphology, 166, 337-386.

Chonghaile, C. (2002). Abandoned chimps highlight conservation challenges in West Africa. The Associated Press 14.09.02, http://www.ni.com/newsflash.

Clark, A. S., Juno, C. J., & Maple, T. L. (1982). Behavioural effects of a change in physical environment: a pilot study of captive chimpanzees. Zoo Biology, 1, 371-380.

Clay, P. (1998). Community-based conservation: an overview of the Conkouati Faunal Reserve in Congo-Brazzaville. Unpublished report.

Clutton-Brock, T. H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In T. H. Clutton-Brock (Ed.), Primate Ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes (pp. 539-538-556). London: Academic Press.

Conly, S. R. (1998). Sub-saharan African at the turning point. The Humanist, 58, 19-23.

Courtenay, J., & Santow, G. (1989). Mortality of wild and captive chimpanzees. Folia Primatologica, 52, 167-177.

Cowlishaw, G., & Dunbar, R. (2000). Primate Conservation Biology. Chicago: The University of Chicago Press.

Cox, D. (1998). Uganda: new homes and new projects. The Jane Goodall Institute World Report, 14-15.

Crawford, M. P. (1937). The cooperative problem-solving by chimpanzees of problems requiring serial responses to colour cues. Journal of Social Psychology, 13, 259-280.

Cullen, P. A., & Swan, R. A. *(2001). A study of factors* associated with the survival of gibbons reintroduced in South-East Asia. *Proceedings of the XVIIIth Congress of* the International Primatological Society: Primates in the new millennium.

Custance, D. M., & Bard, K. A. (1994). The comparative and developmental study of self-recognition and imitation: the importance of social factors. In S. T. Parker, R. W., Mitchell, & M. L. Boccia (Eds.), Self-awareness in animals and humans: developmental perspectives (pp. 207-225). New York: Cambridge University Press.

Custance, D, M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees imitate arbitrary actions? Hayes and Hayes revisited. Behaviour, 132: 839-858.

Custance, D. M., Whiten, A., & Fredman, T. (2002). Social learning and primate reintroduction. International Journal of Primatology, 23(3), 479-499.

DeBournonville, D. (1967). Contribution à l'étude du chimpanzé en Republique de Guinée. Bulletin - Institut Fondamental D'Afrique Noire, Serie A, 29(3), 1188-1269.

DeVore, I., & Hall, K. R. L. (1965). Baboon ecology. In I. DeVore (Ed.), Primate behaviour: field studies of monkeys and apes (pp. 20-52). New York: Holt, Rinehart & Winston.

Didier, S., Roeder, J. J., Krief, J. M., Poullet, S., & Jamart, A. Coprophagy among chimpanzees: a strategy to use unavailable resources? Unpublished manuscript.

Dolhinow, P. J., & Bishop, N. (1972). The development of motor skills and social relationships among primates through play. P. Dolhinow (Ed.), Primate patterns volume 10 (pp. 312-337). New York: Holt, Reinhart & Winston.

Doran, D. (1997). Influence of seasonality on activity patterns, feeding behaviour, ranging, and grouping patterns in Tai chimpanzees. International Journal of Primatology, 18(2), 183-206.

Doumenge, C. (1992). La Reserve de Conkouati: Congo Le secteur sud-ouest. Gland, Switzerland: IUCN.

Dowsett, R. J. (1991). Meterological and hydrological data from the lower Kouilou Basin, Congo. In R. J. Dowsett, & F. Dowsett-Lemaire (Eds.), Flore et faune du Bassin du Kouilou (Congo) et leur exploitation (pp. 7-16). Jupille-Liege, Belgium: Tauraco Press.

Dowsett, R. J., & Dowsett-Lemaire, F. (1991). Flore et faune du bassin du Kouilou (Congo) et leur exploitation. Jupille-Liege, Belgium: Tauraco Press.

Dunbar, R. I. M. (1976). Some aspects of research design and their implications in the observational study of behaviour. Behaviour, 58, 78-98.

Dunbar, R. I. M. (1977). Feeding ecology of gelada baboons: a preliminary report. In T.H. Clutton-Brock (Ed.), Primate ecology: studies of feeding and ranging in lemurs, monkeys and apes (pp. 251-273). London: Academic Press Ltd.

Dunbar, R. I.M. (1988). Primate social systems. London: Chapman & Hall

Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. Folia Primatologica, 57(3), 121-131.

Dunbar, R. I. M., & Sharman, M. (1984). Is social grooming altruistic? Z. Tierpsychol., 64, 163-173.

Dyke, (2001). How much will it cost to keep our chimpanzees? In L. Brent (Ed.), The care and management of captive chimpanzees (pp.266-275). San Antonio, Texas: The American Society of Primatologists.

Erwin, J. (1979). Strangers in a strange land: abnormal behaviour or abnormal environments? In J. Erwin, T. L. Maple, & G. Mitchell (Eds.), Captivity and behaviour (pp.1-28) New York: Van Nostrand.

Farmer, K. H. (1996). Plight of the bushmeat babies. Biologist, 43(3), 134-135.

Fawcett, K. A. (2000). Female relationships and food availability in a forest community of chimpanzees. Unpublished doctoral dissertation, University of Edinburgh, Edinburgh, Scotland.

Fischer, J., & Lindenmayer, D. B. (2000). An assessment of the published results of animal relocations. Biological Conservation, 96, 1-11.

Foddy, W. (1995). Constructing questions for interviews and questionnaires. Cambridge: Cambridge University Press.

Fornos, W. (1998). No vacancy. The Humanist, 58, 15-18.

Fossey, D. (1983). Gorillas in the Mist. Boston: Houghton Mifflin Company.

Fossey, D., & Harcourt, A. H. (1977). Feeding ecology of free ranging mountain gorilla (*Gorilla gorilla beringei*). In T. H. Clutton-Brock (Ed.), Primate ecology: studies of feeding and ranging in lemurs, monkeys and apes (pp. 415-479). London: Academic Press Ltd.

Fouts, R. S. (1972). Use of guidance in teaching sign language to a chimpanzee (Pan troglodytes). Journal of Comparative Psychology, 80: 515-522.

Franklin, I. R. & Frankham, R. (1998). How large must populations be to retain evolutionary potential? Animal Conservation, 1, 69-73.

Fritz, J., Nash, L. T., Martin, T., & Matevia, M. (1992). The relationship between forage material and levels of coprophagy in captive chimpanzees (*Pan troglodytes*). Zoo Biology, 11, 313-318.

Fruth, B. H. G., & Hohmann, G. (1994). Comparative analyses of nest building behaviour in bonobos and chimpanzees. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), Chimpanzee cultures (pp. 109-28). Cambridge, MA: Harvard University Press.

Fruth, B. H. G., & Hohmann, G. (1996). Nest building behaviour in the great apes: the great leap forward? In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), Great ape societies (pp. 225-240). Cambridge, MA: Cambridge University Press.

Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C., & Takayoshi, K. (1998). Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. International Journal of Primatology, 19(6), 1029-1043.

Gadsby, E. L. (2002). Preparing for re-introduction: 10 years of planning for drills in Nigeria. In P. S. Soorae (Ed.), Reintroduction News. Newsletter of the Reintroduction Specialist Group, 21 (pp. 20-23). Abu Dhabi, UAE: IUCN/SSC Reintroduction Specialist Group.

Gardner, R. A., Gardner, B. T., & Cantfort, T. E. (1989). Teaching sign language to chimpanzees. New York: State University of New York Press.

Gardner-Outlaw, T., Engelman, R. (1999). Forest futures: population, consumption and wood resources. Washington DC: Population Action International.

Gautier-Hion, A. (1977). Diet of *Cercocebus a. albigena* in northeast Gabon. Terre et la Vie, 31, 570-585.

Ghiglieri, M. P. (1984). The chimpanzees of Kibale Forest. A field study of ecology and social structure. New York: Columbia University Press.

Gilloux, I., Gurnell, J., & Shepherdson, D. (1992). An enrichment device for great apes. Animal Welfare, 1, 279-289.

Gippoliti, S., & Dell'Omo, G. (1995). Status and conservation of the chimpanzee *Pan troglodytes verus* in Guinea-Bissau. African Primates, 3-5.

Gipps, J. H. W. (1991). Beyond Captive Breeding reintroducing endangered mammals to the wild. Oxford: Clarendon Press.

Goodall, J. (1962). Nest building in the free ranging chimpanzee. Ann. N.Y. Acad. Sci., 102, 455-467.

Goodall, J. (1963). Feeding behaviour of wild chimpanzees: a preliminary report. Symp. Zoo. Soc. Lond., 10, 39-48.

Goodall, J. (1965). Chimpanzees of the Gombe Stream Reserve. In I. DeVore (Ed.), Primate behaviour. Field studies of monkeys and apes (pp. 425-473). New York: Holt, Rinehart & Winston.

Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs, 1(3), 161-311.

Goodall, J. (1970). Tool-using in primates and other vertebrates. In D. S. Lehrman, R. A. Hinde, & E. Shaw (Eds.), Advances in the Study of Behaviour (pp. 195-249). New York: Academic Press.

Goodall, J. (1977). Infant killing and cannibalism in free-living chimpanzees. Folia Primatologica, 28, 259-82.

Goodall, J. (1983). Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park. Z. Tierpsychol, 61, 1-60.

Goodall, J. (1986). The chimpanzees of Gombe. Patterns of behaviour. Cambridge, MA: The Belknap Press of Harvard University Press.

Goodall, J. (1992). The living link between 'man' and 'beast'. Edinburgh: Edinburgh University Press.

Goodall, J., Bandora, A., Bergmann, E., Busse, C., Matama, H., Mpongo, E., Pierce, A., & Riss, D. (1979). Inter-community interactions in the chimanzee population of the Gombe National Park. In D. Hamburg, & E. R. McCown (Eds.), The great apes (pp. 13-53), Menlo Park, California: Benjamin/Cummings.

Goossens, B., Funk, S. M., Vidal, C., Latour, S., Jamart, A., Ancrenaz, M., Wickings, E. J., Tutin, C. E. G., & Bruford, M. W. (in press). Measuring genetic diversity in reintroduced programmes: principles and application to a chimpanzee release project. Animal Conservation.

Grundmann, E., Lestel, D., Boestani, A. N., & Bomsel, M. C. (2001). Learning to survive in the forest: what every orangutan should known. Proceedings from The apes: challenges for the 21st century, Chicago, Chicago Zoological Society, USA.

Grzimek, B. (1971). Among animals of Africa. London: Collins.

Gupta, A. K. (2002). Release of golden langur in Tripura, India. In P. S. Soorae (Ed.), Reintroduction News. Newsletter of the Reintroduction Specialist Group, 21 (pp. 26-28). Abu Dhabi, UAE: IUCN/SSC Reintroduction Specialist Group.

Hall, K. R. L. (1963). Variations in the ecology of the chacma baboon, *Papio ursinus*. Symp. Zool. Soc. Lond., *10*, *1-28*.

Ham, R. (1997). Nationwide chimpanzee census and large mammal survey, Republic of Guinea. Unpublished report for Project de Conservation des Chimpanzés en Guinée.

Hannah, A. C. (1989). Rehabilitation of captive chimpanzees (*Pan troglodytes verus*). Unpublished doctoral dissertation, University of Stirling, Stirling, Scotland.

Hannah, A. C., & McGrew, W. C. (1991). Rehabilitation of captive chimpanzees. In H. O. Box (Ed.), Primate responses to environmental change (pp. 167-186). London: Chapman & Hall.

Harcourt, A. H., & Stewart, K. J. (1978). Coprophagy in wild gorilla. East African Wildlife Journal, 16, 223-225.

Harding, R. S. O. (1981). An order of omnivores: nonhuman primate diets in the wild. In R. S. O. Harding & G. Teleki (Eds.), Omnivorous primates gathering and hunting in human evolution (pp. 191-214). New York: Columbia University Press.

Harrisson, B. (1969). The nesting behaviour of semi-wild juvenile orang-utans. Sarawak Mus. J., 17, 336-384.

Harrison, M. J. S. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, *Cercopithecus sabaeus*. Animal Behaviour, 31, 969-977.

Hasegawa, T. (1990). Sex differences in ranging patterns. In T. Nishida (Ed.), The chimpanzees of the Mahale Mountains: sexual and life history strategies. (pp. 99-114). Tokoyo: University of Tokyo Press.

Hasegawa, T., Hiraiwa, M. Nishida, T., & Takasaki, H. (1983). New evidence on scavenging behaviour in wild chimpanzees. Current Anthropology, 24(2), 231-232.

Hayaki, H. (1985). Social play of juvenile and adolescent chimpanzees in the Mahale Mountains National Park. Primates, 26, 343-360.

Hecketsweiler, P., & Mokoko Ikonga, J. (1991). La reserve de Conkouati: Congo le secteur sud-est. Gland, Switzerland: IUCN.

HELP-INFO (2002). Newsletter of *Habitat Ecologique* et Liberté des Primates (April). Paris, France: HELP.

Heltne, P. G., & Marquardt, L. A. (1989). Understanding chimpanzees. Cambridge, Massachusetts: Harvard University Press.

Hill, C. A. (1966). Coprophagy in apes. International Zoo Yearbook, 251-257.

Hill, K., Boesch, C., Goodall, J., Pusey, A., Williams, J., & Wrangham, R. (2001). Mortality rates among wild chimpanzees. Journal of Human Evolution, 40, 437-450.

Hilton-Taylor, C. (2000). The 2000 IUCN Red List of Threatened Species. Cambridge: IUCN Publications.

Hiraiwa-Hasegawa, M. (1989). Sex differences in the behavioural development of chimpanzees at Mahale. In P. G. Heltne & L. A. Marquardt (Eds.), Understanding chimpanzees (pp. 104-115). Cambridge, MA: Harvard University Press.

Hirata, S., & Celli, M. L. (2002). Learning of tool use by infant chimpanzees: the role of mothers on the acquisition of knowledge. Paper presented at the XIXth Congress of The International Primatological Society, Beijing, China. Abstracts, (pp.55-56).

Hladik, C. M. (1973). Alimentation et activité d'un groupe de chimpanzés reintroduits en forêt Gabonaise. Terre et la Vie, 27, 343-413.

Hladik, C. M. (1974). La vie d'un groupe de chimpanzés dans la forêt du Gabon. Science et Nature, 121, 5-14.

Hladik, C. M. (1977). Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In T. H. Clutton-Brock (Ed.), Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes (pp. 481-501). London: Academic Press Ltd.

Hladik, C. M. (1978). Adaptive strategies of primates in relation to leaf-eating. In G. G. Montgomery (Ed.), The ecology of *arboreal folivores (pp.* 373-393). Washington: Smithsonian Institution Press.

Hladik, C. M. (1981). Diet and the evolution of feeding strategies among forest primates. In R. S. O Harding, & G. Teleki (Eds.), Omnivorous primates (pp. 215-254). New York: Columbia University Press.

Hoff, M. P., Forthman, D. L., & Maple, T. L. (1994). Dyadic interactions of lowland gorillas in an outdoor exhibit compared to an indoor holding area. Zoo Biology, 13, 245-256.

Homsy, J. (1999). Ape tourism and human diseases: how close should we get? A critical review of the rules and regulations governing park management and tourism for the wild mountain gorilla, *Gorillla gorilla beringei.* Unpublished manuscript for International Gorilla Conservation Programme.

Hosaka, K. (1995). Chimpanzee predation on red colobus in Mahale Mountains National Park, Tanzania. Anthropological Science, 103, 160.

Huffman, M. A. (2000). Evaluation of the Rubondo Island National Park chimpanzee habituation project. Unpublished report.

Humle, T., & Matsuzawa, T. (2001). Behavioural diversity among the wild chimpanzee populations of Bossou and neighbouring areas, Guinea and Cote d'Ivoire, West Africa. Folia Primatologica, 72, 57-68.

Hunt, K. D. (1989). Positional behaviour in Pan troglodytes at the Mahale Mountains and the Gombe Stream National Parks, Tanzania. Unpublished doctoral dissertation, University of Michigan, Michigan, USA.

IPPL (2002). Animal dealer offers gorilla babies. IPPL News, 29(1), 3-4.

Irwin, A. (2001). Wild at heart. New Scientist, *2280, 26-31.*

Isabirye-Basuta, G. (1989). Feeding ecology of chimpanzees in the Kibale Forest, Uganda. In P. G. Heltne, & L. A. Marquardt (Eds.), Understanding chimpanzees (pp. 116-127). Cambridge, Massachusetts: Harvard University Press.

Itani, J. (1979). Distribution and adaptation of chimpanzees in an arid area. In D. A. Hamburg, & E. R. McCown (Eds.), The great apes (pp. 55-71). Menlo Park, California: Benjamin Cummings.

IUCN (2000). IUCN 2000 Red list of threatened animals. Gland, Switzerland: IUCN.

IUCN/SSC Re-Introduction Specialist Group. (1995). IUCN Guidelines for Re-introductions. Gland, Switzerland: IUCN.

IUCN/SSC Re-Introduction Specialist Group. (1998). IUCN Guidelines for Re-introductions Gland, Switzerland: IUCN.

IUCN/SSC Re-Introduction Specialist Group. (2002). Guidelines for Nonhuman Primate Re-introductions. Gland, Switzerland: IUCN.

Izawa, K., & Itani, J. (1966). Chimpanzees in Kasakati Basin, Tanganyika: ecological study in the rainy season, 1963-1964. Kyoto University African Studies, 1, 73-156.

Jerome, C. P., & Szostak, L. (1987). Environmental enrichment for adult female baboon (*Papio anubis*). Laboratory Animal Science, 37(4), 508.

Jones, C., & Sabater Pi, J. (1971). Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. Bibliotheca Primatologica, 13, 1-96.

Karesh, W. B. (1995). Wildlife rehabilitation: additional considerations for developing countries. Journal of Zoo and Wildlife Medicine, 26(1), 2-9.

Kawanaka, K. (1981). Infanticide and cannibalism in chimpanzees - with special reference to the newly observed case in the Mahale Mountains. African Study Monographs, 1, 69-99.

Kawanaka, K. (1982). Further studies on predation by chimpanzees of the Mahale Mountains. Primates, 23, 364-384.

Keith-Lucas, T., White, F. J., Keith-Lucas, L., & Vick, L. G. (1999). Changes in behaviour in free-ranging *Lemur catta* following release in a natural habitat. American Journal of Primatology, 47, 15-28.

Kierulff, M. C. M., Beck, B. B., Kleiman, D. G., & Procopio, P. (2002). Reintroduction and translocation as conservation tools for golden lion tamarins in Brazil. In P. S. Soorae (Ed.) Reintroduction News. Newsletter of the Reintroduction Specialist Group, 21 (pp. 7-10). Abu Dhabi, UAE: IUCN/SSC Reintroduction Specialist Group.

Kierulff, M. C. M., Procopio de Oliveira, P., Beck, B. B., Martins, A. (in press). Reintroduction and translocation as conservation tools for golden lion tamarins. D. G. Kleiman, & A. Rylands (Eds.), The lion tamarins of Brazil: twenty five years of research and conservation. Washington: Smithsonian Institution Press.

Kleiman, D. G. (1989). Reintroduction of captive mammals for conservation. Bioscience, 39, 152-161.

Kleiman, D. G., Beck, B. B., Dietz, J. M., Dietz, L. A., Ballou, J. D., & Coimbra-Filho, A. F. (1986). Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies, and reintroduction. In K. Benirschke (Ed.), Primates - the road to self-sustaining populations (pp. 959-979). New York: Springer-Verlag.

Kleiman, D. G., Stanley-Price, M. R., & Beck, B. B. (1994). Criteria for reintroductions. In P.J.S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), Creative conservation: interactive management of wild and captive animals (pp. 287-303). London: Chapman and Hall.

Kohler, W. (1925). The mentality of apes. New York: Liveright.

Kortlandt, A. (1962). Chimpanzees in the wild. Scientific American, 206, 128-138.

Kortlandt, A. (1996). Chimpanzee *Pan Troglodytes* nest-making behaviour in Guinea and Uganda. African Primates, 2(2), 80.

Kummer, H. & Goodall, J, (1985). Conditions in innovative behaviour in primates. Phil. Trans. R. Soc. Lond. B308: 203-214.

Laland, K. N., Richerson, P. J., & Boyd, R. (1996). Developing a theory of animal social learning. In C. M. Heyes, & B. G. Galef (Eds.), Social learning in animals: the roots of culture, (pp.129-154). London: Academic Press Ltd.

Lambert, J. (2000). Urine drinking in wild *Ceropithecus ascanius*: evidence of nitrogen balancing? African Journal of Ecology, 38, 360-362.

Laule, G., & Whittaker, M. (2001). Training for cooperative behaviours and enrichment. In L. Brent (Ed.), The care and management of captive chimpanzees, (pp. 242-265). San Antonio, Texas: American Society of Primtologists.

Leathers, C. W., & Schedewie, H. K. (1980). Diabetes mellitus in a pigtailed macaque (*M. nemestrina)*. Journal of Medical Primatology, 9, 95-100.

Leavens, D. A., Hopkins, W. D., & Bard, K. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology, 113: 396-402.

Lee, P. C. (1984). Ecological constraints on the social development of vervet monkeys. Behaviour, (245-261).

Lee, P.C. (1991). Adaptations to environmental change: an evolutionary perspective. In H. O Box, (Ed.), Primate responses to environmental change (pp.39-56). London: Chapman and Hall.

Leger, D. W. (1977). An empirical evaluation of instantaneous and one-zero sampling of chimpanzee behaviour. Primates, 18, 387-393.

Lethmate, J. (1977). Nest building behaviour of young orang-utans raised in isolation. Primates, 18, 545-554.

Levanduski, S., Bayne, K., & Dexter, S. (1992). Behavioural observations in the detection of diabetes mellitus. Laboratory Primate Newsletter, 31(1), 14-15.

Limongelli, L., Boysen, S. T., & Visalberghi, E. (1995). Comprehension of cause-effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology, 109: 18-26.

Loy, J. (1970). Behavioural responses of free-ranging rhesus monkeys to food shortage. American Journal of Primatology, 33, 263-72.

Lyon, L. (1976). The saving of the gorilla. Africana, 5 (9), 11-23.

Mace, G. (1990). Birth sex ratio and infant mortality rates in captive western lowland gorillas. Folia Primatologica, 55, 156-165.

Mackinnon, J. (1977). The future of orang-utans. New Scientist, 23rd June, 697-699.

Maclean, I. G. (1997). Conservation and the ontogeny of behaviour. In J. R. Clemmons, & R. Buchholz (Eds.), Behavioural approaches to conservation in the wild (pp. 132-156). Cambridge: Cambridge University Press.

Maisels, F. G., & Cruickshank, A. J. (1996). Inventaire et recensement des grands mammiferes. Unpublished report by IUCN (Projet Conkouati) Republic of Congo.

Maisels, F., & Onononga, J. R. (2000). Conkouati-Douli National Park - conservation status, Jan/Feb 2000 large mammals and human impact. Unpublished report by NYZS/The Wildlife Conservation Society, Republic of Congo.

Manning, C. (1996). The Lake Edward Chimpanzee Sanctuary. IPPL Newsletter, 23(2), 25-28.

Maple, T. (1979). Great apes in captivity: the good, the bad and the ugly. In J. Erwin, T. L. Maple, & G. Mitchell (Eds.), Captivity and behaviour. New York: Van Nostrand.

Margalef, R. (1958). Information theory in ecology. General Syst., 3, 36-71.

Markowitz, H., & Spinelli, J. S. (1986). Environmental engineering in primates. In K. Benirschke (Ed.), Primates: the road to self sustaining populations (pp. 489-498). New York: Springer-Verlag.

Marsden née Brewer, S. (1998). The rehabilitation of captive chimpanzees into the wild in Niokolo Koba National Park, Senegal. Unpublished Report.

Marshall, A. J., Holland Jones, J., & Wrangham, R. W. (2000). The plight of the great ape: a global survey of great ape populations. Unpublished report.

Martin, P., & Bateson, P. (1998). Measuring behaviour - an introductory guide. Cambridge: Cambridge University Press.

Matsumoto-Oda, A., & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. Folia Primatologica, 70, 154-162.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. Nature, 315: 57-59.

Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild. In R. W. Wrangham., W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), Chimpanzee cultures (pp. 351-370). Cambridge, MA: Harvard University Press.

Matsuzawa. T., & Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In A. E. Russon, K. A. Bard, & S. Taylor-Parker (Eds.), Reaching into thought - the minds of the great apes (pp. 211-232). Cambridge: Cambridge University Press.

Maughan, J., & Stanford, C. S. (2001). Terrestrial nest building in chimpanzees (*Pan troglodytes schweinfurthi*), Bwindi Impenetrable National Park, Uganda, East Africa. Primate Eye, 75, 28-29.

McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. Journal of Human Evolution, 3, 501-508.

McGrew, W. C. (1979). Evolutionary implications of sex differences in chimpanzee predation and tool use. In D. A. Hamburg, E. R. McCown. (Eds.), The great apes (pp. 440-463). Menlo Park, California: Benjamin Cummings.

McGrew, W. C. (1983a). Chimpanzees can be rehabilitated. Laboratory Primate Newsletter, 22(2), 2-3.

McGrew, W. C. (1983b). Animal foods in the diets of wild chimpanzees. Journal of Ethology, 1, 46-61.

McGrew, W. C. (1985). The chimpanzee and the oil palm: patterns of culture. Social Bio. & Human Affairs, 50, 2-23.

McGrew, W. C. (1992). Chimpanzee material culture: implications for human evolution. Cambridge: Cambridge University Press.

McGrew, W. C., Tutin, C. E. G., & Midgett, P.S. (1975). Tool use in a group of captive chimpanzees. Z. Tierpsychol., 36, 145-162.

McGrew, W. C., Baldwin, P. J., & Tutin, C. E. G. (1988). Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Asserik, Senegal. American Journal of Primatology, 16, 213-226.

McGrew, W. C., Marchant, L., & Nishida, T. (1996). Great ape societies. Cambridge: Cambridge University Press.

McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G., & Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? International Journal of Primatology, 18, 325-374.

Mendoza-Granados, D., & Sommer, V. (1995). Play in chimpanzees of the Arnhem Zoo: self-serving compromises. Primates, 36(1), 57-68.

Mensink, M. (1986). Julia: a gorilla with an identity crisis. New Scientist, 19 June, 68-69.

Menzel, E. W. (1972). Spontaneous invention of ladders in a group of young chimpanzees. Folia Primatologica, 17: 87-106.

Menzel, E. W. (1973). Further observations on the use of ladders in a group of young chimpanzees. Folia Primatologica, 19: 450-457.

Miller, B., Biggins, D., Hanebury, L., & Vargas, A. (1994). Reintroduction of the black-footed ferret (*Mustela nigripes*). In P. J. S Olney, G. M. Mace, & A. T. C. Feistner (Eds.), Creative conservation: interactive management of wild and captive animals (pp. 455-464). London: Chapman & Hall.

Mitani, J. C., & Watts, D. (1999). Demographic influences on the hunting behaviour of chimpanzees. American Journal of Physical Anthropology, 109, 439-454.

Mitani, J. C., & Watts, D. (2001). Why do *chimpanzees hunt and share meat?* Animal Behaviour, 61, 915-924.

Morris, K., & Goodall, J. (1977). Competition for meat between chimpanzees and baboons of the Gombe National Park. Folia Primatologica, 28, 109-121.

Moscovice, L. R., & Huffman, M. A. (2001). Ecology and ranging habits of an introduced group of chimpanzees at Rubondo Island National Park, Tanzania: preliminary report. Unpublished Report.

Moutsambote, J. M. (1997). Etude des differents types de vegetation de la Reserve de Conkouati: secteur ouest. Unpublished report for CERVE/PROGEGAP/GEF Congo.

Moutsambote, J. M., Yumoto, T., Mitani, M., Nishihara, T., Suzuki, S., & Kuroda, S. (1994). Vegetation and list of plant species identified in the Noubale-Ndoki Forest, Congo. Tropics, 3, 277-293.

Muller, M. N., Mpongo, E., Stanford, C. B., & Boehm, C. (1996). A note on scavenging by wild chimpanzees. Folia Primatologica, 65, 43-47.

Myers, N. (1993). Population, environment, and development. Environmental Conservation, 20, 205-16.

Nagell, K., Olguin, R., & Tomasell, M. (1993). Processes of social learning in the imitative learning of chimpanzees and human children. Journal of Comparative Psychology, 107, 174-186.

Nash, L. T., Fritz, J., Alford, P. A., & Brent, L. (1999). Variables influencing the origins of diverse abnormal behaviours in a large sample of captive chimpanzees (*Pan troglodytes)*. American Journal of Primatology, 48, 15-29.

National Research Council. (1998). The psychological well-being of nonhuman primates. Washington: National Academy Press.

Naughton-Treves, L., & Weber, W. (2001). *Human dimensions of the* African rain forest. In W. Weber, L. J. T. White, A. Vedder, & L. Naughton-Treves *(Eds.), African rain* forest ecology and conservation (pp. 30-43). New Haven, CT: Yale University Press.

Nellemann, C., & Newton, A. (2002). The great apes- the road ahead. A global perspective on the impacts of infrastructural development on the great apes. Nairobi, Kenya: United nations Environment Programme.

Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. African Journal of Ecology, 37, 344-354.

Nishida, T. (1973). The ant gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. Journal of Human Evolution, 2, 357-370.

Nishida, T. (1974). Ecology of wild chimpanzees. R. Ohtsuka, J. Tanaka, T. Nishida (Eds.), Human Ecology (pp. 15-60). Tokoyo: Kyoritsu-shuppan.

Nishida, T. (1977). Chimpanzee anting behaviour and its eco-evolutionary significance. In W. Watanabe (Ed.), Ecology: course of physical anthropology (pp. 55-84). Tokyo: Yuzankaku.

Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In D. A. Hamburg, & E. R. McCown (Eds.), The great apes (pp. 73-122). Menlo Park, California: Benjamin Cummings.

Nishida, T. (1980). Local differences in response to water among wild chimpanzees. Folia Primatologica, 33, 189-209.

Nishida, T. (1990). The chimpanzees of the Mahale Mountains. Tokyo: University of Tokyo Press.

Nishida, T., & Hiraiwa, M. (1982). Natural history of a tool-using behaviour by wild chimpanzees in feeding upon wood boring ants. International Journal of Primatology, 11, 73-99.

Nishida, T., & Uehera, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. African Study Monographs, 3, 109-130.

Nishida, T., Takasaki, H., & Takahata, Y. (1990). Demographic and reproductive profiles. In T. Nishida (Ed.), The Chimpanzees of the Mahale Mountains (pp. 3-97). Tokyo: University of Tokyo Press.

Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. Anthropological Science, 107(2), 141-188.

Nissen, H. W. (1931). A field study of the chimpanzee: observations of chimpanzee behaviour and environment in western French Guinea. Comparative Psychology Monograph, 8, 1-122.

Noon, C. (1997). A report on the use of electric fencing as a primary enclosure barrier for chimpanzees, *Pan Troglodytes*. Unpublished report for the National Chimpanzee Research Retirement Task Force.

Oates, J. F. (1987). Food distribution and foraging behaviour. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), Primate societies (pp. 197-209). Chicago: The University of Chicago Press.

Oates, J. (1996). African Primates status survey and conservation action plan. Gland, Switzerland: IUCN.

Paredes, *J. (1997). The adaptation* process of seven released chimpanzees (*Pan t. troglodytes*) in the reserve of *Conkouati – Congo. Unpublished* report.

Paredes, J. (1998). The adaptation process of two groups of rehabilitated chimpanzees (*Pan troglodytes troglodytes*) into the wild, Conkouati Reserve, Republic of Congo Unpublished report.

Parnell, R. J. (2001). An unusual social display by gorillas. Nature, 412, 294.

Parnell, R. J. (2002). Group size and strcuture in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. American Journal of Primatology, 56, 193-206.

Peters, H. (1995). Orangutan reintroduction? Development, use and evaluation of a new method: reintroduction. Unpublished masters dissertation, University of Groningen, Groningen, The Netherlands.

Petersen, R., Smith, G., Kokmen, E., Ivnik, R., & Tangalos, E. (1992). Memory function in normal aging. Neurology, 42, 396-401.

Pfeiffer, A. J., & Koebner, L. J. (1978). The resocialisation of single-caged chimpanzees and establishment of an island colony. J. Med. Primatology, 7, 70-81.

Plumptre, A. J., & Reynolds, V. (1994). The effect of selective logging on the primate populations in the Budongo forest Reserve, Uganda. Journal of Applied Ecology, 31, 631-641.

Povinelli, D. J. (1987). Monkeys, apes, mirrors and minds: the evolution of self-awareness in primates. Journal of Human Evolution, 2: 493-509.

Pusey, A. (1998). Rubondo chimp project. Unpublished Report.

Rahm, U. (1967). Observations during chimpanzee captures in the Congo. In D. Starck, & R. Schneider, & H. J. Kuhn (Eds.), Progress in primatology (pp. 195-207). Stuttgart, Germany: Fischer.

Rapp, P., & Amaral, D. (1989). Evidence for task-dependent memory dysfunction in the aged monkey. Journal of Neuroscience, 9, 3568-3576.

Reader, S. M., & Laland, K. N. (2001). Primate Innovation: sex, age and social rank differences. International Journal of Primatology, 22, 787-805.

Redford, K. H. (1987). Ants and termites as food. Patterns of mammalian myrmecrophagy. In H. H. Genoways (Ed.), Current mammalogy volume 1 (pp. 349-399). New York: Plenum Press.

Remis, M. J. (2002). Food preferences among captive western gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). International Journal of Primatology, 23, 231-249.

Reynolds, V., & Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In I. DeVore (Ed.), Primate behaviour. Field studies of monkeys and apes. (pp. 368-424). New York: Holt, Rinehart & Winston.

Rhine, R. J. & Flanigon F. M. (1978). An empirical comparison of one-zero, focal animal, and instantaneous methods of sampling spontaneous primate social behaviour. Primates, 19, 353-361.

Richard, A. (1985). Primates in nature. New York: W.H. Freemann.

Rijksen, H. D. (1978). A field study on Sumatran orang-utans (*Pongo pygmaeus abelli* Lesson, 1827): ecology, behaviour and conservation. Wageningen, The Netherlands: H. Veenan & Zonen.

Rijksen, H. D., & Meijaard, E. (1999). Our vanishing relative - the status of wild orang-utans at the close of the twentieth century. The Netherlands: Tropenbos.

Rijksen, H. D., & Rijksen-Graatsma, A. G. (1975). Orang-utan rescue work in north Sumatra. Oryx, 13, 65-73.

Riss, D. & Goodall, J. (1977). The recent rise to the alpha-rank in a population of free-living chimpanzees. Folia Primatologica, 27, 134-151.

Ron, T., & McGrew, W. C. (1988). Behavioural assessment for rehabilitating chimpanzees in northern Zambia. Unpublished report.

Rosen, C. (2002). Monkey Tales - The Newsletter of IPPL-UK, Issue 8 (March), 4.

Rosen, N., Russon, A., & Byers, O. (2001). Orangutan reintroduction and protection workshop. Unpublished report. Apple Valley, MN, USA: IUCN/SSC Conservation Breeding Specialist Group.

Rosen, N., Seal, U. S., Montgomery, C., Boardman, W. (2001). Pan-African Sanctuary Alliance (PASA) workshop report. Apple Valley, MN, USA: IUCN/SSC Conservation Breeding Specialist Group.

Rosen, N., Seal, Cox, D., & Montgomery, C. (In press). Pan-African Sanctuary Alliance (PASA) workshop report. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Rowe, N. (1996). The pictorial guide to the living primates. New York: Pogonias Press.

Rumbaugh, D. M. (1977). Language learning in a chimpanzee: The LANA Project. New York: Academic Press.

Russon, A. E. (2001). Rehabilitating orangutans (*Pongo pygmaeus*). Laboratory Primate Newsletter, 40(4), 8-9.

Russon, A. E. (2002). Return of the native: cognition and site-specific expertise in orangutan rehabilitation. International Journal of Primatology, 23(3), 461-478.

Ryder, O. A., & Fleischer, R. C. (1996). Genetic research and its application in zoos. In D. G. Kleiman, M. E. Allen, K. V. Thompson, & S. Lumpkin (Eds.), Wild mammals in captivity (pp. 255-262). Chicago: The University of Chicago Press.

Sabater-Pi, J. (1979). Feeding behaviour and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). Z. Tierpsychol., 50, 265-281.

Sakura, O. (1994). Factors affecting party size and composition of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea. International Journal of Primatology, 15, 167-183.

Sarrazin, F., & Barbault, R. (1996). Reintroduction: challenges and lessons for basic ecology. Tree, 11(11), 474-478.

Sayer, J. (1992). A future for Africa's tropical forests. In J. A. Sayer, C. S. Harcourt, & N. M. Collins (Eds.) Africa: the conservation atlas of tropical forest (pp. 81-93). London: Macmillan.

Savage-Rumbaugh, E. S. (1986). Ape language: from conditioned response to symbol. New York: Columbia University Press.

Savage-Rumbaugh, E. S., Romski, M. A., Hopkins, W. D., & Sevcik, R. (1989). Symbol acquisition and use by *Pan troglodytes, Pan paniscus, Homo sapiens*. In P. Heltne & L. Marquardt (Eds.), Understanding chimpanzees (pp. 266-295). Cambridge, MA: Harvard University Press.

Schaller, G. B. (1963). The mountain gorilla. Ecology and behaviour. Chicago: The University of Chicago Press.

Schoene, C. (2001). Vegetation survey of Ngamba Island, Lake Victoria, Uganda. Unpublished report.

Seddon, P. J., & Soorae, P. S. (1999). Guidelines for subspecific substitutions in wildlife restoration projects. Conservation Biology, 13(1), 177-184.

Sept, J. M. (1992). Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. Current Anthropology, 33(2) 187-207.

Shepherdson, D. (1988). Environmental enrichment in the zoo. In UFAW (24) Why Zoos? (pp. 45-53). Potters Bar, Herts: UFAW.

Shepherdson, D., Carman, M., & Bemment, N. (1989). Auditory enrichment for the lar gibbons at London Zoo. Int. Zoo Yearbook, 28, 256-260.

Simpson, M. J. A., & Simpson, A. E. (1977). One-zero and scan methods for sampling behaviour. Animal Behaviour, 25, 726-731.

Sita, P. (1996). Mission mixte de primatologie et botanique dans le site du Triangle a Conkouati du 02 au 21 fevrier 1996. Unpublished report.

Skorupa, J. P. (1986). Responses of rainforest primates to selective logging in Kibale Forest, Uganda: a summary report. In K. Bemirschke (Ed.), Primates: the road to self-sustaining populations (pp.57-70). New York: Springer-Verlag.

Smith, A. C. (1997). Comparative ecology of saddleback (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins. Unpublished doctoral dissertation, University of Reading, Reading, England.

Soave, O. (1982). The rehabilitation of chimpanzees and other apes. Laboratory Primate Newsletter, 21(4), 3-8.

Soorae, P. S. (2002). Reintroduction News. Newsletter of the Reintroduction Specialist Group (21). Abu Dhabi, UAE: IUCN/SSC Reintroduction Specialist Group.

Spijkerman, R. P., Dienske, H., Van Hooff, J. A. R. A. M., & Jens, W. (1995). Differences in play development of young chimpanzees reared in family groups and in peer groups. Netherlands Journal of Zoology, 45(3-4), 402-421.

Stanford, C. (1998). Chimpanzees and red colobus: the ecology of predator and prey. Cambridge, MA: Harvard University Press.

Stanford, C., Wallis, J., Mpongo, E., & Goodall, J. (1994). Hunting decisions in wild chimpanzees. Behaviour, 131, 1-18.

Stanley-Price, M. R. (1989). Animal reintroductions: the Arabian oryx in Oman. Cambridge: Cambridge University Press.

Stanley-Price, S., & Gordon, I. (1989). How to go wild. New Scientist, 1688, 56-58.

Stoinski, T. S. (2000). Behavioural differences between captive-born reintroduced golden lion tamarins (*Leontopithecus roslia roslia*) and their wild-born offspring. Unpublished doctoral dissertation, Georgia Institute of Technology, Atlanta, USA.

Struhsaker, T. T. (1996). A biologists's perspective on the role of sustainable harvest in conservation. African Primates, 2, 72-75.

Struhsaker, T. T., & Siex, K. S. (1998). Translocation and introduction of the Zanzibar red colobus monkey: success and failure with an endangered island endemic. Oryx, 32(4), 277-284.

Strum, S. C. (2002). Translocation of three wild troops of baboons in Kenya. In P. S. Soorae (Ed.), Reintroduction News. Newsletter of the Reintroduction Specialist Group, 21 (pp.12-15). Abu Dhabi, UAE: IUCN/SSC Reintroduction Specialist Group.

Stuart, S. N. (1991). Reintroductions: to what extent are they needed. In J. H. W. Gipps Beyond captive breeding reintroducing endangered mammals to the wild (pp. 27-37). Oxford: Clarendon Press.

Sugiyama, Y. (1968). Social organisation of chimpanzees in the Budongo Forest, Uganda. Primates, 9, 225-258.

Sugiyama, Y., & Koman, J. (1979). Social structure and dynamics of wild chimpanzees at Bossou, Guinea. Primates, 20(3), 323-339.

Sugiyama, Y., & Koman, J. Bhoye Sow, M. (1988). Ant-catching wands of wild chimpanzees at Bossou, Guinea. Folia Primatologica, 51, 56-60.

Suzuki, A. (1969). An ecological study of chimpanzees in a savanna woodland. Primates, 10, 103-148.

Suzuki, A. (1975). The origin of hominid hunting: a primatological perspective. In R. H. Tuttle (Ed.), Socioecology and psychology of primates (pp. 259-278). The Hague: Mouton Publishers.

Taylor Parker, S. (1996). Apprenticeship in tool-mediated extractive foraging: the origins of imitation, teaching, and self-awareness in great apes. In A. E. Russon, K. A. Bard, & S. Taylor Parker (EDS.), Reaching into thought: the minds of the great apes (pp.348-370). Cambridge: Cambridge University Press.

Taylor Parker, S., & McKinney, M. L. (1999). Origins of Intelligence. The evolution of cognitive development in monkeys, apes, and humans. Baltimore, Maryland: John Hopkins University Press.

Taylor, S. (2000). Standards of captive care for primates in sanctuaries: regulatory and ethical perspectives. Paper presented at the XVIIIth Congress of the International Primatological Society, Adelaide, Australia.

Tear, T. H., Mosley, J. C., & Ables, E. D. (1997). Landscape-scale foraging decisions by reintroduced Arabian oryx. Journal of Wildlife Management, 61, 1142-1154.

Tear, T. H., & Ables, E. D. (1999). Social system development and variability in a reintroduced Arabian oryx population. Biological Conservation, 89, 199-207.

Teleki, G. (1973). The predatory behaviour of wild chimpanzees. Lewisburg, Pennsylvania: Bucknell University Press.

Teleki, G. P. (1977). Spatial and temporal dimensions of routine activities performed by chimpanzees in Gombe National Park, Tanzania: an ethological study of adaptive strategy. Unpublished doctoral dissertation, Pennsylvania State University, Pennsylvania, USA.

Teleki, G. P. (1981). The Omnivorous Diet and Eclectic Feeding Habits of Chimpanzees in Gombe National Park, Tanzania. In . R. S. O. Harding, & G. Teleki (Eds.), Omnivorous Primates. Gathering and Hunting in Human Evolution (pp. 303-343). New York: Columbia University Press.

Teleki, G. (1989). Population status of wild chimpanzees (*Pan troglodytes*) and threats to survival. In P. G. Heltne, & L. A. Marquardt (Eds.), Understanding chimpanzees (pp. 312-353). Cambridge, MA: Harvard University Press.

Teleki, G. (2001). Sanctuaries for ape refugees. In B. B. Beck, T. S. Stoinski, H. Hutchin, T. L. Maple, B. Norton, A. Rowan, E. Stevens, & A. Arluke (Eds.), Great apes and humans the ethics of coexistence (pp. 133-149). Washington: Smithsonian Institution Press.

Tirado Herrera, E. R., & Heymann, E. W. (2000). Mom needs more protein – sex differences in the diet composition of red tit monkeys, *Callicebus cupreus*. Folia Primatologica, 71(4), 244.

Tomasello, M. (1996). Do apes ape? In C. M. Heyes, & B. G. Galef (Eds.), Social learning in animals: the roots of culture (pp.319-346). London: Academic Press Ltd.

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool use by young chimpanzees. Human Evolution, 2, 175-183.

Tomasello, M., Kruger, A., & Ratner, H. (1993). Cultural learning. Behavioural and Brain Sciences, 16, 495-592.

Treves, A., & Naughton-Treves, L. *(1994). Behaviour of a captive,* wild-born chimpanzee before and after release in a habituated community of wild *chimpanzees (Pan troglodytes schweinfurthii)*: In Proceedings of the 1994 Chimpanzoo conference Ridgefield. Can reintroduction succeed for captive chimpanzees? (pp. 79-96). Connecticut: Jane Goodall Institute.

Treves, A., & Naughton-Treves, L. (1997). Case study of a chimpanzee recovered from poachers and temporarily released with wild conspecifics. Primates, 38(3), 315-324.

Tutin, C. E. G. (1979). Mating patterns and reproductive strategies in a community of wild chimpanzees. Behav. Ecol. Sociobiol., 6, 29-38.

Tutin, C. E. G. (1994). Assessment of the possibility of the reintroduction of chimpanzees in the Conkouati Reserve, Congo. Prospection and assessment of potential sites and recommendations for immediate action. Unpublished report for Project Conkouati IUCN/GEF.

Tutin, C. E. G. (1996). Expertise sur les possibilités de reintroduction de chimpanzés en forêt naturelle dans la Reserve de Conkouati, Congo. Unpublished report.

Tutin, C. E. G. (2001). Saving the gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) of the Congo Basin. Reprod. Fertil. Dev., 13, 469-476.

Tutin, C. E. G., & Fernandez, M. (1984). Nationwide census of gorilla (*Gorilla g. gorilla*) *and chimpanzee (Pan t. troglodytes) in Gabon.* American Journal of Primatology, 6, 313-336.

Tutin, C. E. G., & Fernandez, M. (1992). Insect-eating by sympatric lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. American Journal of Primatology, 28, 29-40.

Tutin, C. E. G., Fernandez, M., Rogers, M. E., Williamson, E. A., & McGrew, W. C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. Phil. Trans. R. Soc. Land. B, 334, 179-186.

Tutin, C. E. G., & Fernandez, M. (1993). Composition of the diet chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. American Journal of Primatology, 30, 195-211.

Tutin, C. E. G., White, L. J. T., Williamson, E. A., Fernandez, M., & McPherson, G. (1994). List of plant species identified in the northern part of the Lopé Reserve, Gabon. Tropics, 3, 249-276.

Tutin, C. E. G., Ham, R. M., White, L. J. T., & Harrison, M. J. S. (1997). The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology, 42, 1-24.

Tutin, C. E. G., Ancrenaz M , Paredes. J , Vacher-Vallas, M., Vidal, C., Goossens, B., Bruford, M., & Jamart, A. (2001). Conservation biology framework for the release of wild-born orphaned chimpanzee into the Conkouati Reserve, Congo. Conservation Biology, 15(5), 1247-1257.

Tuttle, R. H. (1986). Apes of the world. New Jersey: Noyes Publications.

Uehera, S. (1982). Seasonal changes in the techniques employed by wild chimpanzees in the Mahale Mountains, Tanzania, to feed on termites (*Pseudacanthotermes spiniger*). Folia Primatologica, 37, 44-76.

Uehara, S. (1986). Sex and group differences in feeding on animals by wild chimpanzees in the Mahale Mountains National Park, Tanzania. Primates, 27(1), 1-13.

Uehara, S. (1997). Predation on mammals by the chimpanzee (*Pan troglodytes*). Primates, 38(2), 193-214.

Uehara, S., Nishida, T., Hamai, M., Hasegawa, T., Hayaki, H., Huffman, M., Kawanaka, K., Kobayashi, K., Mitani, J., Takahata, Y., Takasaki, H., & Tsukahara, T. (1992). In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. de Waal (Eds.), *Characteristics of predation by chimpanzees in the* Mahale Mountains National Park, Tanzania. Topics in primatology volume *1 (pp. 143-158). Tokyo: Tokyo* University Press.

Voisey, B. C. (1995). Seed dispersal by gorillas in the Lopé Reserve, Gabon. Unpublished doctoral dissertation, University of Edinburgh, Edinburgh, Scotland.

DeWaal, F. (1982). Chimpanzee politics: power and sex among apes. New York: Harper Row.

Wallis, J., Mbago, F., Mpongo, E., Chepstow-Lusty, A. (1995). Sex differences and seasonal effects in the diet of chimpanzees. American Journal of Primatology, 36(2), 162.

Warren, S., & Swan, R. A. (2002). Reintroduction of orangutans in Indonesia. In P. S. Soorae (Ed.), Reintroduction News. Newsletter of the Reintroduction Specialist Group, 21 (pp. 24-26). Abu Dhabi, UAE: IUCN/SSC Reintroduction Specialist Group.

White, L. J. T., & Tutin, C. E. G. (2001). Why chimpanzees and gorillas respond differently to logging: a cautionary tale form Gabon. In W. Weber, L. J. T. White, A. Vedder, & L. Naughton-Treves (Eds.), African rain forest ecology and conservation (pp. 449-462). New Haven, CT: Yale University Press.

Whiten, A., Custance, D, M., Gomez, J. C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology, 100: 3-14.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., & Boesch, C. (1999). Cultures in chimpanzees. Nature, 399, 682-685.

Williams-Blangero, S., & Dyke, B. (1992). Genetic management of a chimpanzee colony. In J. Erwin, & J. Landan (Eds.), Chimpanzee conservation and public health: environments for the future (pp. 127-136). Rockville, Maryland: Diagnon Bioqual.

Wolfle, T. L., & April, M. (1994). The US chimpanzee breeding and research program. In G. Eder, E. Kaier, & F. A. King (Eds.), The role of the chimpanzee in research (Symposium on the role of the chimpanzee in research, Vienna, Austria, 1992) (pp.79-86). Basel: Karger.

Wrangham, R. W. (1975). The behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Unpublished doctoral dissertation, University of Cambridge, Cambridge, England.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In T. H. Clutton-Brock (Ed.), Primate Ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes (pp. 503-538). London: Academic Press.

Wrangham, R. W. (1979). Sex differences in chimpanzee dispersion. In D. A. Hamburg, & E. R. McCown (Eds.), The great apes (pp. 481-490). Menlo Park, California: Benjamin/Cummings.

Wrangham , R. W. (1986). Ecology and social relationships in two species of chimpanzee. In D. I. Rubenstein, & R. W. Wrangham (Eds.), Ecological aspects of social evolution: birds and mammals (pp. 352-378). Princeton: Princeton Press.

Wrangham, R. W. (1994). Overview - ecology, diversity, and culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), Chimpanzee cultures (pp. 21-24). Cambridge, MA: Harvard University Press.

Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. J. Reprod. Fert., Suppl., 28, 13-31.

Wrangham, R., & Bergmann Riss, E. (1990). Rates of predation on mammals by Gombe chimpanzees, 1972-1975. Primates, 31, 157-170.

Wrangham, R. W., Conklin, N. L., Chapman, C. A., & Hunt, K. D. (1991). The significance of fibrous foods for Kibale forest chimpanzees. Philosophical Transactions of the Royal Society of London Series B, 334, 171-178.

Wrangham, R. W., Clark, A. P., & Isabirye-Busta, G. (1992). Female social relationships and social organisation of Kibale forest chimpanzees. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, & F. de Waal (Eds.), Human evolution (pp. 87-98). Tokyo: Tokyo University Press.

Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., & Heltne, P. G. (1994). Chimpanzee cultures. Cambridge, MA: Harvard University Press.

Wrangham, R. W., Chapman, C. A., Clark, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In W. C. McGrew, L.F. Marchant, & T. Nishida (Eds.), Great ape *societies (pp. 45-57). Cambridge: Cambridge* University Press.

Yamagiwa, J. (1998). An ossified chimpanzee found in a tree nest. Pan Africa News, *5, 17*-18.

Yamagiwa, J., Yumoto, T., Ndunda, MM., & Maruhashi, T. (1988). Evidence of tool-use by chimpanzees (*Pan troglodytes schweinfurthii)* for digging a bee nest in the Kahuzi-Biega National Park, Zaire. Primates, 29, 405-411.

Yeager, C. P. (1997). Orangutan rehabilitation in Tanjung Putting National Park. Conservation Biology, 11, 802-805.

Yerkes, R. M. (1943). Chimpanzees: a laboratory colony. New Haven, CT: Yale University Press.

Yumoto, T., Yamagiwa, J., Mwanza, N., & Maruhashi, T. (1994). List of plant species identified in Kahuzi-Biega National Park, Zaire. Tropics, 3, 295-308.

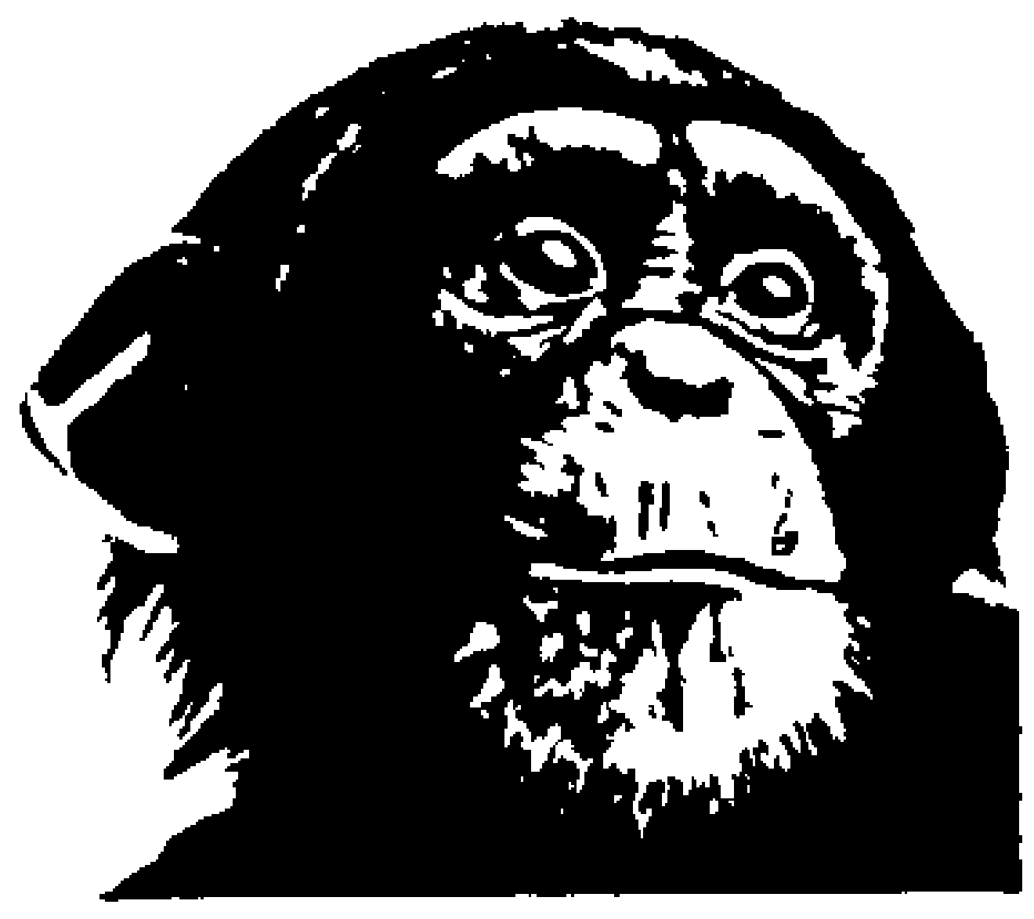
Zhang, Y. (2001). Foraging and social behaviour of rehabilitated orang-utans in a primary forest. Unpublished masters dissertation, University of Edinburgh, Edinburgh, Scotland.

Appendix A: Questionnaire distributed to managers of African ape sanctuaries

This questionnaire was distributed to managers of chimpanzee sanctuaries. The same questionnaire was distributed to gorilla and bonobo sanctuaries with the word chimpanzee substituted with gorilla or bonobo

UNIVERSITY of STIRLING
INNOVATION and EXCELLENCE

African chimpanzee sanctuary questionnaire



Please take some time to carefully complete this questionnaire. The results will be compiled to provide an up-to-date presentation of all African ape sanctuaries; their work, methods and direction. Each sanctuary will be sent a copy of the compilation and results disseminated.

Questionnaire completed by:____

Affiliation to sanctaury:____

1. CONTACT DETAILS

Name of director/contact person:____________________________________

Address:____

____

Telephone/fax:____

Email:____

Web site address:____

2. PROJECT HISTORY

Date sanctuary opened:____

Instigator of sanctuary: ____

____

Focus of project:____

____

3. PROJECT LOCATION

Where is your project located (please tick the relevant box/es):

a. Within a city/town ☐ c. Within a reserve/protected area ☐

b. Within a village ☐ d. Within an isolated location ☐

If you are located within a reserve and/or isolated location, what is the distance to, and the name of the nearest:

a. Village____

b. Major town/city____

If you have more than one site, please detail (using the same criteria as above) the location for the 2nd site:____

____

If you have more than one site please distinguish the purpose/focus for the 2 different sites:

____

____

4. ANIMAL DETAILS

<u>Numbers, age & sex of chimpanzees</u>

(a) How many chimpanzees do you have at your sanctuary:____________

(b) What are the ages of your chimpanzees: (please provide a number for each relevant age category):

0-12 months____________ 8-11 years____________

13-23 months____________ 12-15 years____________

2-4 years____________ 16 years & older____________

5-7 years____________

(c) Number of females____________ Number of males____________

(d) At what age did the chimpanzees arrive (please give an estimated number against each relevant category):

0-12 months____________

8-11 years____________

13 –23 months____________

12-15 years____________

2-4 years____________

16 years & older____________

5-7 years____________

(e) Are you still accepting chimpanzees into your sanctuary (please tick the relevant box):

Yes ☐

No ☐

If you are no longer accepting chimpanzees, what are the reasons (please *tick the relevant box/es*):

Financial ☐

Space ☐

Other (please specify) ☐

What is the maximum number of chimpanzees that you could hold? Please provide a figure

____

Origin of chimpanzees

(a) How did the chimpanzees come to arrive at your project (please provide an estimated number against each relevant category):

Confiscation____________

Other (please specify)____________

Donation____________

(b) What had been the circumstances of the chimpanzees before their arrival at your project (please provide an estimated number against each relevant category):

Kept as a pet____________

Tourist attraction (bar/hotel/zoo)____________

Awaiting sale/transportation to place of sale/market at a camp/village____________

Other (please specify)____________

(c) Are all the chimpanzees at your sanctuary known to be from the country where your project is based (please tick the relevant box):

Yes ☐ **Do not know** ☐

No ☐ **Other (please specify** ☐

If you have chimpanzees at your sanctuary that originate from another country, please state the countries of origin here:____________________________________

____

(d) For those chimpanzees that originate from the country where your sanctuary is based, for how many chimpanzees do you know the region in which they were originally captured (please provide a figure) :____

____

(e) For those chimpanzees where you know the region of origin, how many different regions do the chimpanzees come from (please provide a figure):____________________________

If you know the names of the regions please specify here:________________________

____

Health of the chimpanzees

(a) In what state of overall general health have your chimpanzees arrived (please give an estimated number of chimpanzees against each relevant category):

Excellent:____________ **Poor:**____________

Good:____________ **Very poor:**____________

Fair:____________ **Other (please state):**____________

(b) Using a scale of 1-10, rate how common the following conditions/injuries are when a chimpanzee first arrives at your sanctuary. The lower end of the scale (0) represents never and the higher end (10) represents all the time (please circle the appropriate number):

RARE **COMMON**

Bullet wound

1 2 3 4 5 6 7 8 9 10

Wound due to wire/chain

1 2 3 4 5 6 7 8 9 10

Infected wound

1 2 3 4 5 6 7 8 9 10

Broken bones

1 2 3 4 5 6 7 8 9 10

External parasites

1 2 3 4 5 6 7 8 9 10

Malnutrition

1 2 3 4 5 6 7 8 9 10

Malaria

1 2 3 4 5 6 7 8 9 10

Internal parasites

1 2 3 4 5 6 7 8 9 10

Behavioural abnormalities (please specify)

1 2 3 4 5 6 7 8 9 10

Other (please specify) ____

1 2 3 4 5 6 7 8 9 10

(c) How many chimpanzees have died as a direct result of their medical condition upon arrival? Please specify a number: _______________

(d) How may chimpanzees have died in total? Please specify a number for males and females:

Males________________ Females________________

(e) Do you use (or plan to use) some form of contraception for the chimpanzees (please tick the relevant box):

Yes ☐

No ☐

Please specify which method you use (are planning to use):___________________________________

____

Other species at the sanctuary

Do you house any other species of wildlife at your sanctuary (please tick the relevant box):

Yes ☐

No ☐

If you do have any other species of wildlife, please specify the species and their numbers:__________

____

____

5. CHIMPANZEE HOUSING

(a) How do you accommodate your chimpanzees: (please tick the relevant box/es):

Cage/s	☐	**Islands**	☐
Enclosure/s	☐	**Other (please specify)**	☐

(b) If you ticked the box for enclosures, what method/s do you employ to prevent the animals from escaping (please tick the relevant box/es):

Electric fence	☐	**Wire**	☐
Water/moat	☐	**Other (please specify)**	☐
Wall	☐		

(c) Please state the size of the islands and/or enclosures: ______________________________

____

6. CHIMPANZEE DIET

(a) Are the chimpanzees nutritionally self-sufficient in their accommodation (please tick the relevant box):

Yes ☐

No ☐

(b) If not nutritionally self-sufficient, how many times per day are the chimpanzees fed (please tick the relevant box):

Once ☐

Twice ☐

Three ☐

Four ☐

Other (please specify) ☐

(c) If not nutritionally self-sufficient what types of food are your chimpanzees fed:

Fruits ☐

Vegetables ☐

Milk ☐

Cerelac ☐

Natural vegetation/fruits ☐

Other (please specify) ☐

If you have ticked the box natural vegetation & fruits, please list the types that are fed to the chimpanzees: ______________________________

____

7. DAILY ROUTINES OF THE CHIMPANZEES

Do your chimpanzees remain the whole day within their accommodation (please tick the relevant box):

Yes ☐

No ☐

Sometimes ☐

Group dependent ☐

Other (please specify) ☐

If your chimpanzees do not remain the whole day in their accommodation, please specify their routine. If this varies according to group, please explain how and why:____________________

____

____

8. SANCTUARY STRUCTURE

(a) How does your sanctuary operate (please tick relevant box/es):

Independently as a local NGO	☐
Part of an international NGO	☐
In collaboration with a national governmental department	☐
Other (please specify)	☐

(b) Is your project involved in any of the following in conjunction with the work in the sanctuary:

Local education	☐	Tourism	☐
Local development	☐	Collection of scientific data	☐
Habitat protection/anti-poaching	☐	Other (please specify)	☐

If you have ticked any of the boxes please describe how you are achieving this: ____________

(i) Local education______________________________

____

____

(ii) Local development______________________________

____

____

(iii) Habitat protection/anti-poaching________________________

____

____

(iv) Tourism____________________________________

____

____

*(v) Collection of scientific data*____

(vi) Other (please specify):____

9. SANCTUARY FINANCE

(a) Using a scale of 1-10 (where 0 represents least important and 10 represents most important), please provide a figure for each category to represent how much each contributes to your overall funding. The same rating figure can be used more than once.

Personally financed	____	**Zoo**	____
Local NGO	____	**Local individual donations**	____
Overseas NGO	____	**Overseas individual donations**	____
Local commercial sponsorship	____	**Government**	____
Overseas commercial sponsorship	____	**Tourism/visitors**	____
Volunteer programmes	____	**Other (please specify)**	____

(b) How much approximately does it cost to run the sanctuary per annum in US dollars (please tick a box):

Up to $50,000	☐	**$101,000-$150,000**	☐
$51,000-$100,000	☐	**$151,000-$200,000**	☐

If you have a more accurate figure and do not mind providing this information, please state here. Also if you hold non-apes species, can you also provide a figure for apes only:____________________

If you do have 2 sites and can distinguish the costs between the sites, please state here:________________

10. SANCTUARY STAFFING

(a) How many local staff do you employ:____________________

(b) How many ex-patriate staff do you employ:____________________

(c) Do you have any volunteers working at your site (please tick a box) :

Yes ☐

No ☐

Do your volunteers pay to work at the site (please tick a box) :

Yes ☐

No ☐

If you have volunteers, are they part of a volunteer programme (please tick a box) :

Yes ☐

No ☐

If you have answered yes, who organises the volunteer programme and recruitment:_______________

____

11. THE FUTURE

What are the future priorities of your project (please specify):______________________________

____

____

THANK-YOU FOR YOUR CO-OPERATION

Kay Farmer from the Department of Psychology at the University of Stirling has compiled this questionnaire as part of a doctorate thesis focused on chimpanzee reintroduction.

For further details please contact:

Kay Farmer,
Scottish Primate Research Group,
Department of Psychology,
University of Stirling,
Stirling. FK9 4LA.
Scotland. UK.
Tel:- 00 44 (0) 1786 466373
Fax:- 00 44 (0) 1786 467641
Email:- k.h.farmer@stir.ac.uk

Appendix B: Mammal species identified in the Triangle

Common name	Scientific name	Direct observation	Sign (print/faeces)
ARTIODACTYLA			
Bay duiker	*Cephalopus dorsalis*	√	
Black-fronted duiker	*Cephalopus nigriforns*	√	
Blue duiker	*Cephalopus monticola*		√
Forest buffalo	*Syncerus caffer nanus*		√
Peter's duiker	*Cephalopus callipygus*	√	
Red-flanked duiker	*Cephalophus rufilatus*	√	
Red river hog	*Potamochoerus porcus*	√	√
Sitatunga	*Tragelapus speki*	√	√
Water chevrotain	*Hyemoschus aquaticus*		√
Yellow-backed duiker	*Cephalopus silvicultor*		√
CARNIVORA			
African clawless otter	*Aonyx capensis*	√	
Civet	*Virerra civetta*	√	
Leopard	*Panthera pardus*	√	√
PHOLIDOTA			
Long-tailed pangolin	*Uromanis tetradactyla*	√	
PRIMATES			
Chimpanzee	*Pan troglodytes troglodytes*	√	√
Dwarf galago	*Galagoides demidoff*	√	
Gorilla	*Gorilla gorilla gorilla*	√	√
Mandrill	*Mandrillus sphinx*	√	√
Moustached monkey	*Cercopithecus cephus*	√	
Putty-nosed monkey	*Cercopithecus nictitans*	√	
PROBOSCIDEA			
Forest elephant	*Loxodonta africana cyclotis*	√	√
RODENTIA			
Brush-tailed porcupine	*Atherurus africanus*	√	
Flying squirrel	*Anomalurus* sp.	√	

(Source: Paredes, 1997, 1998)

Appendix C: Main check-sheet used to collect behavioural data

Date: **Group:** **Height of water:** **Weather:** **Forest type:** **Observer:**

Time	Chimp	Feed	Rest	Groom	Aggr	Play	Move	Other	Height	Location	Comments
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									
		FR SD L ST FL SP OTH									

Height: 0=ground 1 = <5m 2 = 5-15, 3 = >15m Weather: HR = heavy rain, R = rain, C = cloudy, S = sunny Height of water: 0 = none 1 = <ankle, 2 = <knee, 3 = >knee
Forest type: I = inundated, S = swamp, P = primary Feed: Fr = fruit, SD = seed, L = leaf, ST = stem, FL = flower, SP = sap, OTH = other (specify in comments)

Appendix D: Plant species identified and consumed on the three pre-release islands in comparison to the presence of these species in wild and other reintroduced chimpanzee diet

FAMILY Name scientific	Life form	Species present on island(s)	Eaten on island/s	Species present at WC site	Eaten by WC	Species present at RC site	Eaten by RC	Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
ANGIOSPERMAE																		
DICOTYLEDONEAE																		
ANACARDIACEAE																		
Mangifera indica	Tree	1, 3	√	L	√	C	x	•										
BIGNONIACEAE																		
**Kigelia africana*	Tree	3	x	L	x	C	x											
**Spathodea campanulata*	Tree	1	x	L	x	C	x											
CAESALPINIACEAE																		
**Anthonotha* sp.	Tree	1, 2	x	L/NN/KB	x	C	x											
**Dialium* sp.	Tree	1, 3	x	L/NN/KB	√	C	√	•	C		C	C	C					C
CELASTRACEAE																		
**Salacia* sp.	Liana	3	x	x	x	C	√	•			•							
CLUSIACEAE																		
**Symphonia globulifera*	Tree	1, 2	x	x	x	C	√	•			•	•	•					
COMBRETACEAE																		
**Terminalia superba*	Tree	2	√	NN	x	C	x				•							

Family Name scientific	Life form	Species present on island/s	Eaten on island/s	Species present at WC site	Eaten by WC	Species present at RC site	Eaten by RC	Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
DILLENIACEAE																		
**Tetreacera alnifolia*	Liana	2	x	x	x	C	x											
**Tetracera podotricha*	Liana	1	x	L/NN	x	C	√				•							
**Tetracera* sp.	Liana	3	x	KB	x	C	√											
EUPHORBIACEAE																		
**Alchornea cordifolia*	Tree	2	√	L/NN/KB	x	C	x			•								
**Anthostema aubryanum*	Tree	1, 2, 3	x	x	x	C	x											
**Macaranga* sp.	Tree	1, 3	x	L/NN/KB	x	I/C	I	•										
HUMIRIACEAE																		
**Sacoglottis gabonensis*	Tree	1	x	L	√	C	√	•										C
IRVINGIACEAE																		
**Klainedoxa* sp.	Tree	3	x	L/NN/KB	√	C	√	•			KB/C	KB		C				
LOGANIACEAE																		
**Anthocleista* sp.	Tree	1	x	L/NN	x	C	x											
MELIACEAE																		
Carapa procera	Tree	3	x	L/NN	x	x	x											
MORACEAE																		
**Musanga cecropioides*	Tree	1	x	L/NN/KB	NN/KB	I/C	I	•	I						I			
MYRTACEAE																		
Psidium guajava	Shrub	1	√	x	x	x	x											•

FAMILY **Name scientific**	**Life form**	**Species present on island/s**	**Eaten on island/s**	**Species present at WC site**	**Eaten by WC**	**Species present at RC site**	**Eaten by RC**	**Part/s eaten**										
								Fruit/pulp	**Seed**	**Stem/pith**	**Leaf**	**Young Leaves**	**Sap**	**Flower**	**Bark**	**Shoots**	**Liquid**	**Not known**
PAPILIONACEAE																		
Haplormosia monophylla	Herb	2	√	x	x	x	x	•										
**Milletia comosa*	Liana	1, 2, 3	x	x	x	C	√	•			•	•		•				•
PIPERACEAE																		
**Piper guineense*	Liana	2	x	NN	x	C	x											
RHIZOPHORACEAE																		
**Rhizophora racemosa*	Tree	1, 2	x	x	x	C	x											
STERCULIACEAE																		
**Cola* sp.	Tree	1, 2, 3	1,2,3	L	√	C	√	1, 2, L/ C		2, C	1, L/ C	C		2				3, C
**Pterygota* sp.	Tree	1, 3	x	L/NN	x	I/C	√	•	C		C	C	C	C	I	•		
VERBENACEAE																		
**Vitex doniana*	Tree	1	√	L/NN	L	C	√	L/C										1
**Vitex* sp.	Tree	2, 3	2	x	x	C	√	C		C	•	C	C					C
MONOCOTYLEDONEAE																		
AGAVACEAE																		
Dracaena arborea	Shrub	2	√	NN	x	C	x				•							
**Dracaena* sp.	Shrub	1	x	L/NN	x	C	x											
Sansevieria sp.	Herb	1, 3	x	L	x	C	x											

FAMILY Name scientific	Life form	Species present on island/s	Eaten on island/s	Species present at WC site	Eaten by WC	Species present at RC site	Eaten by RC	Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
ARACEAE																		
**Anchomanes difformis*	Shrub	1	x	L	x	C	x											
**Cyrtosperma senegalense*	Herb	1	x	NN	x	C	x											
ARECACEAE (PALMAE)																		
Borassus aethiopum	Palm	1, 2	2	x	x	x	x	•										
**Calamus* sp.	Palm	2	x	L	x	I/C	√	•										
**Elaeis guineensis*	Palm	1, 2, 3	1,2,3	NN	x	C	√	•	C	2, C	C			C				1,C
Phoenix reclinara	Palm	2	x	x	x	x	x											
**Podococcus barteri*	Palm	2	x	x	x	√	•		•									
**Raphia* sp.	Palm	1, 2, 3	x	L/NN	x	C	√	•	•	•	•		•	•		•		•
COMMELINACEAE																		
**Palisota* sp.	Herb	1, 2	x	L/NN/KB	NN/KB	C	√	NN		KB/C	C			C				
CYPERACEAE																		
**Scleria boivinii*	Herb	1	x	L/NN	x	C	x											
DIOSCORACEAE																		
Dioscorea sansibarensis	Liana	1, 3	x	x	x	x	x											
MARANTACEAE																		
**Marantaceae* sp.	Herb	1	x	L/NN/KB	√	I/C	√	•	L/NN/I	L/NN/ I/C	L/NN I/C			I/C		I/C	C	C
SIMAROUBACEAE																		
**Odyendyea gabonensis*	Tree	2	√	L	x	x	x				•							

FAMILY Name scientific	Life form	Species present on island/s	Eaten on island/s	Species present at WC site	Eaten by WC	Species present at RC site	Eaten by RC	Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
ZINGIBERACEAE																		
**Aframomum* sp.	Herb	1, 2, 3	√	L/NN	√	I/C	√	1, 2, L/NN/ I/C		1, 2, L/C	NN/C			2, C	I			3, C
**Costus* sp.	Herb	1, 2	x	L	√	C	√	C		•	C	C						
NON-IDENTIFIED																		
*Liana (non-identified)	Liana	1	√	L/NN/KB	√	C	√	•	C	C	L/C	C	C	C	L/C			C
Nucuna (LN)	Liana	1	x	x	x	x	x											
Palétuvier (LN)	Shrub	1, 2, 3	√	x	x	x	x				1							2,3
*Succis (LN)	Liana	2	x	x	C	√	x			•	2							

Notes: sp. = species; LN = local name; Island 1 = Yombe Island, 2 = Yvette Island, 3 = Pepere Island; WC = wild chimpanzees; RC = reintroduced chimpanzees
Wild chimpanzee site: L = Lopé, NN = Noubalé-Ndoki, KB = Kahuzi-Biega; Reintroduced chimpanzee site: I = Ipassa, C = Conkouati; * = found within Triangle release site
x = no, √ = yes, empty cells = part not eaten, • = all chimpanzee sites listed eating the plant part, code letters represent group/site that eats the part

Appendix E: Plant species and parts consumed post-release

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem-pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
ANGIOSPERMAE																		
DICOTYLEDONEAE																		
ANACARDIACEAE																		
**Antrocaryon klaineanum*	Tree	L/NN	√	x	-	√	x	•										
Lannea welwitschii	Tree	L	√	-	-	x	x								•			
Mangifera indica	Tree	L	√	-	-	x	x	•										
**Pseudospondias longifolia*	Tree	L	√	-	-	√	√	•			C							
**Pseudospondias microcarpa*	Tree	L/KB	√	-	x	√	x	•										
**Trichoscypha* sp. (5)	Tree					√	√	•			C							
-*Trichoscypha acuminata*	Tree	L/NN	√	x	-	?	?	•										
-*Trichoscypha abut*	Tree	L	√	-	-	?	?	•										
-**Trichoscypha ferruginea*	Tree	NN	-	x	-	?	?											
-*Trichoscypha heterophylla*	Tree	-	-	-	-	?	?											
-**Trichoscypha laxiflora*	Tree	-	-	-	-	?	?											
ANNONACEAE																		
Anonidium mannii	Tree	NN/KB	-	√	√	√	x	•										
**Cleistophilis patens*	Tree	NN	-	x	-	x	√	•										
Enanthia chlorantha	Tree	L	√	-	-	x	√	•	C		C	C	C					C
Hexalobus crispiflorus	Tree	L	√	-	-	x	√	•										
**Isolona hexaloba*	Tree	NN	-	√	-	√	x	•										
**Monoanthotaxis diclina*	Liana	L	x	-	-	x	√	•										
**Pachypodanthium staudi*	Tree	L	x	-	-	√	√	•		C	C							•

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
ANNONACEAE *cont...*																		
**Polyalthia suaveolons* sp. (2)	Tree						√	•										
-**Polyalthia suaveolens* var. *gabonica*	Tree	L	√	-	-	√	?	•										
-**Polyalthia suaveolens* var. *suaveolens*	Tree	L/NN/KB	√	√	√	√	?	•										
**Uvaria brazzavillensis*	Liana	NN	-	x	-	x	x											
Uvaria comerei	Liana	NN	-	x	-	x	x											
Uvaria psorosperma	Liana	L	√	-	-	x	x	•										
Uvaria sp. SEGC 253	Liana	L	√	-	-	-	-	•										
Uvaria sp. SEGC 256	Shrub	L	√	-	-	-	-	•										
**Uvariastrum pierreanum*	Tree	L/NN	√	√	-	x	√	•										
Uvariopsis congolana	Tree	KB	-	-	√	x	x	•										
**Xylopia* sp. (14)	Tree						√	•	•				•	•				
-**Xylopia aethopica*	Tree	L/NN/KB	√	x	x	√	?	•	I									
-**Xylopia africana*	Tree	-	-	-	-	x	?											
-*Xylopia gilbertii*	Tree	-	-	-	-	x	?											
-**Xylopia hypolampra*	Tree	L/NN	√	x	-	√	?	•	I									
-**Xylopia le-testui*	Tree	-	-	-	-	x	?											
-**Xylopia mildbraedii*	Tree	-	-	-	-	x	?											
-**Xylopia parviflora*	Tree	L	x	-	-	x	?											
-**Xylopia phoidora*	Tree	L	x	-	-	x	?											
-**Xylopia pynaertii*	Tree	NN	-	x	-	x	?											
-**Xylopia quintasii*	Tree	L	√	-	-	√	?	•	I									
-**Xylopia rubscens*	Tree	NN	-	x	-	x	?											
-**Xylopia staudtii*	Tree	L	x	-	-	√	?	•	•									
-**Xylopia toussaintii*	Tree	-	-	-	-	x	?											
-**Xylopia wilwerthii*	Tree	-	-	-	-	x	?											

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not *known*
APOCYNACEAE																		
Dictyophleba stipulosa	Liana	-	-	-	-	√	x	•					•					
**Landolphia foretiana*	Liana	NN	-	√	-	x	x	•										
Landolphia cf. *jumelei*	Liana	L	√	-	-	x	x	•										
**Landolphia mannii*	Liana	(L)	-	-	-	x	√	•										
Landolphia owariensis	Liana	KB/NN		x	√	x	x	•										
Landolphia sp. SEGC 526	Liana	L	√	-	-	-	-	•										
Landolphia sp. LJTW 0079	Liana	L	x	-	-	-	-											
Pleiocarpa mutica	Shrub	NN	-	√	-	x	x	•										
**Saba comorensis*	Liana	NN	-	√	-	x	x	•										
Tabernaemontana crassa	Tree	NN	-	√	-	x	x	•										
BIGNONIACEAE																		
Newbouldia laevis	Tree	L	x	-	-	√	x					•						
BOMBACACEAE																		
Ceiba pentandra	Tree	L/NN	x	√	-	x	x							•				
BURSERACEAE																		
**Aucoumea klaineana*	Tree	L	√	-	-	x	x							•				
**Canarium schweinfurthii*	Tree	L/KB	√	-	√	√	x	•										
**Dacroydes* sp. (7)	Tree	-	-	-	-	x	√	•										
Dacroydes ebatom	Tree	-	-	-	-	x	?											
Dacryodes edulis	Tree	L/KB	√	-	√	x	?	•										
Dacroydes heterotricha	Tree	-	-	-	-	x	?											
**Dacroydes igaganga*	Tree	-	-	-	-	√	√	•			C			C				
Dacroydes klaineana	Tree	L	x	-	-	√	?	•										
Dacroydes le-testui	Tree	-	-	-	-	x	?											
**Dacroydes rubescens*	Tree	NN	-	x	-	x	?											

FAMILY Name scientific	Life Form	Species present at WC site	Eaten by WC			Eaten by RC		Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
BURSERACEAE *cont....*																		
Dacroydes sp. LJTW 0641	Tree	L	x	-	-	-	-											
**Santiria trimera*	Tree	L/NN	√	√	-	√	√	•		C	C							
CAESALPINIACEAE																		
Afzelia bipendensis	Tree	L	x	-	-	√	x	•	•									
**Berlinia* sp. (3)	Tree						√				•	•	•	•				
-**Berlinia bracteosa*	Tree	L	x	-	-	x	?											
-**Berlinia confusa*	Tree	-	-	-	-	x	?											
-**Berlinia grandiflora*	Tree	-	-	-	-	x	?											
Cryptosepalum congolanum	Tree	-	-	-	-	√	x		•					•				
**Cryptosepalum staudtii*	Tree	L	√	-	-	x	x		•		•				•			
**Dialium* sp. (9)	Tree	-	-	-	-	x	√	•	•		•	•	•					•
**Dialium bipindense*	Tree	L/NN	x	√	-	x	?	•										
**Dialium densiflorum*	Tree	-	-	-	-	x	?											
**Dialium dinklagei*	Tree	L	√	-	-	x	?	•										
**Dialium gossweileri*	Tree	-	-	-	-	x	?											
Dialium laurentii	Tree	-	-	-	-	x	?											
**Dialium pachyphyllum*	Tree	L/NN	√	√	-	x	?	•										
Dialium polyanthum	Tree	NN/KB	-	√	√	x	?	•										
Dialium soyauxii	Tree	L	x	-	-	x	?											
**Dialium tessmannii*	Tree	NN	-	√	-	x	?	•										
Dialium sp. SEGC 525	Tree	L	x	-	-	-	-											
**Erytrophleum ivorense*	Tree	L/NN	x	√	-	√	x		I	NN				NN				
Gilbertiodendron dewevrei	Tree	L/NN/KB	x	√	x	x	x		•									
Guibourtia tessmannii	Tree	L	√	-	-	x	x		•									
**Julbernardia brieyi*	Tree	L	√	-	-	x	√		•		L				L			
Scorodophloeus zenkeri	Tree	L	x	-	-	√	x		•									

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
CAESALPINIACEAE *cont....*																		
Tessmannia africana	Tree	NN	-	√	-	x	x		•									
**Tessmannia anomala*	Tree	NN/KB	-	x	x	x	√	•										
CELASTRACEAE																		
**Salacia* sp. (?)	Liana	-	-	-	-	x	√	•			•							
**Hippocratea* sp. (?)	Liana	-	-	-	-	x	√		•									
CHRYSOBALANACEAE																		
**Acioa pallenscens*	Tree	L	x	-	-	x	√				•							
Parinari excelsa	Tree	L/NN	x	√	-	x	x	•										
CLUSIACEAE																		
**Pentadesma butyracea*	Tree	-	-	-	-	x	√	•					•	•				•
**Symphonia globulifera*	Tree	-	-	-	-	x	√	•			•	•	•					
CONNARACEAE																		
Byrsocarpus dinklagei	Liana	NN	-	x	-	√	x	•	•									
**Roureopsis obliquifoliolata*	Liana	NN	-	x	-	√	x				•							
CONVOLVULACEAE																		
Neuropeltis acuminata	Liana	-	-	-	-	√	x				•							
DICHAPETALCEAE																		
**Dichapetalum* sp. (2)	Liana	-	-	-	-	x	√	•										
Dichapetalum brazzae	Liana	NN	-	x	-	x	?											
Dichapetalum chalotii	Liana	-	-	-	-	x	?											
Dichapetalum sp. LJTW 0048	Shrub	L	√	-	-	-	-	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
DICHAPETALCEAE *cont…*																		
Dichapetalum sp. LJTW 0414	Liana	L	√	-	-	-	-	•										
Dichapetalum sp. LJTW 0140	Liana	L	x	-	-	-	-											
DILLENIACEAE																		
**Tetracera podotricha*	Liana	L	x	-	x	x	√				•							
EBENACEAE																		
**Diospyros* sp. (16)	Tree	-	-	-	-	√	√	•			C							
-**Diospyros bipindensis*	Tree	KB	-	-	x	x	?											
-*Diospryos crassiflora*	Tree	NN	-	√	-	√	?	•										
-**Diospyros conocarpa*	Tree	-	-	-	-	-	?											
-*Diospryos dendo*	Tree	L/NN	√	√	-	x	?	•	L									
-**Diospyros fragrans*	Tree	-	-	-	-	x	?											
-**Diospyros hoyleana*	Tree	KB	-	-	x	x	?											
-*Diospryos mannii*	Tree	L	√	-	-	x	√	•										
-**Diospyros obliquifoliolata*	Tree	-	-	-	-	x	?											
-**Diospyros physocalycina*	Tree	-	-	-	-	x	?											
-**Diospyros piscatoria*	Tree	L/NN	√	√	-	x	?	•										
-**Diospyros polystemon*	Tree	L	√	-	-	x	?	•	•									
-*Diospyros simulans*	Tree	-	-	-	-	x	?											
-**Diospyros suavelons*	Tree	L/NN	√	√	-	x	√	•										
-**Diospyros vermoesenii*	Tree	-	-	-	-	x	?											
-*Diospyros viridicans*	Tree	L	x	-	-	x	?											
-**Diospyros zenkeri*	Tree	L/KB	√	-	x	x	√	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
EBENACEAE *cont....*																		
-*Diospyros* sp. LJTW 409	Tree	L	x	-	-	-	-											
-*Diospyros* sp. LJTW 1004	Tree	L	x	-	-	-	-											
EUPHORBIACEAE																		
**Alchornea floribunda*	Shrub	KB/NN	-	x	√	x	x			•	•							
**Dichostemma glaucescens*	Tree	NN	-	x	-	√	x		•									
**Discoglypremna caloneura*	Tree	L	√	-	-	x	x	•			•							
**Macaranga barteri*	Tree	L/NN	x	x	-	√	x	•										
**Macaranga monandra*	Tree	L/NN/KB	x	x	x	√	x	•										
**Phyllanthus sp.* (2)	Tree					x	√	•										
-*Phyllanthus amarus*	Tree	-	-	-	-	x	?											
-**Phyllanthus capillaris*	Tree	-	-	-	-	x	?											
Plagiostyles africana	Tree	L	√	-	-	x	x	•										
**Uapaca* sp. (3)	Tree					x	√	•										
**Uapaca guinennsis*	Tree	L/NN/KB	√	x	√	x	√	•										
Uapaca heudelotii	Tree	L/NN	√	x	-	√	√	•										
Uapaca paludosa	Tree	L/KB	√	-	√	√	?	•										
FLACOURTIACEAE																		
**Caloncoba glauca*	Tree	L/NN	x	x	-	√	x	•						•				
**Caloncoba welwitschii*	Tree	NN	-	√	-	x	x	•										
**Scottellia coriacea*	Tree	L	x	-	-	x	√	•										
HUMIRIACEAE																		
**Sacoglottis gabonensis*	Tree	L	√	-	-	x	√	•										C

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC at three sites			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
ICACINACEAE																		
**Lavigeria macrocarpa*	Liana	-	-	-	-	x	√				•							
IRVINGIACEAE																		
**Irvingia gabonensis*	Tree	L/NN	√	√	-	√	√	L/NN /C	L/C/I	C	C			C				C
**Irvingia grandifolia*	Tree	L/NN	√	√	-	x	x	•	L									
**Irvingia robur*	Tree	L/NN/KB	√	x	x	x	x	•										
**Klainedoxa gabonensis*	Tree	L/NN/KB	√	√	√	x	√	•			C			C				
**Klainedoxa microphylla*	Tree	-	-	-	-	x	√				•	•						
LAURACEAE																		
Beilachmiedia fulva	Tree	L	√	-	-	x	x	•										
Beilachmiedia sp. LJTW 37	Tree	L	√	-	-	-	-	•										
LOGANIACEAE																		
**Strychnos congolana*	Liane	L/KB	x	-	x	x	√	•	•								•	•
MELASTOMATACEAE																		
**Dinophora spenneroides*	Herb	NN	-	x	-	√	x				•							
**Warnecka* sp. (4)	Shrub	-			-	x	√	•								•		
- **Warnecka macrantha*	Shrub	-	-	-	-	x	?											
-*Warnecka membranifolia*	Shrub	NN	-	x	-	x	?											
-**Warnicka pulcherrima*	Shrub	-	-	-	-	x	?											
-**Warnicka wildeana*	Shrub	-	-	-	-	x	?											
MELIACEAE																		
Trichilia welwitschii	Tree	KB	-	-	√	x	x	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
MENISPERMACEAE																		
**Triclisia dictyophylla*	Liana	NN	-	√	-	x	x	•										
MIMOSACEAE																		
**Calpocalyx dinklagei*	Tree	-	-	-	-	√	x	•										
**Parkia bycolor*	Tree	L/KB	√	-	x	x	√	•			C			C				
**Pentaclethra* sp. (2)	Tree					x	√				•							
**Pentaclethra eetveldeana*	Tree	L	√	-	-	x	?				•							
**Pentaclethra macrophylla*	Tree	L/KB	√	-	x	x	?				•			•				
**Piptadeniastrum africanum*	Tree	L/NN/KB	x	x	x	x	√	•			•	•	•					
Tetrapleura tetraptera	Tree	L/NN/KB	x	√	x	√	x		NN		I							
MORACEAE																		
**Ficus* sp. (3)	Tree					√	√	•		C			C					
Ficus elasticoides	Tree	L/NN	x	√	-	x	√	•					C					
**Ficus ovata*	Tree	L/KB	x	-	x	x	?											
**Ficus vogeliana*	Tree	KB	-	-	x	x	?											
Ficus sp. SEGC 443	Epip-phyte	L	√	-	-	-	-	•										
**Musanga cercopioides*	Tree	L/NN/KB	x	√	√	√	x	•	I						I			
**Myrianthus* sp. (2)	Tree	-	-	-	-	-	√	•										
**Myrianthus arboreus*	Tree	L/NN/KB	√	√	√	√	?	•			KB							
**Myrianthus scandens*	Tree	-	-	-	-	x	?											
**Treculia africana*	Tree	L/NN/KB	√	x	x	√	x	I	•					•				
Trilepisium madagascariensis	Tree	KB	-	-	√	x	x	•										
MYRISTICACEAE																		
**Coelocaryon preussi*	Tree	L	x	-	-	√	√	•			C	C		C				

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC at three sites			Eaten by RC		Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
MYRISTICACEAE *cont…*			L	NN	KB	I	C											
**Pycnanthus angolensis*	Tree	L/NN/KB	√	x	√	√	√	•			C		C					
**Staudia gabonensis*	Tree	L/NN/KB	√	x	x	√	√	•		C	C	C						
MYRTACEAE																		
**Syzygium rowlandii*	Tree	KB	-	-	√	x	x	•										
OLACACEAE																		
**Coula edulis*	Tree	L	x	-	-	√	√	•										
Heisteria parvifolia	Tree	L/NN/KB	√	x	x	√	x	•										
**Strombosia grandiflora*	Tree	NN	-	√	-	x	x				•							
**Strombosia schefferi*	Tree	L/KB	x	-	√	x	x	•										
Strombosiopsis tetrandra	Tree	L/NN/KB	x	√	x	x	x	•										
**Ongokea gore*	Tree	L/NN	√	x	-	√	x	I			•							
PANDACEAE																		
**Panda oleosa*	Tree	L/NN	x	√	-	√	√	•			C							
PASSIFLORACEAE																		
**Barteria fistulosa*	Tree	L/NN	√	x	-	x	x	•										
POLYGALACEAE																		
Carpolobia glabrescens	Shrub	KB	-	-	√	x	x	•			•							
RHAMNACEAE																		
Maesopsis eminii	Tree	NN/KB	-	x	√	x	x	•										
RUBIACEAE																		
Atractogyne gabonii	Liana	L	√	-	-	√	√	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
RUBIACEAE *cont…*																		
**Massularia acuminta*	Tree	NN/KB	-	x	x	√	√	•	C									
**Nauclea* sp. (3)	Tree						√	•	•		•							
-**Nauclea diderrichii*	Tree	L/NN/KB	√	√	x	√	√	•	I		C							
-*Nauclea latifolia*	Tree	L	√	-	-	x	?	•										
-**Nauclea pobeguinii*	Tree	NN	-	√	-	√	?	•										
**Porterandia cladantha*	Tree	L/NN	√	x	-	-	?	•										
**Psychotria* sp. (9)	Tree					x	√	•										
-**Psychotria bifaria*	Tree	-	-	-	-	x	?											
-**Psychotria calva*	Tree	-	-	-	-	x	?											
-*Psychotria ceratalabastron*	Shrub	L	x	-	-	x	?											
-**Psychotria comperei*	Tree	-	-	-	-	x	?											
-**Psychotria dermatophylla*	Tree	-	-	-	-	x	?											
-**Psychotria ealensis*	Tree	-	-	-	-	x	?											
-**Psychotria ebenensis*	Tree	-	-	-	-	x	?											
-**Psychotria kimuenzee*	Tree	-	-	-	-	x	?											
- *Psychotria venosa*	Tree	-	-	-	-	x	?											
**Sherbournia* sp. (3)	Tree	-	-	-	-	-	√	•										
-**Sherbournia batesii*	Tree	-	-	-	-	x	?											
-**Sherbournia bignoniifolia*	Tree	-	-	-	-	√	√	•	I									
-**Sherbournia bignoniifolia* var. *brazzei*	Tree	-	-	-	-	x	?											
RUTACEAE																		
**Zanthoxylum* (*Fagara*) sp. (5)	Tree	-	-	-	-	x	√	•			•							
Zanthoxylum bouetensis	Tree	-	-	-	-	x	?											
Zanthoxylum gilletii	Tree	-	-	-	-	x	?											

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC at three sites			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
RUTACEAE *cont…*																		
Zanthoxylum heitzii	Tree	NN	-	x	-	x	?											
Zanthoxylum macrophylla	Tree	L/NN/KB	x	x	x	x	?											
Zanthoxylum tessmannii	Tree	L	x	-	-	x	?											
SAPINDACEAE																		
Blighia welwitschii	Tree	L/NN	x	x	-	√	x	•	•									
**Chytranthus talbotii*	Tree	L/NN	x	x	-	x	√				•							
**Eriocoelum marcrocarpum*	Tree	L	x	-	-	x	√	•										
**Eriocoelum oblongum*	Tree	-	-	-	-	x	√	•										
Eriocoelum sp. LJTW 132	Tree	L	x	-	-	-	-											
**Pancovia* sp. (3)	Tree					x	√	•										
**Pancovia harmsiana*	Tree	L/NN/KB	x	x	x	x	?											
**Pancovia laurentii*	Tree	NN	-	x	-	x	?											
**Pancovia pedicellaris*	Tree	NN	-	x	-	x	?											
Paullinia pinnata	Liana	NN	-	x	-	√	x	•										
SAPOTACEAE																		
Baillonella toxisperma	Tree	L/NN	√	x	-	√	x	•										
**Gambeya africana*	Tree	L/NN/KB	√	x	√	x	x	•										
Gambeya subnuda	Tree	L	√	-	-	x	x	•										
Omphalocarpum procerum	Tree	L	x	-	-	√	x	•						•				
Pachystela brevipes	Tree	L/NN	√	x	-	√	x	•										
**Synsepalum longecuneatum*	Tree	NN	-	√	-	√	x	•										
SCYTOPETALACEAE																		
**Scytopetalum klaineanum*	Tree	-	-	-	-	x	√	•										
Scytopetalum sp. LJTW 0017	Tree	L	√	-	-	-	-	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC at three sites			Eaten by RC		Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
STERCULIACEAE																		
**Cola* sp. (9)*	Tree						√	•										
**Cola accuminata*	Tree	NN/KB	-	x	x	x	?											
Cola attiensis	Tree	-	-	-	-	x	?											
**Cola cabindensis*	Tree	-	-	-	-	x	?											
**Cola ficifolia*	Tree	-	-	-	-	x	?											
Cola gabonensis	Tree	NN	-	x	-	x	?											
Cola griseiflora	Tree	-	-	-	-	x	?											
**Cola lizae*	Tree	L	√	-	-	x	√	•		C	•							
Cola rostrata	Tree	NN	-	x	-	√	?	•										
Cola sp. (Maccata = LN)	Tree	-	-	-	-	x	√	•			•	•						•
Cola sp. SEGC 332	Tree	L	x	-	-	-	-											
**Sterculia tragacantha*	Tree	L/NN/KB	√	x	x	x	x				•							
**Pterygota bequaerti*	Tree	L/NN	x	x	-	√	√	•	C		C	C	C	C	I	•		
TILIACEAE																		
**Desplatsia dewevrei*	Tree	NN	-	x	-		√	•										
**Duboscia macroparpa*	Tree	L/NN	√	√	-	√	x	•	L									
**Grewia sp. (4)*	Tree					√	√	•										
-**Grewia barombiensis*	Tree	-	-	-	-	x	?											
-**Grewia coriacea*	Tree	NN	-	x	-	√	√	•					C					
-**Grewia oligoneura*	Tree	NN	-	x	-	x	√	•	•	•			•					
-**Grewia seretti*	Tree	NN	-	√	-	x	?	•										
ULMACEAE																		
**Celtis tessmannii*	Tree	L/NN	√	x	-	x	√	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
URTICACEAE																		
**Urera* sp. (4)	Liana	-	-	-	-	x	√	•		•	•							
-**Urera cameroonensis*	Liana	-	-	-	-	x	?											
-**Urera hypselodendron*	Liana	KB	-	-	√	x	?				•							
-**Urera repens*	Liana	-	-	-	-	x	?											
VERBENACEAE																		
**Vitex* sp. (4)	Tree						√	•		•	•	•	•					•
-**Vitex doniana*	Tree	L/NN	√	x	-	x	√	•										
-*Vitex grandifolia*	Tree	-	-	-	-	x	?											
-*Vitex ferruginea*	Tree	-	-	-	-	x	?											
Vitex madiensis	Tree	-	-	-	-	x	?											
VIOLACEAE																		
**Rinorea oblongifolia*	Shrub	KB	-	-	√	x	x				•							
VITACEAE																		
Cissus dinklagei	Liane	L/NN/KB	√	√	√	√	x	•		I						•		
MONOCOTYLEDONEAE																		
ARECACEAE (PALMAE)																		
**Ancistrophyllum secundiflorum*	Liana	-	-	-	-	x	√			•								
**Calamus deerratus*	Palm	-	-	-	-	√	√	•										
**Elaeis guineensis*	Palm	NN	-	x	-	x	√	•	•	•	•			•				
**Erempospatha wendleana*	Palm	-	-	-	-	√	x	•		•								
**Podococcus barteri*	Palm	-	-	-	-	x	√	•		•								

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
ARECACEAE *cont…*																		
**Raphia* sp. (3)	Palm						√	•	•	•	•		•	•		•		•
-*Raphia hookeri*	Palm	-	-	-	-	x	?											
-**Raphia sudanica*	Palm	-	-	-	-	x	?											
-*Raphia vinifera*	Palm	-	-	-	-	x	?											
COMMELINACEAE																		
**Palisota* sp. (4)	Herb						√			•	•			•				
-**Palisota ambigua*	Herb	L/NN/KB	x	√	√	x	?	NN		KB								
-**Palisota barteri*	Herb	-	-	-	-	x	?											
-**Palisota hirsuta*	Herb	NN/KB	-	√	√	x	?	NN		KB								
-**Palisota schweinfirthii*	Herb	KB	-	-	x	x	?											
Palisota sp. SEGC 551	Herb	L	x	-	-	-	-											
MARANTACEAE																		
**Hypselodelphys* sp. (4)	Herb						√	•		•	•							•
-**Hypselodelphys poggeana*	Herb	L/NN	√	x	-	x	?		•		•							
-**Hypselodelphys scandens*	Herb	-	-	-	-	x	?											
-**Hypselodelphys violacea*	Herb	L/NN	√	√	-	√	?	I	•		L/NN			I		I		
-**Hypselodelphys zenkeriana*	Herb	-	-	-	-	x	?											
**Ataenidia conferta*	Herb	L/NN	√	x	-	√	?	I			L/NN							
**Haumania danckelmaniana*	Herb	NN	-	√	-	√	?			•								
**Haumania liebrechstiana*	Herb	L/KB	√	-	√	x	?	KB	L		L							
**Marantaceae* sp.	Herb						√	•		•	•			•		•	•	•
**Megaphrynium macrostachyum*	Herb	L/NN	√	√	-	x	√	•		L/NN	L			C				

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
MARANTACEAE *cont…*																		
**Sarcophrynium priogonium*	Herb	NN	-	√	-		√	C		C	NN							
**Sarcophrynium schweinfurthianum*	Herb	NN	-	x	-	√	x	•										
**Trachyphrynium braunianum*	Herb	L/NN	x	x	-	√	√	•		C								
**Marantachola* sp. (6)	Herb	-					√			•								
-Marantachola congensis	Herb	NN	-	x	-	x	?											
*-*Marantachola cordifolia*	Herb	L	x	-	-	x	?											
*-*Marantachola filipes*	Herb	L/NN	x	x	-	x	?											
*-*Marantachola holostachya*	Herb	KB	-	-	x	x	?											
*-*Marantachola leucantha*	Herb	KB	-	-	x	x	?											
*-*Marantachola purpurea*	Herb	L	x	-	-	x	?											
ORCHIDACEAE																		
Angraecum distichum	Herb	NN	x	-	-	x	x											
**Bulbophyllum congolanum*	Herb	-	-	-	-	x	√	•	•		•							
**Epiphyte* sp. (?)	Herb	-	-	-	-	x	√	•		•	•			•				
PAPILIONACEAE																		
**Milletia comosa*	Liana	-	-	-	-	x	√	•			•	•		•				•
ZINGIBERACEAE																		
**Aframomum* sp. (8)	Herb						√	•		•				•				•
-Aframomum citratum	Herb	NN	-	√	-	x	?				•							
*-*Aframomum giganteum*	Herb	NN	-	x	-	√	?	•								•		
*-*Aframomum le-testuanum*	Herb	NN	-	x	-	x	?											
*-*Aframomum limbatum*	Herb	-	-	-	-	x	?											
*-*Aframomum longipetiolatum*	Herb	L	√	-	-	x	?	•		•								

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC			Eaten by RC		Item eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
ZINGIBERACEAE *cont...*																		
-**Aframomum manusianum*	Herb	-	-	-	-	x	?											
-**Aframomum pseudostipulare*	Herb	-	-	-	-	x	?											
-*Aframomum stipulatum*	Herb	-	-	-	-	x	?											
Aframomum sp. SEGC 152	Herb	L	√	-	-	-	-	•		•								
Aframomum sp. SEGC 239	Herb	L	√	-	-	-	-	•		•								
Aframomum sp. SEGC 323	Herb	L	√	-	-	-	-	•		•								
**Costus afer*	Herb	L/NN/KB	√	x	x	x	x			•								
**Costus albus*	Herb	-	-	-	-	x	√	•		•	•	•						
PTERIDOPHYTES																		
ASPLENIACEAE																		
**Asplenium africanum*	Fern	L	x	-	-	x	√				•							
MARATTIACEAE																		
**Marattia fraxinea*	Fern	L/KB	x	-	√	x	x			•								
NON-IDENTIFIED SPECIES AT CONKOUATI																		
**Liane* sp. (general)	Liana		(13)	(9)	(4)	(27)	√	•	•	•	•	•	•	•	•			•
**Liane* sp. no.3	Liana						√	•										
**Liane* sp. no. 6	Liana						√	•	•		•							
**Liane* sp. no.8	Liana						√	•			•							
**Liane* sp. no.10	Liana						√	•			•							
**Liane* sp. no.12	Liana						√	•			•							
**Liane* sp. no. 16	Liana						√	•			•							
**Liane* sp. no. 17 (LN=Tsah)	Liana						√	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC at three sites			Eaten by RC		Part/s eaten										
			L	NN	KB	I	C	Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
NON-IDENTIFIED SPECIES AT CONKOUATI *cont...*																		
*Un-identified sp. no. 8	?						√	•										
*Un-identifed sp. no. 11	?						√	•										
*Un-identified sp. no. 14	?						√						•					
*Unidentified sp. no. 22	?						√	•			•							
*Unidentified sp. no. 27	?						√	•										
*Unidentified sp. no.29	?						√		•									
*Unidentified sp. no. 31	?						√	•										
*Unidentified sp. no. 33	?						√	•										
*Un-identified sp. no. 107	?						√	•										
*Un-identified sp. no. 109	?						√	•										
*Un-identified sp. no. 110	?						√	•										
*Un-identified sp. no. 111	?						√	•										
*Unidentified sp. no. 118	?						√	•										
*Unidentified sp. no. 121	?						√	•										
*Unidentified sp. no. 122	?						√	•										
*Unidentified sp. no. 124	?						√	•										
*Unidentified sp. no. 125	?						√	•										
*Unidentified sp. no. 127	?						√	•										
*Unidentified sp. no. 131	?						√		•									
*Unidentified sp. no. 158	?						√	•										
*Unidentified sp. no. 159	?						√	•										
*Unidentified sp. no. 161	?						√	•										
*Unidentified sp. no. 162	?						√	•										
*Unidentified sp. no. 214	?						√							•				
*Unidentified sp. no. 226	?						√	•										
*Unidentified sp. no. 231	?						√	•										

FAMILY Name scientific	Life form	Species present at WC site	Eaten by WC at three sites			Eaten by RC		Part/s eaten										
								Fruit/pulp	Seed	Stem/pith	Leaf	Young leaves	Sap	Flower	Bark	Shoots	Liquid	Not known
			L	NN	KB	I	C											
NON-IDENTIFIED SPECIES																		
*Unidentified sp. no. 237	?						√	•										
*Mougama/mouyama (LN)	?						√	•			•							
*Moukouyi (LN)	?						√											•
*Succis (LN)	Liana						√				•							
*Vindou (LN)	Tree						√	•					•					
*Fungi (non-identified)	Fungi						√											
Unidentified tree (general)	Tree						√		•	•	•	•	•	•		•		
Unidentified young tree	Tree						√				•							
Unidentified shrub	Shrub						√		•		•							
Unidentified plant	Other						√				•			•				

Notes:
sp. = species. When sp. is followed by brackets, the number within details the possible species eaten and lists them below (as identified in one of the four selected surveys).
WC = wild chimpanzees. Wild chimpanzee site: L = Lope, NN = Nouabalé-Ndoki, KB = Kahuzi-Biega.
RC = reintroduced chimpanzees. Reintroduced chimpanzee site: C = Conkouati (present data) I = Ipassa,
x = not eaten, √ = eaten, - not eaten/present, empty cells = part not eaten
• all chimpanzee sites listed eating the particular feeding item, code letters are when that group/site only is known to eat the feeding item.
* identified in Triangle

Appendix F: Description of insect consumption and extraction

Date of episode	Name of chimpanzee involved and description of behaviour
17.02.1997	Jeanette broke open a piece of wood to look for insects
03.03.1997	Choupette used a stick to try and get termites from a log
09.03.1997	Yvette and Choupette caught a chameleon – they touched and played with it as did Bougnoule and Rosette, but it was not eaten
14.03.1997	Bougnoule took a leaf from its stem to try and get at a caterpillar. Choupette tried the same but could not remove the leaves from the stem. Both failed in getting at the caterpillar.
14.03.1997	Bougnoule broke a piece of wood in an attempt to access insect larvae, she successfully extricated and ate the larvae.
25.03.1997	Jeanette found a broken branch. She removed the leaves from the stem and inserted the stem into a branch, extricated a wasp and ate it.
20.07.1997	Rosette fished for ants (no mention on check sheet what she used).
03.04.1999	David broke a very dry branch in a tree and it fell to the ground. David, Sophie and Agathe all removed leaves from stems and poked at the hole in the rotten wood with the stem. The insect (a bee) escaped but all the chimpanzees successively continued to poke at the hole in the wood. David finally tried to use his teeth to get at the larvae inside but failed. After five minutes the task was abandoned by all and none had succeeded (author's observation).
27.03.2000	Sophie used a tool to extricate insect larvae. She tried to break the wood against a mound. She successfully extracted and ate the larvae.

NB: The above descriptions were copied directly from check-sheets completed by a number of observers

Appendix G: Description of vertebrate prey consumption

Date of episode	Name of chimpanzee involved and description of behaviour
07.02.1997	Bougnoule and Rosette killed a mouse but did not eat it
07.02.1997	Bougnoule examined an old bird nest and looked inside – nothing there
16.02.1997	Bougnoule, Yvette, Jeanette, Choupette and Rosette found a turtle and played with it
17.02.1997	Bougnoule tried to catch a flying squirrel but failed
18.02.1997	Rosette caught and ate a flying squirrel. Bougnoule and Jeanette were in the group and followed Rosette in the trees. Yvette picked a piece up that had been dropped on the ground by Rosette. Bougnoule and Choupette food begged from Yvette, but Yvette shared the piece she found on the ground with Rosette
22.02.1997	Jeanette chased a snake
10.03.1997	Bougnoule, Yvette, Jeanette and Choupette found a turtle (*Kinyxis erosa)* – they were initially scared but they threw it, hit the shell against a tree and jumped on it. Due to the poor physical condition of the turtle as a consequence of the action of the chimpanzees, the observer killed the turtle and offered it to the chimpanzees to eat. They only took the stomach and intestines to eat which at the time were full of *Sacoglottis gabonensis* fruit pulp
19.03.1997	Bougnoule, Yvette and Mekoutou try to catch a flying squirrel. Bougnoule was seen eating it
21.04.1997	Jeanette found a turtle (*Kinyxis erosa)*; she first smashed the shell several times with some force against a tree trunk on which she was sat - some of the shell was broken. Jeanette then inserted twigs and prodded at the wounded turtle; she licked the blood from the twig. She tried to get at the body of the turtle with her fingers and teeth but failed and eventually abandoned the turtle
05.07.1997	Yvette was seen consuming an owl that was found dead on the ground
29.11.1997	Bougnoule, Yvette and Jeanette found a pangolin at 20m and threw it to the ground. Jeanette descended, threw the pangolin again and then threw a stick at it. It was not killed or eaten
05.12.1997	Rosette was seen eating a bird egg
16.08.1998	Massabi and Mossendjo were seen eating a birds egg
07.11.1998	Massabi and Mossendjo caught a bird, killed and ate it
28.05.1999	Agathe, Sophie and Koutou hunted, killed and ate a *Periodicticus potto*; Sophie led the hunt and the others joined the chase. Mekoutou was with the group but did not eat the potto.
31.05.1999	Hinda found a pangolin in a tree and threw it to the ground. Agathe quickly descended to the ground and picked it up, she took it into a tree, bit and ate the very end of its tail. The pangolin rolled into a ball and she could not get at the main trunk of the animal. She threw it to the ground. Koutou hit the pangolin several times with a stick and Mekoutou used a stick to prod it. They all quickly lost interest and moved away from the pangolin. The group consisted of Sophie, Koutou, Rosette, Mekoutou and Hinda (personal observation)
10.11.1999	Agathe, Sophie and Koutou were seen consuming a pangolin; there was no mention on the check sheet whether the pangolin was already dead when found or killed by the chimpanzees. It was eaten with leaves from a tree.

NB: The above descriptions were copied directly from check-sheets completed by a number of observers. Incidents on 10.03.1997 and 31.05.1999 were in descriptive format only and not included in scan observations

Appendix H: Check-sheet used to collect data on nests

Date: **Group:** **Height of water:** **Weather:** **Forest type:** **Observer:**

Time	Chimp	Location	Height of nest (m)	Height of tree (m)	DBH (cm)	Closest nest		Canopy cover	No. of nests in a tree	No. of tree to make nest	Comments
						Chimp	Distance (m)				
											Includes tree species, distance from last eating place, if nest was built in feeding tree, number of marked nest and tree

Height of water: 0 = none 1 = <ankle, 2 = <knee, 3 = >knee Weather: HR = heavy rain, R = rain, C = cloudy, S = sunny
Forest type: I = inundated, S = swamp, P = primary Canopy cover: 1 = covered, 2= intermediate, 3 = open