1 The Monkeys of the Taï forest: an introduction

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Introduction

With several notable exceptions (e.g. Schaller 1963, Goodall 1965, 1968), early field primatology in Africa was practically equivalent to observing baboons on the savannah. Because of the prominence of open-country primates in models of human evolution as well as the difficulties of seeing and habituating cercopithecids in dense forest, many of the first studies of African primates focussed on terrestrial monkeys such as Olive baboons (Washburn & Devore 1961a, 1961b), Chacma baboons (Hall 1962), Hamadryas baboons (Kummer 1968), Yellow baboons (Altmann & Altmann 1970), Gelada baboons (Crook 1966, Crook & Aldrich-Blake 1968, Dunbar & Dunbar 1974), patas monkeys (Hall 1965) and vervet monkeys (Struhsaker 1967) (but see Haddow 1952, Rowell 1966, Aldrich-Blake 1968, 1970, Chalmers 1968a, 1968b, Gautier & Gautier-Hion 1969, Struhsaker 1969, Gartlan & Struhsaker 1972). Interest in arboreal primates eventually prompted more biologists to venture beneath the closed canopy and with Struhsaker’s (1975) classic monograph on red colobus monkeys as a reference point, our knowledge of forest-dwelling African monkeys has grown significantly over the last 30 years. The result has been a burgeoning literature on African cercopithecoids including detailed treatments of guenons (e.g. Gautier-Hion et al. 1988, Glenn & Cords 2002), colobines (Davies & Oates 1994) and monkeys throughout the Congo Basin (Gautier-Hion et al. 1999). These and other contributions on both extant and extinct cercopithecoids (e.g. Whitehead & Jolly 2000) represent the state of the art in phylogeny reconstruction, functional morphology and behavioral biology and have provided significant insight into the habits of forest dwelling African monkeys that as recently as 35 years ago were largely unknown (Napier & Napier 1970).
Much of what we know about African monkeys is based on work at several well-known sites including Kibale Forest, Uganda (e.g. Struhsaker 1978, Chapman & Chapman 1996), Tiwai Island, Sierra Leone (e.g. Oates & Whitesides 1990), Makokou Forest, Gabon (e.g. Gautier & Gautier-Hion 1969), Lope Reserve, Gabon (Tutin et al. 1997), and Kakamega Forest, Kenya (e.g. Cords 1984). The elegant research carried out at these localities has generated a wealth of long-term data for several monkey species, some of whom are among the best known — and thoroughly studied — of all primates (e.g. red colobus). At the same time, there have been few attempts to summarize the interactions between food, predators, habitat and social life for all members of any particular cercopithecid community living in sympatry. After reviewing research conducted by the ~40 students involved in our project since 1989, we felt we could describe some of the principle machinations within a single African monkey community in a manner similar to Terborgh’s study of New World monkeys (Terborgh 1983). Ideally, the result would be a multi-disciplinary overview that could inform anthropological, psychological (Gleitman 1999), philosophical (Allen & Bekoff 1997) and linguistic (Tallerman 2005) disciplines in ways a collection of papers scattered throughout specialty journals could not.

In this book, we report on a community of eight Old World monkeys living in the Taï forest of western Ivory Coast. We summarize results of approximately 15 years of research conducted by a large number of individuals, all of whom carried out fieldwork at Taï. From the start, it has been our intention to understand the behavior of these primates as determined by habitat characteristics, predators, food availability, other group members and neighbors. A volume summarizing the behavior of one Taï primate — the chimpanzee — already exists (Boesch & Boesch-Achermann 2000) and one aim of the present book is to complement information on the Taï ape with that on the lesser-known cercopithecids sharing the same forest. Eventually, we hope the third group of Taï primates — the nocturnal lorises and galagos — are similarly studied so that the entire Taï primate community can be examined collectively. Ultimately, data sets from additional sites can be used to compare communities so that the ecological, phylogenetic and historical factors responsible for the composition of faunas we observe — and conserve — today are better understood (Fleagle et al. 1999). This chapter provides background information on the Taï forest, presents a brief history of the Taï Monkey Project, and introduces the eight monkey species with general remarks on their natural histories. We then discuss the content of subsequent chapters.
Taï National Park
Taï National Park is the last substantial block of intact forest remaining in West Africa. The forest was once part of a large forest belt, the Upper Guinea Forest that covered a vast area from Ghana to Sierra Leone. Its decline in size has been dramatic, particularly in the twentieth century (Martin 1991). The official area today is 330,000 ha in addition to a 20,000 ha buffer zone, which is contiguous to the 73,000 ha “Réserve de Faune du N’Zo” to the north of the park. The park is located in the southwest corner of Ivory Coast near the Liberian border about 200 km south of Man and 100 km from the Gulf of Guinea coast in the districts of Guiglo and Sassandra (0°15′−6°07′N, 7°25′−7°54′W) (see Figure 1.1).

The park was declared a UNESCO World Heritage Site in 1982; detailed information about its features and history can be found on the UNESCO website (http://whc.unesco.org). Briefly, the Taï forest first obtained protection in 1927 when it was declared a “Forest and Wildlife Refuge.” About half a century later, in 1972, it obtained National Park status. Five years later, 20,000 ha of buffer zone were added, and the park became

Figure 1.1. Approximate location of the Taï National Park.

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internationally recognized as a Biosphere Reserve under UNESCO’s Man and the Biosphere Programme. In 1982 it became part of the UNESCO World Heritage List.

The park contains some 1,300 species of higher plants including 150 identified as endemic. Vegetation is predominantly dense evergreen ombrophilous forest of a Guinean type with 40–60 m high continuous canopy and large numbers of epiphytes and lianas (see Figure 1.2). The forest is recovering from commercial timber exploitation, which officially ceased in 1972. The park contains a fauna typical of West African forests. Some noteworthy non-primate mammals include giant pangolins (*Manis gigantea*), tree pangolins (*M. tricuspis*) and long-tailed pangolins (*M. tetradactyla*), golden cats (*Felis aurata*), leopards (*Panthera pardus*), elephants (*Loxodonta africana*), bushpigs (*Potamochoerus porcus*), giant forest hogs (*Hylochoerus meinertzhageni*), pygmy hippopotamus (*Choeropsis liberiensis*), water chevrotains (*Hyemoschus aquaticus*), bongos (*Tragelaphus euryceros*), buffalos (*Syncerus caffer*), and several species of forest duikers and rodents. Almost 1,000 species of vertebrates including over 230 bird species have been identified in the park. Altitudes range from 80 m to 396 m with Mount NiénoKoué as the highest peak (see Figure 1.3). It comprises an ancient sloping granitic peneplain, broken by several inselbergs, which were formed by volcanic intrusions. The soils
are ferralitic of generally low fertility. There are two distinct climatic zones with annual average rainfall of 1,700 mm in the north and 2,200 mm in the south. The rains peak in June and September and there is a marked dry season from December to February. Temperatures range from 24°C to 27°C and the relative humidity is constantly high at between 85 and 90 per cent.

The principal conservation problems facing the Taï National Park are illegal poaching, logging, farming, and gold mining. There is increasing degradation of and human encroachment into the forest, particularly in the surrounding buffer zone that is generally not respected by local farmers. Destabilization of the country following a failed 2002 military coup has led to an increase in poaching activity in and around the park. The impact of these activities on the local fauna is likely to be enormous.

**Background of the Taï Monkey Project**

Most early publications dealing with African monkeys were largely taxonomic and contained little behavioral information, particularly on the habits of West African cercopithecids (e.g. Pocock 1907, Elliot 1913, Schwarz 1928, 1929, Rode 1937, Sanderson 1940, Dekeyser 1955). Before his tragic death at age 30, Angus Booth provided some of the earliest observations on West African monkeys in a series of influential papers.
Booth 1954, 1955, 1956a, 1956b, 1957, 1958a, 1958b, 1960), but it was not until the 1970s that the behavior of the Taï Forest primates first came to light (e.g. Struhsaker & Hunkeler 1971). Intensive studies on the forest’s chimpanzees began in 1976 (Boesch & Boesch-Achermann 2000) and work on monkeys began shortly thereafter (Galat 1978, Galat & Galat-Luong 1985). In addition to primates, there have been numerous studies on the forest’s non-primate fauna including those on leopards (Hoppe-Dominik 1984, Jenny 1996), elephants (Alexandre 1978, Roth et al. 1984, Merz 1986, Roth & Hoppe-Dominik 1987), crocodiles (Waitkuwait 1981), pygmy hippos (Galat-Luong 1981), duikers (Newing 2001), and birds (Thiollay 1985, Balchin 1988, Gartshore 1989). These contributions have been vital in informing our research.

The Taï Monkey project was founded in 1989 when Ronald Noe¨ and Bettie Sluijter, then at the University of Zurich, undertook a pilot study on red colobus monkeys. The eminent primatologist Hans Hummer (University of Zurich) had suggested to Noe¨ and Sluijter that they investigate whether some of the peculiarities of red colobus monkeys, especially their large group size, male philopatry and tendency to form polyspecific associations, could be explained as adaptive responses to chimpanzee predation (see Figure 1.4). At the time, the Taï chimpanzees were already well-known monkey hunters and red colobus were their preferred prey (Boesch & Boesch 1989). Kummer envisioned a long-term cooperative endeavor in which one research group studied the predators while the other studied the prey.

A successful four-month pilot study led to additional funding and the project’s first students, Klaus Zuberbühler and Kathy Holenweg, arrived in January 1991. Klaus and Kathy were responsible for habituating the first group of red colobus and Diana monkeys as well as establishing the primary study grid. They selected an area with a high density of monkeys near the field station of the “Institute d’Ecologie Tropicale” (IET) on the western border of the park. The IET research station is approximately 20 km from the nearest village and 25 km from the Cavally River that forms the border with Liberia. The grid established in 1991 has since been enlarged but still forms the core of the project’s study site (see Figure 1.5).

The following three years witnessed significant expansion in research activity as a growing number of students travelled to Taï, primarily to investigate the anti-predation adaptations of monkeys. In January 1992, Redouan Bshary (Max Planck Institut für Verhaltensphysiologie) started a three-year study on the relationship between red colobus — Diana monkey associations and chimpanzee hunting behavior. In November 1992, Kauri Adachi (University of Kyoto) initiated a study of guenon socio-ecology.
Figure 1.4. The Taï Monkey Project began as an attempt to determine whether peculiar features of red colobus monkeys — including large group sizes, male philopatry and frequent formation of polyspecific associations — were adaptations to predation by chimpanzees. Here, part of a red colobus monkey group rests and grooms during the late afternoon (Photo: Scott McGraw).

Figure 1.5. The Audrenisrou River near the research station of the Taï Monkey Project (Photo: Klaus Zuberbühler).
and five months later, Scott McGraw (SUNY Stony Brook) started work on comparative positional behavior and habitat use. As the number of students grew, so too did the number of field assistants. By the end of 1994, there were — on average — six students and six field assistants studying monkeys at any one time. The breadth of research has increased over the years, but the number of personnel in the forest has remained stable. Table 1.1 provides an overview of Masters and Ph.D. students including the general topics of study and date of thesis.

A community of West African monkeys

There are eight monkey species in the Taï forest. Seven occur throughout the park: the Diana monkey *Cercopithecus diana*, Campbell's monkey *Cercopithecus campbelli*, the lesser spot-nosed monkey *Cercopithecus petaurista*, the red colobus monkey *Procolobus badius*, the King (or Western black and white) colobus monkey *Colobus polykomos*, the olive colobus monkey *Procolobus verus* and the sooty mangabey *Cercocebus atys*. The eighth species, the putty-nosed monkey *Cercopithecus nictitans stampflii*, is found at significantly lower densities and mainly in northern portions of the forest. The low densities and patchy distribution of putty-nosed monkeys at Taï and elsewhere in West Africa can be explained by competitive exclusion from the Diana monkey *C. diana* (Oates 1988a, Eckardt & Zuberbühler 2004). Although we have studied *C. nictitans*, the species is not part of the monkey community near the IET research station; most of the project’s research — and that comprising the majority of this book — is focused on the seven species found within our 2 × 2 km² study grid.

It is not clear how long each species has existed in the Taï region, nor is the exact order of their arrival known. Most authorities agree that Taï monkeys are early descendents from primates that migrated from central Africa and that they have been isolated in the Upper Guinea forest for a considerable period of time (Grubb 1978, 1982, Oates & Trocco 1983, Kingdon 1989, Disotell & Raaum 2002, Tosi et al. 2005). Some version of Holocene refuge theory is routinely used to explain the presence of multiple species at a single locality (Lonnberg 1929, Livingstone 1975, 1982, Kukla 1977, Grubb 1982, Hamilton 1988) and while the Taï forest is situated midway between the two proposed West African refugia — one in Sierra Leone/Liberia and the other in eastern Ivory Coast/western Ghana (Booth 1958a, 1958b, Hamilton 1988, Oates 1988b) — there is growing evidence that the guenons and mangabeys diverged as early as the late Miocene (see Figure 1.6). Such early divergence dates are problematic for arguments that rely on Pleistocene glaciers and concomitant forest oscillations to
Table 1.1. Thesis research conducted in the Taï Monkey Project

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<tr>
<th>Topic</th>
<th>Reference</th>
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<tr>
<td><strong>Feeding behavior</strong></td>
<td>Mangabeys: Rutte (1998); Bergmüller (1998); Red colobus: Schabel (1993); Wachter (1993); King colobus: Nijsen (1999); all colobines: Schaff (1995); Korstjens (2001); Diana monkeys: Schabel (1993), Wachter (1993); Eckardt (2002); putty-nosed monkeys Eckardt (2002); all guenons: Buzzard (2004)</td>
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<td><strong>Social behavior</strong></td>
<td>Mangabeys: Benneton (2002); Range (1998, 2004); Meystre-Storrer (2002); Olive colobus: Deschner (1996); Schippers (1999); Krebs (1998); Red colobus: Von Oirschot (1999); Korstjens (2001); King colobus: Paukert (2002); Nijsen (1999); Korstjens (2001); Diana monkeys: Wolters (2001); Eckardt (2002); Campbell’s monkeys: Wolters (2001); putty-nosed monkeys: Eckardt (2002); guenons: Buzzard (2004)</td>
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<td><strong>Conservation</strong></td>
<td>Refisch (2001); Kone (2004)</td>
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<td><strong>Positional behavior</strong></td>
<td>Cercopithecids: McGraw (1996); putty-nosed monkeys: Bitty, E. A. (in prep)</td>
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<tr>
<td><strong>Non-primate studies</strong></td>
<td>Crowned eagle: Shultz (2003); mongooses: Dunham (2003); bats: Gordon (2001); hornbills: Rainey (2004)</td>
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explain the recent evolution of at least several cercopithecid groups. In any case, the colobus monkeys (*Procolobus* and *Colobus* spp.) and mangabeys (*Cercocebus* sp.) may have been the first monkeys to radiate into the Upper Guinea forest (Kingdon 1989). Early members of these groups may have met significant ecological competition by westerly radiating guenons which could explain why the colobines at Taï today (*Procolobus badius*, *P. verus*, and *Colobus polykomos*) are specialist in terms of their niches, diets, and ecological strategies (Kingdon 1989). The three common guenon species are descendants of distinct radiations, each of a different age. For example, the Diana monkey has no East African equivalent and may be descendants of the first arboreal lineage that migrated into the narrow coastal forests of Upper Guinea (see Disotell & Raaum 2002, Tosi *et al.* 2002). *C. campbelli* represents the most conservative member of the mona super-species, while *C. petaurista* may be the contemporary descendant of ancestors of the moustached or red-tail group (Kingdon 1989).

The diversity of sympatric species at Taï and their ecological profiles seem typical for an African forest. Several recent studies have compared the ecological characteristics and taxonomic makeup of primate communities globally (Fleagle & Reed 1996, 1999, Chapman *et al.* 1999) and these analyses have demonstrated that primates in African forested areas typically are characterized by, “a fairly high number of arboreal frugivores, 2–3 arboreal folivores, terrestrial cryptic foragers of the Papionin tribe, and 2–5 nocturnal gumivores/insectivores” (Reed & Bidner 2004:23). This accurately describes the Taï primate community and is similar to that at Kibale, Uganda (Struhsaker 1997) and Lope, Gabon (Tutin *et al.* 1997). The concordance of taxa occupying specific