PRIMATES

Monkeys of the Taï Forest

An African Primate Community

Edited by W. Scott McGraw,
Klaus Zuberbühler and
Ronald Noë

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Cambridge Studies in Biological and Evolutionary Anthropology 51

Monkeys of the Taï Forest

A great deal has been written about primates; however few volumes have focused on an entire community of sympatric monkeys at a single site. The primary purpose of this book is to provide a multi-thematic snapshot of the entire monkey community of the Taï forest (Ivory Coast), drawing upon diverse sets of data collected by researchers over the years. The major themes covered include the following: feeding ecology, social behavior, positional behavior and habitat use, predator-prey interactions, vocal communication, and conservation. In addition, portraits of all species are provided, summarizing the major behavioral characteristics of each, as little is known about these West African monkeys.

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CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 8RU, UK
Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521816335

First published in print format 2007

ISBN-13 978-0-511-28460-1 eBook (MyiLibrary)
ISBN-10 0-511-28540-X eBook (MyiLibrary)

ISBN-13 978-0-521-81633-5 hardback
ISBN-10 0-521-81633-5 hardback

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Preface

The study of primate behavior and ecology has been an ongoing area of research for over 50 years, building on the pioneering work of such people as C. R. Carpenter, Washburn and DeVore, C. R. L. Hall, J. J. Petter, and the Altmanns. There are relatively few of the 300 plus species of living primates that have not been the object of at least a survey; many have been studied for a complete year; and a few taxa have been the subject of long-term efforts lasting decades (e.g. Strier *et al*. 2006). Primatology has grown to become an integral part of anthropology or zoology in most parts of the world and a discipline that is the focus of numerous national and international organizations, more than half a dozen specialist journals and numerous book series.

Although year-long studies of a single species have long been the standard research protocol in primatology, some of the greatest advances in our understanding of primate behavioral ecology have come from coordinated studies of numerous species at a single site. Because all of the species are living in the same habitat with identical climatic and phonological variations, they enable a clearer insight into species-specific differences and similarities in adaptive strategies. The comparative, synecological studies of the primate assemblages such as those conducted at Makokou in Gabon, Morondava in Madagascar, Kibale Forest in Uganda, Kuala Lompat in Malaysia, Raleighvallen-Voltsberg in Suriname, and Manu in Peru stand out as milestones in the history of primatology and have disproportionately advanced our understanding of the relationship between behavior and ecology in primate evolution. With this volume, the Taï Forest joins this pantheon and offers an in-depth, comparative view of the diurnal primate fauna of west-central Africa.

In addition, this volume clearly demonstrates the sophisticated and diverse nature of studies in primatology at the beginning of the twenty-first century. In addition to providing the critical baseline data on behavior and ecology of the monkey taxa at Taï, these papers use both observational and experimental methods to probe the nature of locomotion and posture, communication, and predator-prey interactions. Most significantly research on the Taï monkey is fully integrated with conservation work to make possible effort to ensure that this extraordinary assemblage of primates, and research to understand ever more about their behavior and ecology will continue for generations to come.

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1 The Monkeys of the Taï forest: an introduction

W. S. McGraw and K. Zuberbühler

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).

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

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.

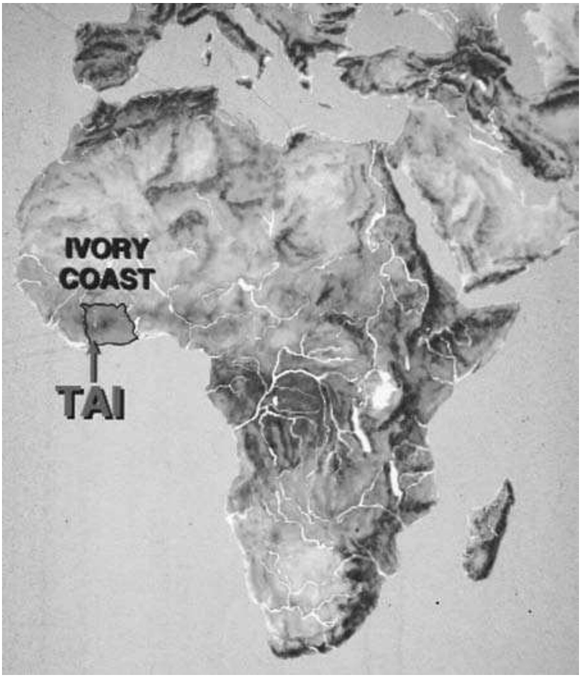

Figure 1.1. Approximate location of the Taï National Park.

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 1.2. Under story of the Taï forest (Photo: Scott McGraw).

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 gigantean*), 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

Figure 1.3. Taï forest canopy viewed from top of Mount Nienokoue (Photo: Scott McGraw).

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, Dekeyeser 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 Noë 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 Noë 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 $2 \times 2\,\text{km}^2$ 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*

Topic	Reference
Anti-predator behavior	Mangabeys: Range (2004); Olive colobus: van der Hoeven (1996); Korstjens (2001); Red colobus: Zuberbühler (1993); Bshary (1995); Korstjens (2001); King colobus: Korstjens (2001); Diana monkeys: Zuberbühler (1993), Bshary (1995); Shultz (2003); Campbell's monkeys: Wolters (2001); all guenons: Hansen (1996)
Association behavior	Mangabeys: Bshary (1995); McGraw (1996); Olive colobus: Bergmann (1998); Korstjens (2001); King colobus: Bergmann (1998); Korstjens (2001); Red colobus: Blank (1997); Holenweg 1992; Bshary (1995); Höner (1993); Leumann (1994); Korstjens (2001); Diana monkeys; Bshary (1995); Wolters (2001); Holenweg (1992); Leumann (1994); Eckardt (2002); Höner (1993); Campbell's monkeys: Wolters (2001); Putty-nosed monkeys: Eckardt (2002); all guenons: Buzzard (2004); Adachi-Kanazawa (2004)
Feeding behavior	Mangabeys: Rutte (1998); Bergmüller (1998); Red colobus: Schabel (1993); Wachter (1993); King colobus: Nijssen (1999); all colobines: Schaaff (1995); Korstjens (2001); Diana monkeys: Schabel (1993), Wachter (1993); Eckardt (2002); putty-nosed monkeys Eckardt (2002); all guenons: Buzzard (2004)
Ranging behavior	Mangabeys: Janmaat (2006); Förderer (2001); Olive colobus: Schippers (1999); Korstjens (2001); Red colobus: Korstjens (2001); Höner (1993); King colobus: Paukert (2002); Bitty (2001); Korstjens (2001); Diana monkeys: Höner (1993); Eckardt (2002), Wolters (2001); Campbell's monkeys: Wolters (2001); putty-nosed monkeys: Eckardt (2002); all guenons: Buzzard (2004)
Vocal behavior	Mangabeys: Range (2004); Red colobus: Zuberbühler (1993); Bshary (1995); Olive colobus: Koffi (in prep); King colobus: Tranquilli (2003); Diana monkeys: Zuberbühler (1993, 1998); Bshary (1995); Uster (2000); Eckardt (2002); Campbell's monkeys: Wolters (2001); putty-nosed monkeys: Eckardt (2002)
Social behavior	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); Nijssen (1999); Korstjens (2001); Diana monkeys: Wolters (2001); Eckardt (2002); Campbell's monkeys: Wolters (2001); putty-nosed monkeys: Eckardt (2002); guenons: Buzzard (2004)
Conservation	Refisch (2001); Kone (2004)
Positional behavior	Cercopithecids: McGraw (1996); putty-nosed monkeys: Bitty, E. A. (in prep)
Non-primate studies	Crowned eagle: Shultz (2003); mongooses: Dunham (2003); bats: Gordon (2001); hornbills: Rainey (2004)

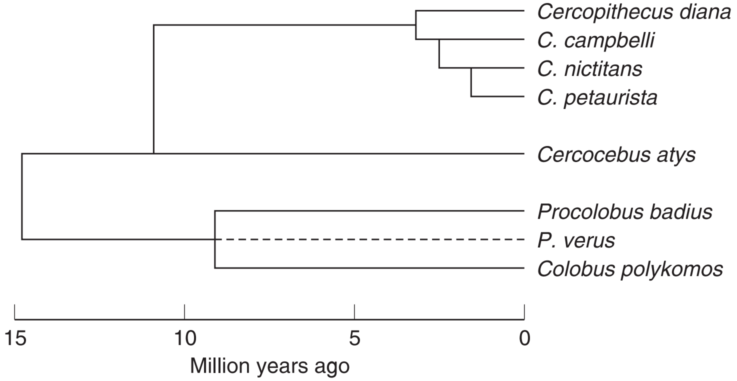

Figure 1.6. Approximate divergence dates of the eight cercopithecid species in the Taï forest (after Kingdon 1997, Disotell & Rauum 2002, Tosi *et al*. 2005).

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

Table 1.2. *Estimated annual percentage of food items consumed by Taï monkeys*

	DIA[a]	CAM[b]	PET[b]	NIC[a]	BAD[d]	POL[e]	VER[e]	ATY[c]
Fruit	70.9	46.3	33.6	58.9	28.8	48.0	9.0	68.4
Foliage	1.6	8.4	39.7	4.2	50.0	48.0	91.0	2.4
Invertebrate	26.5	33.1	12.3	31.3	–	–	–	26.4
Flower	0.4	1.0	6.2	2.5	19.5	3.0	–	1.3
Fungi	0.2	1.6	1.1	1.3	–	–	–	0.9
Other	0.5	9.3	6.4	1.8	2.1	1.0	–	0.6
N samples	1,828	953	924	1,424	6,480	4,090	991	406

DIA (*Cercopithecus diana*); CAM (*Cercopithecus campbelli*); PET (*Cercopithecus petaurista*); NIC (*Cercopithecus nictitans*); BAD (*Procolobus badius*); POL (*Colobus polykomos*); VER (*Procolobus verus*); ATY (*Cercocebus atys*)
Source: [a] Buzzard (2004); [b] Eckardt (2002); [c] Bergmüller (1998); Bergmüller *et al*. submitted; [d] Korstjens unpublished data; [e] Korstjens & Galat-Luong in press; Oates *et al*. in press

niches defined by body size, diet, locomotion, and activity patterns, strongly suggests that the structure of the primate community at Taï and elsewhere in Africa is the product of a complex but common series of evolutionary events and limiting agents including forest productivity, availability of keystone resources, predation pressure and, perhaps, historical anthropogenic factors (Fleagle & Reed 1996, Tutin & White 1999, Struhsaker 1999, Reed & Bidner 2004). These factors are discussed throughout this volume. Table 1.2 summarizes general feeding data on each species while Table 1.3 provides species means for group size, home range size, number of adult males per group, canopy use, and group density.

Procolobus badius badius ***(Kerr 1792) Western red colobus***

The Western red colobus monkey *Procolobus badius badius* is the most abundant monkey in the study area and prior to reductions by human poachers, the most common primate in the park. Red colobus are medium-sized, slender monkeys that exhibit little sexual dimorphism: mean male body weight is 8.3 kg and mean female body weight is 8.2 kg (Oates *et al.* 1990). Individuals are predominantly red with a black band running the length of the dorsum and a rust-colored tail (see Figure 1.7). Adult females exhibit large sexual swellings when in estrus. The inter-membral index of *P. badius badius* is 87 (Fleagle 1999).

Red colobus monkeys have a wide distribution across equatorial Africa. Their taxonomy is in need of revision, however recent classifications recognize at least five species including 15 subspecies (Grubb *et al.* 2003).

Table 1.3. *Summary overview of some socio-ecological features of the Taï monkeys*

Species	Group size[a]	Home range	N males[a]	Habitat[b]	Density[a]
Procolobus badius	52.9	0.58	10.1	0.4	123.8
Procolobus verus	6.7	0.56	1.43	1.3	17.3
Colobus polykomos	15.4	0.78	1.42	13.2	35.5
Cercopithecus diana	20.2	0.63	1	6.1	48.2
Cercopithecus campbelli	10.8	0.60	1	36.8	24.4
Cercopithecus petaurista	17.5	0.69	1	9.9	29.3
Cercopithecus nictitans	10.5	0.96	1	0.7	2.1
Cercocebus atys	69.7	4.92	9.0	88.9	11.9

Density: estimated number of individuals per square kilometer
Group size: average number of individuals per group
N males: average number of adult males per group
Habitat: per cent time observed in lower forest strata
Home range: estimated size of annual range in km^2
[a] Data compiled by Zuberbühler and Jenny (2002);
[b] Data from McGraw (1998a, 2000); Eckardt (2002)
Home range data from the following studies: *C. diana*: Eckardt (2002): 0.66 km^2; Buzzard (2004): 0.59 km^2; *C. campbelli*: Buzzard (2004): 0.67 & 0.52 km^2; *C. petaurista*: 0.74 & 0.64 km^2; *C. nictitans*: Eckardt (2002): 0.96 km^2; *P. badius*: Korstjens (2001): 0.50 & 0.66 km^2 *P. verus*: Korstjens (2001): 0.54 & 0.58 km^2, *C. polykomos*: Korstjens (2001): 0.83 & 0.72 km^2; *Cercocebus atys*: Rutte (1998): 4.92 km^2

The Taï subspecies, *P. badius badius*, is found from the Ivory Coast's Bandama River in the east to Sierra Leone in the west and except for an outlying population on the Gambia River (*Procolobus badius temminckii*), represents the most western extent of the red colobus radiation (Kingdon 1989, Starin 1991, 1994, Galat-Luong & Galat 2005).

The red colobus is possibly the best-known forest monkey in Africa, having been the subject of many important studies in East Africa (Clutton-Brock 1973, 1974, 1975a, 1975b, Struhsaker 1974, 1975, 1978, 1980, Struhsaker & Oates 1975, Busse 1977, Marsh 1979a, 1979b, 1981, Baranga 1982, 1983, 1986, Isbell 1984, Struhsaker & Leland 1985, Decker 1994, Stanford *et al.* 1994, Stanford 1995, Chapman & Chapman 1996, 2002, Chapman *et al.* 2002a, 2002b), Central Africa (Maisels *et al.* 1994), and West Africa (Gatinot 1977, Galat & Galat-Luong 1985, Starin 1990, 1991, 1994, 2001, Fimbel 1992, Teichroeb *et al.* 2003). These studies have highlighted great variation in red colobus socio-ecology, diet preferences, group sizes, association tendencies and anti-predator adaptations across the continent.

At Taï, red colobus monkeys live in loud, large groups of between 40 and 90 individuals. These groups often divide into subgroups during periods

Figure 1.7. Western red colobus monkey *Procolobus badius badius* (Photo: Scott McGraw).

of low resource availability (Höner *et al*. 1997). Group composition is multi-male, multi-female and groups exhibit male philopatry. Solitary females are regularly observed in mono-specific and mixed-species groups. Red colobus are frequently found in association with other monkey species, primarily as a response to predation pressure (Holenweg *et al*. 1996, Honer *et al*. 1997, Wachter *et al*. 1997, Bshary & Noe 1997a, 1997b). They are the favored monkey prey of chimpanzees which appear to specifically target them during the rainy season. The response to monkey-hunting chimpanzees by Taï red colobus differs markedly from that of red colobus at sites in East Africa (e.g. Boesch 1994, Stanford 1998). Red colobus are frequent leapers who suffer a high incidence of injuries from falls (Hellmer & McGraw 2005) (see Figure 1.8). They use all layers of the forest but prefer the main canopy (McGraw 1996, 1998a). Taï red colobus

Figure 1.8. Red colobus monkeys are spectacular leapers. Here, an adult is passing between a large discontinuity at the top of the main canopy forest layer (Photo: Scott McGraw).

feed predominantly on leaves, fruit, and flowers (Korstjens 2001). The vocal behavior of red colobus has been described by Struhsaker (1975); to date, no thorough vocal studies have been conducted at Taï. The IUCN Red List of Threatened Species considers this taxon as Endangered, based on an estimation of rate of population decline (www.redlist.org). The species is now rare or absent in parts of Taï National Park.

Procolobus verus *(van Beneden 1838) Olive colobus*

The monotypic olive colobus is the smallest colobine monkey. The species is not particularly dimorphic: average body mass for males is 4.7 kg and for females is 4.2 kg (Oates *et al.* 1990). It is cryptically colored with a dull grayish underside and a greenish olive upper side. The face is hairless of a dark gray color and framed by a dull-white ruff (see Figure 1.9). The drab coat of *Procolobus verus* makes locating this species extremely difficult, particularly in the shadows of the forest understory where it spends the majority of its time feeding and resting in vine tangles and other areas of dense vegetation.

Olive colobus are characterized by a unique combination of features. These small, mysterious monkeys are restricted to West Africa and most authors believe they are the most primitive African colobine having

Figure 1.9. An adult male olive colobus *Procolobus verus* (Photo: Scott McGraw).

retained many ancestral traits (Kingdon 1989, Davies & Oates 1994). Olive colobus have the most reduced thumb and the largest feet of any African colobine (Fleagle 1999). The inter-membral index is 80 (McGraw, this study) and they are the most frequent leapers at Taï, capable of propelling themselves over distances many times their body lengths. They prefer the forest understory for all activities where they frequent dense vine tangles (McGraw 1996, 1998a). Olive colobus are the only anthropoids known to carry their dependent offspring in their mouth for as yet unknown reasons (Booth 1957, 1960).

Olive colobus are extremely cryptic monkeys who vocalize infrequently and primarily when alarmed (Koffi, B. J.-C. in prep). They are nearly always found in association with other monkey species, especially Diana monkeys (*Cercopithecus diana*) (see Figure 1.10). Oates and Whitesides (1990) argue that this small colobine has evolved a specific strategy to associate with other monkey species – most likely for anti-predation benefits – without compromising its dietary strategy.

Group structure of olive colobus varies significantly, however a typical social unit consists of several adult males, three or more adult females and their infants (Korstjens & Schippers 2003, Korstjens & Noë 2004). Females display prominent sexual swellings during estrus. The diet of olive colobus has been well studied in an area of old secondary forest on Sierra Leone's

Figure 1.10. Olive colobus monkeys are found in association with Diana monkeys (*Cercopithecus diana*) over 95 per cent of the time. Here, a female Diana monkey is resting with an adult male olive colobus (Photo: Florian Möllers).

Tiwai Island, (Oates 1988a, Oates & Whitesides 1990). The most preferred food item is young leaves with fruit comprising between 10 and 20 per cent of the annual diet (Korstjens 2001). The IUCN Red List of Threatened Species considers this taxon as *Near Threatened*.

Colobus polykomos polykomos *(Zimmerman 1780) King Colobus*

Most authorities recognize five species of black and white colobus; the King colobus *Colobus polykomos* is the western most species and is separated from *Colobus vellerosus* to the east by the Sassandra River. *C. polykomos* has more conservative features than the well-known *C. guereza* of East Africa (Oates 1977a, 1977b, 1977c), perhaps because

Figure 1.11. An adult male king colobus *Colobus polykomos* (Photo: Scott McGraw).

this species is the direct descendant of a lineage that has continued to evolve further east (Kingdon 1989). Analyses of loud calls, cranial morphology and pelage indicate that King colobus diverged early from the ancestral black and white colobus while *C. vellerosus* and *C. guereza* to the east are more recent, derived forms (Oates & Trocco 1983, Oates *et al.* 2000a).

King colobus are the largest arboreal monkeys at Taï. Adults are dimorphic in size: average male body weight is 9.9 kg and average female body weight is 8.3 kg (Oates *et al.* 1990). The inter-membral index is 78 (McGraw, this study). Adults possess jet-black coats and a long, rope-like tail with no tuft. The monkey's black face is fringed by tufts of white or gray hair, which often extends to the shoulders in adults (see Figure 1.11). Infants are born completely white and develop their adult coat within a few months. Females show no evidence of sexual swelling during estrus.

The typical social unit of *C. polykomos* consists of one or two adult males, 3 to 7 adult females and between 6 and 12 infants, juveniles and subadults (Korstjens *et al.* 2002). Neighboring groups have strongly overlapping home ranges. The species is generally cryptic and tends to actively avoid associating with sympatric species. In these respects, it provides a striking contrast to the closely related red colobus sharing the same forest. King colobus males emit roaring loud calls, which function in predator defense and may also serve in intergroup spacing (Walek 1978, Tranquilli 2003). Contact calls are soft and consist of snorts and grunts.

Species of black and white colobus are generally not as sensitive to habitat disturbance, nor as reliant on primary forest, as are red colobus (e.g. Saj & Sicotte 2004). Several studies have shown that densities of black and white colobus may actually be greater in areas of colonizing forest or secondary growth (Oates 1977a, 1977b, Struhsaker 1997). In the undisturbed forest at Taï, King colobus can be found exploiting all layers of the canopy, particularly lianas in the understory, although they most frequently use large supports of the main canopy. The diet of *C. polykomos* at Taï and elsewhere is characterized by a marked preference for seeds from fruit, particularly those of *Pentaclethera macrophylla*, as well as liana leaves (Dasilva 1992, 1994, Hayes *et al.* 1996, Davies *et al.* 1999, Daegling & McGraw 2001). The IUCN Red List of Threatened Species considers this taxon as *Near Threatened.*

Cercocebus atys atys (*Audebert 1797*) *sooty mangabey*

Mangabeys are diphyletic and consist of two groups: the arboreal members are placed in the genus *Lophocebus* with three species (*aterrimus*, *albigena* and *kipunji*) and the predominately terrestrial members are placed in the genus *Cercocebus* with upwards of six species (*atys*, *torquatus*, *agilis*, *galeritus*, *sanjei*, *chrysogaster* (Cronin & Sarich 1976, Groves 1978, Disotell 1994, Nakatsukasa 1996, Fleagle & McGraw 1999, 2002). *Cercocebus atys atys* is the western-most species and the Ivory Coast's Sassandra River serves as the approximate boundary separating it from *C. atys lunulatus* (the White-naped mangabey) further east (Booth 1956a, 1956b). It is the former that is found in the Taï forest.

Sooty mangabeys are large, long-limbed, predominantly terrestrial monkeys (McGraw 1998a, 1998b). Their coat color is charcoal gray and they have lighter, flesh-colored faces (see Figure 1.12). Sexual dimorphism is high: mean male body weight is 11 kg while mean female body weight is 6.2 kg (Oates *et al.* 1990). The inter-membral index is 84 (McGraw, this study).

Apart from some anecdotal observations (Booth 1956a, 1956b, Struhsaker 1971, Harding 1984, Galat & Galat-Luong 1985), the monkey had not been systematically studied under natural conditions prior to our project. A well-established colony at the Yerkes National Primate Research Center has been the subject of numerous studies and

Figure 1.12. The sooty mangabey *Cercocebus atys* is the only predominantly terrestrial monkey at Taï (Photo: Scott McGraw).

most early information on this species was based on this captive population (Bernstein 1971a, 1971b, 1976, Hadidian & Bernstein 1979, Aidara *et al*. 1981, Busse & Gordon 1984, Ehardt 1988a, 1988b, Fultz *et al*. 1986, Gordon *et al*. 1991, Gust & Gordon 1991, 1993, 1994, Gust 1994).

Studies on the dynamics of social behavior in Taï sooty mangabeys (Range & Noe 2002, 2005, Range & Fischer 2004, Range 2005) provide an interesting contrast to conclusions based on observations of captive individuals (Ehardt 1988a, 1988b). A typical sooty mangabey group at Taï numbers approximately 100 individuals. Groups frequently splinter into subgroups as an adaptation to seasonal fluctuations of preferred resources. Group structure is multi-male, multi-female with female philopatry. Solitary or groups of non-resident males are frequently observed and are known to invade resident groups during the breeding season. Females exhibit marked swellings during estrus.

Sooty mangabeys obtain most of their food from within the leaf litter on the forest floor (see Figure 1.13). Here, members search through the forest debris looking for insects and fallen hard object foods that resist decomposition and are generally too hard for other cercopithecines to process. It is the suite of adaptations for manual foraging and hard object

Figure 1.13. Sooty mangabeys spend a large portion of their foraging time searching for fallen fruits and nuts amid the leaf litter on the forest floor. Many of these hard object foods resist decomposition and are not available as resources to other Taï monkeys because they are too difficult to open (Photo: Ralph Bergmüller).

feeding – including powerful forelimbs, large teeth and strong jaws for crushing – that links *Cercocebus* mangabeys with their sister taxon, *Mandrillus* (Fleagle & McGraw 1999, 2002). The vocal behavior of the species has been described by Range & Fischer (2004).

In recent years, sooty mangabeys have received considerable attention from the biomedical community. The human immunodeficiency virus type 2 (HIV-2) is thought to have originated from simian immunodeficiency viruses, which occur naturally in sooty mangabeys (SIVsm). Chen *et al.* (1996) showed that viruses of eight feral sooty mangabeys from West Africa belonged to the SIVsm/HIV-2 family, although they were widely divergent from SIVs found earlier in captive monkeys at American primate centers. Their findings support the hypothesis that each HIV-2 subtype in West Africans originated from widely divergent SIVsm strains transmitted by independent cross-species events in the same geographic locations (see also Marx *et al.* 1991, Gao *et al.* 1992). One current research topic concerns the question why SIV does not induce acquired immuno-deficiency syndrome (AIDS) in sooty mangabeys (Silvestri 2005). Surprisingly, the mangabeys' immune system does not suffer any damage despite highly replicating viruses. It may thus be the case that sooty mangabeys have evolved a special mechanism for resisting AIDS development (Ling *et al.* 2004), suggesting that understanding this mechanism may provide clues to understanding the pathogenesis of immunodeficiency in HIV-infected humans (Santiago *et al.* 2005). Research into this and related questions is being carried out cooperatively by the TMP and Yerkes National Primate Research Center. The IUCN Red List of Threatened Species considers this taxon as *Near Threatened.*

Cercopithecus diana diana *(Linnaeus 1758) Diana monkey*

There are two subspecies of Diana monkeys: *Cercopithecus diana roloway* (Roloway monkeys) east of Ivory Coast's Sassandra River and *C. diana diana* (Diana monkey, proper) to the west. All reports indicate that both subspecies require high, primary rainforest and that they do not fare well in disturbed areas and secondary forest (Booth 1958a, 1958b, Oates 1988a, 1988b, Whitesides 1989). The Roloway monkey is one of the world's 25 most endangered primates and the Diana monkey appears to be not far behind (McGraw 1998b, McGraw & Oates in press).

Diana monkeys are the most active, acrobatic and conspicuous monkeys at Taï. They are beautifully adorned, with black faces, short white beards, white chests, black/auburn coats, bright reddish orange hair on the rump and inner thighs and black tails (see Figure 1.14). The monkey is sexually dimorphic; mean male body weight is 5.2 kg and mean female body weight is 3.9 kg (Oates *et al.* 1990). The inter-membral index for *C. diana* is 79.

The first intensive studies of Diana monkeys were conducted at Tiwai Island, Sierra Leone where it was revealed that the typical Diana monkey social unit consisted of a single adult male, 6 or 7 females and their offspring (Whitesides 1989, Oates *et al.* 1990, Hill 1994). At Tiwai, Diana monkeys are almost always found in association with other monkey species (Oates & Whitesides 1990, Whitesides 1991). The same is true for Diana monkeys at Taï (Bshary & Noe 1997b, Wachter *et al.* 1997, Korstjens *et al.* 2002). Previous dietary information is available from Tiwai Island (Oates & Whitesides 1990) and from Taï (Galat & Galat-Luong 1985). These studies, as well as those at Taï, indicate that Diana monkeys eat large amounts of fruit and insects with smaller amounts of flowers and leaves.

Diana monkeys are noisy, active, fast and agile primates that appear to be in constant motion throughout the forest, from the top of the emergent layer to the ground (see Figure 1.15). Their foraging regime, alert nature and constant vigilance make them excellent early warning signallers for predators. Evidence from Taï indicates that at least one monkey – red

Figure 1.14. The Diana monkey *Cercopithecus diana* (Photo: Scott McGraw).

colobus – preferentially associates with Diana monkeys because of its ability to detect monkey-hunting chimpanzees (Bshary & Noe 1997a, 1997b, Noe & Bshary 1997) (see Figure 1.16). Detailed studies of the acoustic and semantic properties of Diana monkey vocalizations, particularly their loud calls, have revealed that males and females produce acoustically distinct alarm calls for two of their predators, leopards and crowned eagles (see Chapter 8). For several reasons, Diana monkeys can be regarded as the central species in the Taï monkey community: two colobine species frequently associate with Diana monkeys (one – *Procolobus verus*, permanently), Diana monkey groups dominate those of the two other guenon species (*C. campbelli* and *C. petaurista*) that share a common home range, and Diana monkeys have competitively displaced a third guenon at Taï (*C. nictitans*). Thus, an understanding of the Taï monkey community depends to a large extent on exploring the relationship of all cercopithecids to *C. diana*. The 2000 IUCN Red List of Threatened Species considers this taxon as *Endangered*,

Figure 1.15. Diana monkeys are agile, active foragers that are found at all layers of the forest canopy (Photo: Scott McGraw).

Figure 1.16. Red colobus monkeys associate with Diana monkeys because of their ability to detect monkey-hunting chimpanzees. The active foraging strategy, extensive use of all forest layers and alert nature of Diana monkeys make them excellent sentinels (Photo: Scott McGraw).

Figure 1.17. An adult male Campbell's monkey *Cercopithecus campbelli* (Photo: Florian Möllers).

facing a very high risk of extinction in the wild in the near future (Hilton-Taylor 2000).

Cercopithecus campbelli campbelli ***(Waterhouse 1838)*** ***Campbell's monkey***

Campbell's monkey – *Cercopithecus campbelli campbelli* – is one of several species in the Mona super-species of guenons (Booth 1955, 1956a, 1956b, 1958a, 1958b). It is found from Senegal to parts east of the Taï Forest meaning that the Cavallay River forming the Ivory Coast-Liberia border is not an effective barrier to dispersion. The species is capable of exploiting many habitats including highly disturbed areas and low, secondary forest (Booth 1955, 1956a, 1956b, 1958a, 1958b, Bourliere *et al*. 1970, Hunkeler *et al*. 1972, Galat-Luong & Galat 1979, Harding 1984, Oates 1988b). For this reason, Campbell's monkey is one of the most abundant monkeys in West Africa (McGraw 1998b, Oates *et al*. 2000b).

The coat of Campbell's monkey is drab olive-gray with darker hair towards the distal ends of the limbs (see Figure 1.17). A yellow brow band above the darkened blue shading around the orbits marks the face. Campbell's monkeys are among the most sexually dimorphic of all guenons with mean male body weights of 4.5 kg and mean female body weights of 2.7 kg (Oates *et al.* 1990). The inter-membral index for *C. campbelli* is 85 (McGraw, this study).

C. campbelli has not been studied intensively outside of Taï, however available reports suggest that the behavior of Campbell's monkey at Taï is representative of this species throughout its range. *C. campbelli* is a cryptic monkey that, like the olive colobus, is adapted to the shadows of the dark understory. Group sizes average approximately 11 individuals and consist of single adult male, 3–4 adult females and their offspring. In contrast to the raucous Diana monkey, Campbell's monkeys produce much softer contact calls, travel and forage primarily at levels below the main canopy (including the ground) and are generally inconspicuous. They can be found in association with all other cercopithecid species, but show a marked tendency to move and feed with another cryptic guenon at Taï – the lesser spot-nosed monkey *Cercopithecus petaurista*. Indeed, the niches of these two species are quite similar and adult males of associated groups perform an unusual three-unit loud call duet, initiated by the male Campbell's monkey's two booms, which are immediately answered by the male lesser spot-nosed monkey's loud calls, completed by the Campbell's monkey's hacks. The function of this intricate behavior is currently under investigation but preliminary data suggest that it may serve as a means of joint territorial defense. The IUCN Red List of Threatened Species considers Campbell's monkeys as *Not Threatened*.

Cercopithecus petaurista buettikoferi ***(Jentink 1886) Western lesser spot-nosed monkey***

There are two subspecies of lesser spot-nosed monkeys: *C. petaurista petaurista* is found east of the Cavally River and *C. petaurista buettikoferi* to the west, including Taï. Intermediate forms have been reported between Sassandra-Cavally-N'zo river systems. The lesser spot-nosed monkey is part of the *cephus* group of guenons whose members are characterized by small body size, frugivorous diet, cryptic behavior, and habitat flexibility (Lernould 1988, Oates 1988b). These shy, cryptic monkeys are quite difficult to follow in the forest because of their ability to quickly and quietly leave an area (all members of our team have – at one time or another – been frustrated by the ability of this monkey to seemingly vanish!). This quality, combined with the ability to exploit multiple habitat types including degraded forest, explains why this small and adaptable guenon is one of the most common primates in West Africa (McGraw 1998a, 1998b, Oates *et al.* 2000b).

Lesser spot-nosed monkeys are the smallest monkeys at Taï; mean body weight for males is 4.4 kg, and females average 2.9 kg (Oates *et al.* 1990).

Figure 1.18. An adult female lesser spot-nosed monkey *Cercopithecus petaurista* (Photo: Scott McGraw).

Their coat is agouti-brown and the underside of the limbs and chest are light colored (see Figure 1.18). A white stripe marks the side of the dark face but it is the white or pinkish heart-shaped spot on the nose that is the most recognizable feature of this monkey. The inter-membral index is 80 (McGraw, this study). The Western lesser spot-nosed monkey has not been intensively studied outside of Taï. Data culled from various reports indicate that like *Cercopithecus campbelli*, *C. petaurista* is generally found in small, single male groups that exploit the lower levels of forests. Lesser spot-nosed monkeys associate frequently with all other cercopithecids in the forest (see Figure 1.19). Their diet consists of large percentages of fruit, flowers and insects. Their vocal behavior has not yet been studied intensively. The IUCN Red List of Threatened Species considers lesser spot-nosed monkey as *Not Threatened.*

Cercopithecus nictitans stampflii *(Jentinck 1888) Stampfli's putty-nosed monkey*

Putty-nosed monkeys are large, long-tailed, arboreal primates with dark, grizzled olive fur on the back, crown, cheeks, and base of the tail. The limbs and distal half of the tail are black or dark gray. The brilliant white nose spot in a dark face is striking (see Figure 1.20).

Figure 1.19. Like all Taï guenons, lesser spot-nosed monkeys frequently associate and interact with other cercopithecids in the forest. This photograph shows a red colobus monkey grooming a female lesser spot-nosed monkey (Photo: Scott McGraw).

Putty-nosed populations east of the River Cross, Nigeria, are generally numerous (e.g. Mitani 1991, Garcia & Mba 1997). In contrast, population densities of Stampfli's putty-nosed monkeys in Côte d'Ivoire and Liberia are very low, suggesting that they may have been recent and non-competitive colonists to habitats already occupied by other primates, particularly the lesser spot-nosed monkeys (*C. petaurista*) and Diana monkeys (*C. diana*). For example, in the Odzala National Park, Republic of the Congo, density was estimated to be about 1.4 groups/km^2 (Bermejo 1999). Similarly, in the Campo-Ma'an area, Southwestern Cameroon, group density was 1.43 groups/km^2 (Mathews & Matthews 2002), while in Ipassa-Makou, north-east Gabon, density was estimated at 56.43 ind./km^2 (Okouyi *et al*. 2002).

Putty-nosed monkeys live in groups of 12 containing a single adult male and four adult females (Eckardt & Zuberbühler 2004). The feeding ecology of *C. nictitans* has been documented at Lope, Gabon (Tutin *et al*. 1997) and Taï (Eckardt 2002, Eckardt & Zuberbühler 2004). Other ecological work has been conducted at Bioko Island, Republic of Equatorial Guinea (Gonzalez-Kirchner 1996). The vocal behavior of *C. nictitans* has been studied at Taï where males exhibit an interesting pattern of combining two

Figure 1.20. Stampfli's putty-nosed monkey, *Cercopithecus nictitans stampflii*. This monkey is probably a recent arrival to the Taï Forest having migrated from northern savannah regions. It lives at low densities and is dominated by groups of Diana monkeys (Photo: Winnie Eckardt).

basic types of alarm calls – the pyows and the hacks – into structurally more complex sequences with novel meanings (Eckardt & Zuberbühler 2004). The positional behavior of putty-nosed monkeys is currently being investigated (Bitty & McGraw 2006, in press).

The taxonomic position of Stampfli's putty-nosed monkeys is debated (Groves 2001, Grubb *et al*. 2003). If afforded full species status, the species is considered *Critically Endangered* and faces a high risk of extinction due to its very patchy distribution in areas of heavy hunting pressure.

Format of the book

The book contains 11 chapters authored by 22 researchers. The chapters are grouped into four parts dealing with questions of social behavior, anti-predator strategies, habitat use, and conservation.

Part I – Social behavior

The first section consists of three chapters, each covering key elements of social behavior in the three radiations of Taï monkeys: guenons, mangabeys, and colobines. Buzzard and Eckardt describe the social systems of the four guenon species, reviewing a set of previously unpublished material. Obtaining social data from forest guenon species has proven to be challenging, which makes Buzzard and Eckardt's contribution particularly important. The authors find dramatic differences in group-densities with Diana monkeys, Campbell's monkeys, and lesser spot-nosed monkeys being relatively equally common, while putty-nosed monkeys are much rarer. The typical group structure was single male/multi-female, although occasionally two adult males were observed for certain periods. Stable all male groups were only observed in Campbell's monkeys. Buzzard and Eckardt then provide data on these species' social behavior, noting that levels of social interactions are substantially lower than those of macaques or baboons. Across species, grooming rates were comparable, although Diana monkeys were characterized by higher rates of agonistic behavior to other group members (e.g. McGraw *et al.* 2002).

There are few forests in Africa that boast three sympatric species of colobus monkeys. Because the red colobus, King colobus, and olive colobus differ in so many aspects of their behavior, Taï provides a superb opportunity to explore the determinants of group size, dispersal patterns, diet and anti-predation defenses in a comparative context while controlling for phylogeny. Perhaps not surprisingly, the three colobus species have been the most studied monkeys at Taï and over a dozen students have carried out long-term projects on the socio-ecology of one or more social groups. The chapter by Korstjens *et al.* represents the work of nine students whose combined data address the relationship between food competition, contestability and social structure within the framework of current socio-ecological theory. Among other things, these authors demonstrate that the King colobus is the most frugivorous and has the highest intra-group feeding competition of the three colobine species present. Females of all three species disperse at least occasionally suggesting that affiliative relationships among females are weak.

Range *et al.*'s chapter deals with social relationships among sooty mangabeys. These authors demonstrate that females are the philopatric sex and form linear, stable dominance hierarchies. Range *et al.* show how high rank is beneficial in terms of feeding competition and particularly predator avoidance. Among males, access to females was rank-dependent, suggesting that social dominance is closely linked with reproductive success in both sexes. Finally, Range *et al.* show that individuals of both sexes form well-differentiated relationships with preferred partners, whom they groomed, associated with and supported during agonistic interactions. These authors demonstrate that high-ranking females tended to form close relationships with high-ranking males. In several interesting ways, these results contrast with what is known about this species in captivity.

Part II – Anti-predation strategies

Understanding the evolution and mechanisms underlying the anti-predator behavior of the Taï monkeys has been a major focus of the project, particularly in its early stages. This interest was prompted by earlier work by Boesch and Boesch (1989), showing the extraordinary high hunting pressure exerted by the Taï chimpanzees on the sympatric cercopithecids. Recognizing predation as a key selective factor, an over-arching hypothesis was that the Taï monkeys have responded to chimpanzees by evolving species-specific anti-predator strategies. It quickly became apparent that chimpanzees were part of a larger, more complex system in which three other monkey predators played a major role: crowned eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*) and, more recently, human poachers. Over the years, it has been possible to collect a large set of behavioral data on these monkey predators and we are now able to provide a near complete picture on the impact of these predators both individually and collectively.

Zuberbühler and Jenny review their work on the impact of leopard predation on the primate community. These authors studied the content of leopard feces as well as the ranging behavior of several radio-tagged individuals in relation to the ecological characteristics of each monkey species. A number of unexpected findings have emerged. First, Taï leopards appear to be selective hunters that develop individual prey preferences. Monkeys and duikers are particularly targeted. Second, it became apparent that the various species differed in how vulnerable each was to leopard predation, in ways that often contradicted current theory. For instance, larger species living in larger groups suffered disproportionately high losses suggesting that body size, group size, and the number of males per group are not adaptive traits to avoid predation by leopards. Zuberbühler and Jenny show how the various species use their vocal behavior in response to different predators and demonstrate how the hunting techniques of each predator have resulted in the evolution of species-specific anti-predator strategies.

The next chapter by Bshary concerns the interactions between red colobus monkeys and chimpanzees. Bshary carried out experiments using recordings of chimpanzee vocalizations and drumming on tree buttresses to simulate the sounds produced with chimpanzees prior to a hunt. He was primarily interested in the responses of red colobus monkeys, who routinely fall victim to chimpanzees, as well as those of Diana monkeys, who rarely do. Bshary's data strongly indicate that a major "anti-chimpanzee" strategy of red colobus is to seek out associations with the vigilant Diana monkeys. Bshary shows that red colobus monkeys respond to the sounds of chimpanzees by moving towards and remaining in association with Diana monkeys and that chimpanzees tend to avoid groups of red colobus when they determine that Diana monkeys are in the vicinity. The red colobus-chimpanzee relationship at Taï differs strikingly from that at sites in East Africa and can be explained by differences in forest structure, the size of red colobus groups and the hunting tactics required in each system (Boesch 1994, Stanford 1998). Bshary concludes by discussing the adaptations and counter adaptations in this evolving arms race.

The sudden and fleeting nature of attacks by raptors on forest dwelling primates does not lend itself to systematic scrutiny and long-term studies on the relationship between arboreal cercopithecids and monkey-eating crowned eagles are few. Nevertheless, Shultz and Thomsett use a combination of techniques to provide a detailed look at the interactions between crowned eagles and their jungle prey. Data from radio-transmitters affixed to two adult and two juvenile eagles provide information on ranging behavior and activity budgets. Feeding remains in the form of bones collected from within and beneath 12 eagle nests are used to compile prey profiles that are then examined in light of specific ecological characteristics of each prey species. In so doing, Shultz and Thomsett highlight the biases in eagle diets and discuss the criteria eagles use to preferentially hunt different taxa. These data are complemented by the author's observations of eagle attacks as well as the responses of monkeys to eagle alarm calls to present a complex portrait of eagle-monkey interactions (Shultz 2001 and Shultz *et al.* 2004).

The section on anti-predator strategies concludes with a review of one of the most prominent aspects of monkey anti-predator behavior: alarm calls. All Taï monkeys produce these vocalizations in response to danger, but there are substantial inter-species differences. A chapter by Zuberbühler provides a survey of the experimental work conducted on the alarm call behavior of the various monkey species. Although still incomplete, the emerging picture is one of remarkable species-specific differences in alarm calling behavior. In the case of guenons the idiosyncratic solutions are especially apparent: although Diana monkeys, Campbell's monkeys, and spot-nosed monkeys are all hunted by the same predators, the natural selection pressure exerted by them has led to widely different vocal behavior. The conclusion from these observations is that the vocal repertoire of a species has evolved in response to the

Figure 1.21. A Diana monkey twines its tail around a vertical trunk as it scans the under story for fruit, insects and, perhaps, predators (Photo: Scott McGraw).

particularities of their species-specific ecological niche and social organization. How exactly the monkeys use their various calls, however, is a rather flexible affair. Compliant call usage allows individuals to respond adaptively to differences in type and degree of predation pressure, which are likely to occur over evolutionary times. It also leads to dramatic species difference in calling behavior.

Part III – Habitat use

The single chapter in this section is a comparative examination of the locomotion, posture and habitat use of the seven species found in the study area's central grid. McGraw provides positional behavior, canopy use, and support use profiles for all species and discusses how these can be used to understand additional aspects of each monkey's natural history (see Figure 1.21). He then evaluates the extent that variables known to co-vary in other primate groups are similarly related in the Taï monkeys. The results show that canopy partitioning is critical for permitting monkey sympatry and that species with similar canopy preferences tend to avoid one another. Maintenance activities are not strongly associated with particular canopy levels, but rather with support size. There is a strong relationship between body size and large supports, but not with medium and small supports. Body size is only weakly associated with particular locomotor behaviors and inter-membral index is not a consistent predictor of leaping frequencies. McGraw discusses the significant differences in the postural behavior between cercopithecid subfamilies and argues that these are almost certainly related to the spatial configuration and digestive requirements of colobines versus cercopithecine foods.

Part IV – Conservation

The future of the Taï monkeys is uncertain. Hunting for bushmeat is a daily event, and those who have worked in Taï are unlikely to forget the sound of gunshots that shatter the forest calm. Due to the continuous presence of researchers, poaching is low in some areas of the park, but the vast majority of the forest is used as a hunting ground for both commercial and local subsistence hunters. Some success has been made in curbing illegal hunting activity, but we have yet to detect a widespread political will to aggressively confront the problem. Bushmeat is very popular in large segments of West African society suggesting that until habits change, demand will remain high (see Figure 1.22). The monkeys have little means to protect themselves against these activities. Nevertheless, some adaptations have occurred and Koné and Refisch examine the impact of the most dangerous monkey predator – humans – on two Taï cercopithecids. These authors compare the behavior of Diana monkeys and red colobus monkeys in an area of high poaching with that in a region not frequented by human hunters. They conclude the behavior of Diana monkeys differs significantly between localities but that of red colobus monkeys does not. The inability of red colobus to alter its behavior in response to poaching pressure significantly increases its vulnerability, an idea explored in more detail in the next chapter.

In the final paper, McGraw uses data from preceding chapters, including those on habitat sensitivity, diet, and response to predators to assess the extirpation risk of the seven main monkey species at Taï. He discusses the synergistic factors responsible for putting several species at great risk and concludes that naturally high densities do not necessarily

Figure 1.22. An Ivorian soldier holds a red colobus monkey being sold immediately adjacent to Taï National Park. Poaching is widespread in the forest (Photo: Scott McGraw).

provide protection if naturally abundant primates are conspicuous and ill-equipped to avoid and flee from poachers. The chapter concludes with a discussion of the threats to the Taï fauna as well as recommendations for the conservation of the park and its inhabitants.

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I *Social behavior*

2 The social systems of the guenons

P. Buzzard and W. Eckardt

Introduction

The social system of a species includes the nature of the interactions of individuals between and within social units and the spatial distribution of different age/sex classes. For primates, theories concerning the evolution of social systems are typically based on field data from a restricted number of species, with a clear bias towards species living in more open habitats (Sterck *et al.* 1997). This is problematic because the forest is a major primate habitat, housing a large number of primate species. The social behavior of most forest-living primates is not well described, primarily due to the difficulties in accessibility and observation conditions. In this respect the forest guenons (*Cercopithecus* spp.) are of particular interest for evolutionary theories because they represent a major group of Old World primates.

It is theorized that female primates live in social groups because of anti-predation benefits (van Schaik 1983, van Schaik & van Hoof 1983) and because group-living improves their capacity to defend resources against other groups of conspecifics (Wrangham 1980). Across species, female primates differ in the types of social relations they maintain with one another to achieve these goals. It has been proposed that the relative strengths of inter- and intra-group competition are the two main factors that determine the nature of the females' social relationships and their social system (Sterck *et al.* 1997, Table 2.1).

Across primate species, inter-group encounters can vary from friendly intermingling to hostile fights. Home ranges may overlap completely with neighboring groups ignoring or avoiding each other or they may be defended vigorously against neighbors. In most baboons and in some colobines, for example, home ranges overlap largely and adjacent groups normally do not fight but avoid each other (e.g. Rowell 1988, Korstjens 2001). In contrast, guenon groups usually maintain territories by defending a particular geographical area (Rowell 1988, Butynski 1990, Rowell *et al.* 1991, Cords 2000a, Payne *et al.* 2003). For example, blue monkey (*C. mitis*)

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

Table 2.1. *A classification scheme of primate social systems (see Sterck* et al. *1997)*

In dispersal-egalitarian populations, females disperse from their natal group and do not show clear hierarchical relationships. In the remaining types, females remain in their natal group showing either unclear or clear hierarchical relationships in resident-egalitarian and resident-nepotistic populations respectively. In resident-nepotistic-tolerant populations, females show clear hierarchical relationships, but the benefits of cooperating against other female groups in territorial defense prevents highly despotic behavior of higher-ranking individuals.

	Competition			
Type	Within group	Between group	Female philopatry	Social dominance
Dispersal-Egalitarian	Weak	Weak	No	Weak
Resident-Egalitarian	Weak	Strong	Yes	Weak
Resident-Nepotistic	Strong	Weak	Yes	Strong
Resident-Nepotistic-Tolerant	Strong	Strong	Yes	Weak

females form alliances almost daily against neighboring females and as much as half of a group's home range is used exclusively (Cords 2000a).

A prevalent belief about guenons is that these are animals with low rates of social interactions. Several authors have stated that individuals only engage in low frequencies of agonistic and affiliative behavior and that individual relationships are difficult to discern (Bourlière *et al.* 1970, Glenn 1996, Cords 2000a, Pazol 2001). For example, female baboons and macaques may interact agonistically 1.5 to 20 times more often than female blue monkeys (Seyfarth 1976, Barton 1993, Barton *et al.* 1996, Sterck & Steenbeek 1997, Cords 2000a, Pazol 2001). Consequently, forest guenons were categorized as "resident-egalitarian" and baboons as "resident-nepotistic," using terminology listed in Table 2.1 (Sterck *et al.* 1997).

However, it is possible that guenon behavior has been misrepresented due to the difficult observation conditions and because interactions may be more subtle than in other primate species. For example, long-term data on blue monkey social behavior at Kakamega forest (Kenya) showed that these primates form highly linear and matrilineally-based dominance hierarchies where individuals maintain stable rank positions over several years (Cords 2002a). Thus, the low rates of social interactions may simply be a consequence of high social stability in these groups. Analogous results have recently been obtained from captive Campbell's monkeys (*Cercopithecus campbelli campbelli*) (Lemasson *et al.* 2003, Lemasson & Hausberger 2004), questioning whether the guenons as a whole should be classified as "resident-egalitarian" (Sterck *et al.* 1997, Cords 2002a). More field data on guenon social systems are needed to resolve this controversy.

Unlike the baboons and some colobines, forest guenons typically live in single-male groups for most of the year (Rowell 1988, Cords 2000b). During the breeding season, single-male groups are sometimes invaded by non-resident males who may stay from several days to months and occasionally manage to expel the resident male (Cords 1988, 2000b, 2002b, Macleod *et al.* 2002). It is possible that male forest guenons follow two alternative reproductive strategies. While resident males try to remain with a female group throughout the year non-resident males may try to associate with a female group during the breeding season only. Alternatively, non-resident males may simply try to make the best of a bad situation by joining groups at times when the cost-benefit ratio is most in their favor (Macleod *et al.* 2002). During the non-breeding season, non-resident males have been observed to range solitarily, to form a poly-specific association with other primate species, or to associate in all-male groups. The latter two strategies are thought to be advantageous in providing anti-predation and foraging benefits (Struhsaker 1969, Wrangham 1980, van Schaik & van Horstermann 1994, Noë & Bshary 1997). All-male groups may additionally provide opportunities to form coalitions, which may improve the chances of successfully invading a group of females (Pusey & Packer 1987). In sum, one of the main reasons for guenon males to live in social groups is to gain access to females during the breeding season, and the relative costs and benefits at any one time appear to be the main determinant of male sociality.

In this chapter, we present several sets of data on the four guenon species present in the Taï forest, the Diana monkeys (*Cercopithecus diana*), Campbell's monkeys (*C. campbelli*), lesser spot-nosed monkeys (*C. petaurista*), and putty-nosed monkeys (*C. nictitans*). The Taï primates are of particular interest for evolutionary theories because their habitat, the Taï forest, could be representative of a typical primate forest habitat, containing natural densities of the major primate predators and relatively low levels of human activity. We will first provide data on the population density for each species because of the potential impact of this variable on social systems (Smuts *et al.* 1987). Next, we will describe the typical group compositions for each species and assess the nature of the social relations of individuals between and within social groups. Finally, we will utilize these sets of information to contribute to the debate about the proper classification of guenon social systems.

Methods

Study animals

Data were collected from seven habituated study groups, two each of Diana monkeys, Campbell's monkeys and lesser spot-nosed monkeys, as well as one putty-nosed monkey group. We conducted additional group counts and some behavioral observations on a third Diana monkey group, on two all-male Campbell's monkey groups, and on several partly habituated neighboring groups of Campbell's monkeys, lesser spot-nosed monkeys, and one group of putty-nosed monkeys.

Sampling procedure

On most observation days we followed one group from about 7:30 to 18:00 hrs until the monkeys stopped moving in sleeping trees. At other times, we followed the groups for half-days from about 7:30 to 12:30 hrs or from 12:00 to 18:00 hrs. Groups were followed for 2–4 consecutive days. The observation regime for the putty-nosed monkey group was slightly different because the group's home range was much further away, outside the main study area. This group was followed from 8:00 to 17:00 hrs (8:00 to 12:30 hrs or 12:30 to 17:00 hrs). Paul Buzzard (PB) and a trained field assistant followed the Diana monkeys, Campbell's monkeys, and lesser spot-nosed monkeys from August 2000 until November 2001. Winnie Eckardt (WE) followed the putty-nosed monkey group from June to December 2001. Data collection was based on scan sampling (Altmann 1974). Scans were conducted twice per hour throughout the day, and individual scans lasted for up to 15 min. During each scan we attempted to sample as many different individuals as possible once per scan by walking through the group.

Group composition

We classified individuals into five different age/sex classes: adult males, adult females, sub-adults, juveniles, and infants. Adult males were slightly bigger than other adult individuals and they produced loud calls (Gautier & Gautier 1977, Zuberbühler *et al.* 1997, Zuberbühler 2001, Eckardt & Zuberbühler 2004). Individuals were classified as adult females if they appeared to be pregnant or had pendulous nipples, suggesting that they had given birth before. Sub-adult males were the same size or slightly smaller than adult males but did not give loud calls. Sub-adult females were the size of adult females but were not pregnant and had no pendulous nipples. Juveniles were smaller than adult females but were no longer carried by them and, if at all, only suckled infrequently. Infants were frequently carried by their mothers and were still suckling regularly.

Home range size, home range overlap, and population density

At the end of each scan, we determined the group's center of mass (Cords 1987) and marked it on a grid system that was made up of 0.25 ha quadrants. Since the putty-nosed monkey group was outside this grid system, their position was determined with a GPS receiver (GARMIN XL16). We estimated home range overlap by noting the position of neighboring groups on an all-occurrence basis while we followed a study group or during days when we collected other data (2–4 days/month).

Home range sizes and overlap with neighboring groups were determined and used to calculate group density, using the "block method" (Struhsaker 1981, Whitesides *et al*. 1988, Fashing and Cords 2000). Blocks (i.e. grid quadrants) used by one group only contributed with a value of 1.0; quadrants used by two conspecific groups contributed with 0.5, quadrants used by three groups contributed with 0.33, and so forth. Each group's value was then summed up to produce an "adjusted home range size." Group density (groups/km^2) was determined by using the inverse of the average adjusted home range sizes for each species. Individual density (individuals/km^2) was determined by multiplying group density with the average group size for each species. Putty-nosed monkeys are extremely rare in the Taï forest and adjacent groups did not overlap in home range use (see Eckardt & Zuberbühler 2004). We calculated this group's home range by assigning GPS readings to an imaginary grid system equivalent to one used for the other study groups. We located a total of four different putty-nosed monkey groups in a 73 km^2 area surrounding the main study grid, which provided the basis for our population density estimates.

Inter-group encounters

An inter-group (or between-group) encounter was recorded when a study group was less than 50 m apart from a neighboring group of conspecifics. Since our study groups were often in mixed-species associations (60–90 per cent of monthly scans: Wolters & Zuberbühler 2003, Buzzard 2004, Eckardt & Zuberbühler 2004), we were able to recognize some inter-group encounters while following other study groups. Only data from PB were included for inter-group encounters since PB followed Diana, spot-nosed and Campbell's, and only these species were involved in inter-group encounters. If another group was associated with the study group for more than eight hours, we were able to enlarge our sample size and counted such days as possible days of encounters for both groups. While sampling a study group, PB walked not only through that study group but also through most of the other associated groups to look for inter-group encounters. We distinguished between passive and aggressive types of inter-group encounters. An aggressive encounter was scored if individuals gave acoustically distinct vocalizations at high amplitude, or if individuals chased or were chased by members of the neighboring group. During aggressive encounters the males frequently exchanged loud calls. Passive encounters did not involve any of the behavioral patterns described. Instead, the two groups simply stayed in each other's vicinity for a while and then travelled on to other areas of their home range.

Intra-group interactions

To assess the nature of relationships between individuals within the same group, we recorded all affiliative and agonistic behaviors during the scans. Grooming and mounting were scored as affiliative behaviors; attacks, threats, and avoidances were scored as agonistic behaviors. Grooming behavior was defined as the manual inspection of another individual's fur with one or both hands or with the mouth. Mounts, which also occurred between females, could take place with or without pelvic thrusts. An attack was scored if one individual engaged in a physical confrontation with another individual involving biting and/or hitting. A threat was scored if one individual lunged at another individual with bared teeth. Finally, an avoidance occurred if one individual moved away in response to another individual's approaching to a distance of two meters or less. We calculated relative rates of affiliative and agonistic behaviors for each species by dividing the number of behaviors by the number of individuals scanned.

To further describe the social dynamics in these groups we determined the age/sex-specific interaction patterns of affiliative and agonistic behaviors. In particular, we compared the expected and the observed number of agonistic and affiliative behaviors for each age/sex class combination. To calculate expected frequencies, we multiplied the total number of grooming or agonistic bouts by the random interaction frequency ratios for each age/sex class combination. To obtain the random interaction frequency ratio, the marginal totals of the actor and recipient were each divided by the total number of grooming or agonistic bouts and then multiplied together. The observed number was then tested to see if it was significantly greater or less than the expected number by using the binomial (or z-test approximation to the binomial) wherever the expected number exceeded 10 (Siegal & Castellan 1988, Bernstein 1991).

Results

Group composition

The average group size for Diana monkeys was 23.5 individuals, more than twice the number of an average Campbell's monkey (9.3 individuals),

Table 2.2. *Typical group compositions of the Taï forest guenons (November 2001)*

Group	Adult male	Adult female	Sub-adult	Juvenile	Infant	Total
Diana monkeys						
DIA1[a]	1	11	2	7	0	21
DIA2[a]	1	13	2	10	0	26
DIA3	1	11	?	?	?	>15
Campbell's monkeys						
CAM1[a]	1	6	0	2	1(?)	9 (10?)
CAM2[a]	1	5	1	2	0	9
CAM3	1	5	0	4	0	10
Spot-nosed monkeys						
PET1[a]	1, (2)[b]	8	1	6	0	16
PET2[a]	1	4	0	2	0	7
PET3	1	5	1	4	0	11
Putty-nosed monkeys						
NIC1[a]	1	4	5	2	0	12
NIC2[c]	1	2(?)	0(?)	2	1(?)	6(?)

[a] Study groups; [b] PET 1 frequently contained 2 males from February 2001 to December 2001; [c] Census in 2000

lesser spot-nosed monkey (11.3 individuals) and putty-nosed monkey group (11.3 individuals). All study groups contained one resident male through most of the study period (see Table 2.2). However, in February 2001, a sub-adult male in a lesser spot-nosed monkey group (PET1) became adult but remained in the group resulting in two adult males. About five months later, the original male was involved in several fights and chases with the male from a neighboring group (PET2). Soon thereafter, both males of PET1 disappeared and the PET2 male took over the PET1 group. In addition, a new adult male was often seen with the PET1 group until the end of the study period. After the PET2 male successfully transferred to the PET1 group another new male took over the PET2 group quickly.

In addition, we observed two all-male groups of Campbell's monkeys in the study area. One of them (CAMAM1) contained two to four adult males and one juvenile male and was often (68.7 per cent, N = 115) observed in association with one Diana monkey (DIA1) and one lesser spot-nosed monkey group (PET2). The other all-male group (CAMAM2) contained two adult males and was observed five times in the home range of a Campbell's monkey group (CAM2). Individuals in both all-male groups were observed to give loud calls in response to Diana monkey loud calls, falling trees, or other disturbances.

Table 2.3. *Home range size, home range overlap, and population density of the Taï guenons*

Group	Home range (ha)	Overlap (%)	Adjusted range (ha)	Density Groups (/km^2)	Density Individuals (/km^2)
DIA1	59.3	67	37.0	2.7	63
DIA2	58.5	65	38.8	2.6	61
CAM1	67	54	42.0	2.4	24
CAM2	52	56	37.6	2.7	25
PET1	73.5	60	49.3	2	23
PET2	64	69	38.5	2.6	29
NIC1	93	–	93.0	0.05	0.45

Diana monkeys (DIA); Campbell's monkeys (CAM); Spot-nosed monkeys (PET); Putty-nosed monkeys (NIC)

Home range size, home range overlap, and population density

Diana monkeys were the most common guenons in the Taï forest (62 ind./km^2) followed by lesser spot-nosed monkeys (26 ind./km^2), Campbell's monkeys (24 ind./km^2) and putty-nosed monkeys (0.6 ind./km^2). Group densities (groups/km^2) were similar for Diana monkeys (2.6 groups per km^2), Campbell's monkeys (2.5 groups per km^2) and lesser spot-nosed monkeys (2.3 groups per km^2), but lower for putty-nosed monkeys (0.05 groups per km^2; Table 2.3). Diana monkeys used an average home range of 56.8 ha. About 66 per cent of it was shared with neighboring groups, resulting in an average adjusted home range of 37.9 ha. Campbell's monkeys used an average home range of 56.0 ha. About 55 per cent was shared with neighboring groups, resulting in an average adjusted home range of 39.8 ha. Lesser spot-nosed monkeys used an average home range of 65.3 ha. About 64 per cent was shared with neighboring groups, resulting in an average adjusted home range of 43.9 ha. The putty-nosed monkey group used a home range of 93.0 ha, and there was no overlap with neighboring groups.

Inter-group encounters

Although the group densities were roughly equal, the three species in the study grid differed greatly in how frequently they encountered neighboring groups and in the consequences of these encounters (see Table 2.4). Campbell's monkeys were least likely to encounter neighboring groups, although the few times this happened it was usually of an aggressive nature. Additionally, the all-male group CAMAM1 was observed in two

Table 2.4. *Inter-group encounters in the Taï guenons*

Species (observation days)	Encounter rate (N/day)	Aggressive encounters	Male calling
Diana monkeys (N = 95)	0.358	35%	24% (N = 34)
Campbell's monkeys (N = 91)	0.033	67%	67% (N = 3)
Spot-nosed monkeys (N = 104)	0.125	31%	31% (N = 13)

inter-group encounters with a neighboring group. All males from the all-male group exchanged repeated loud calls and threats with the resident male from the neighboring group. Inter-group encounters were four times more common in spot-nosed monkeys compared to Campbell's monkeys, although during encounters groups typically ignored each other and aggressive interactions were uncommon. Three of the four observed aggressive encounters were over access to a feeding tree. In all cases, the males took an active role, engaging in loud calling and threatening neighboring group members. Finally, Diana monkeys had the highest rates of inter-group encounters, about ten times more frequent than Campbell's monkeys. However, only a minority of them resulted in aggressive interactions, often about access to a feeding tree. Males called in 8 out of 12 aggressive encounters (66.7 per cent). The home ranges of putty-nosed monkey groups were over one kilometer apart and inter-group encounters were never observed.

Intra-group interactions

We conducted a total of 7,258 scans on the seven different study groups (see Table 2.5). Grooming rates were relatively similar for all species and highest in putty-nosed monkeys, followed by Campbell's monkeys, spot-nosed monkeys, and Diana monkeys (see Table 2.5). Only Diana monkey adult females, however, mounted each other (N = 5 bouts). The order was different for agonistic interactions. Diana monkeys showed the highest rates of agonistic behaviors, followed by putty-nosed monkeys, spot-nosed monkeys, and Campbell's monkeys (see Table 2.5). Diana monkey females were also the only ones observed to form coalitions with one another. In six instances, two or more individuals chased or threatened one or more other group members. Coalitions occurred frequently during conflicts with members of another species (Buzzard 2004).

In each species, the adult females were involved in the majority of grooming bouts (see Table 2.6). Diana and lesser spot-nosed adult females groomed other adult females more than expected, but the differences were

Table 2.5. *Intra-group affiliative and agonistic interactions*

Species (N observation days)	N scans	N individual samples	Relative frequency (bouts/ind. $\times 10^3$) Affiliative	Agonistic
Diana monkeys (N=75)[a]	1,320	9,243	9.6	4.9
Campbell's monkeys (N=145)	2,262	9,093	12.5	0.8
Spot-nosed monkeys (N=156)	2,362	9,425	10.3	1.0
Putty-nosed monkeys (N=90)	1,314	5,577	17.6	2.7

[a] Includes the 5 mounts

not significant ($z = -0.86, -0.11$; $p = 0.19, 0.46$, respectively; Table 2.6). Males groomed rarely, in some cases never (see Table 2.6). In Diana monkeys and Campbell's monkeys the majority of agonistic interactions involved adult females, but in lesser spot-nosed monkeys most agonistic interactions involved juveniles (see Table 2.7). Adult female Diana monkeys were involved in more agonistic bouts than expected with other females, but the difference was not significant (see Table 2.7, $z = -0.62$, $p = 0.27$). In addition, juvenile Diana monkeys were involved in fewer agonistic bouts than expected with other juveniles, but this difference was not significant either (see Table 2.7, $p = 0.24$).

Discussion

Group composition

All study groups lived in single-male groups for the majority of the time, as documented in other forest guenons (Rowell 1988, Cords 2000b). The numbers of adult females per group was comparable to other published records (e.g. Cords 2000b), and group sizes for Diana monkey, Campbell's monkeys and spot-nosed monkeys were comparable to data reported from another West African study site, Tiwai Island, Sierra Leone (Oates *et al*. 1990, Hill 1994). Putty-nosed monkey groups were smaller at Taï than at other field sites, probably due to higher inter-specific competition with Diana monkeys (Gautier & Gautier-Hion 1969, Struhsaker 1969, Gautier-Hion & Gautier 1974, Whitesides 1981, Mitani 1991, White 1994, Eckardt & Zuberbühler 2004).

Resident forest guenon males defend their group against intruding males, but extra-group male influxes have still been reported in some forest guenons, particularly during the breeding season (Cords 2000b). Our documentation of a male take-over, the likely eviction of the resident PET1 male by his neighbor, suggests that this may also be part of the

Table 2.6. *Number of observed (expected) grooming bouts between each age/sex class in (a)* C. diana*, (b)* C. campbelli*, (c)* C. petaurista*, and (d)* C. nictitans

Marginal totals are for observed bouts; for each species the total number of bouts is in bold. To calculate the expected values, the marginal totals of the actor and recipient were each divided by the total number of bouts and then multiplied together; this product was then multiplied by the total number of bouts (see Methods). The differences between observed and expected bouts were insignificant in all cases (see Results).

	Recipient					
Groomer	Adult male	Adult female	Sub-adult	Juvenile	Unknown	Marginal totals
(a) *C. diana*						
Adult male	—	0 (0)	0 (0)	0 (0)	—	0
Adult female	0 (0)	28 (21)	2 (5)	10 (14)	—	40
Sub-adult	0 (0)	6 (8)	2 (2)	6 (5)	—	14
Juvenile	0 (0)	11 (16)	6 (3)	13 (10)	—	30
Marginal totals	0 (0)	45	10	29	—	**84**
(b) *C. campbelli*						
Adult male	—	1 (1)	0 (0)	0 (0)	—	1
Adult female	10 (9)	63 (65)	2 (1)	15 (15)	—	90
Sub-adult	0 (0)	2 (3)	0 (0)	2 (1)	—	4
Juvenile	1 (2)	16 (14)	0 (0)	2 (3)	—	19
Marginal totals	11	82	2	19	—	**114**
(c) *C. petaurista*						
Adult male	0 (0)[a]	0 (0)	0 (0)	0 (0)	—	0
Adult female	13 (14)	45 (43)	3 (3)	12 (14)	—	73
Sub-adult	1 (1)	1 (2)	0 (0)	1 (1)	—	3
Juvenile	4 (4)	11 (12)	1 (1)	5 (4)	—	21
Marginal totals	18	57	4	18	—	**97**
(d) *C. nictitans*						
Adult male	—	0 (0)	0 (0)	0 (0)	0 (0)	0
Adult female	6 (4)	23 (24)	0 (0)	7 (11)	11 (9)	47
Sub-adult	0 (0)	4 (2)	0 (0)	0 (1)	0 (1)	4
Juvenile	2 (4)	23 (22)	0 (0)	15 (10)	3 (8)	43
Unknown	0 (0)	0 (2)	0 (0)	0 (1)	4 (1)	4
Marginal totals	8	50	0	22	18	**98**

[a] In *C. petaurista*, adult male interaction with other adult males in the group was possible since PET1 frequently contained 2 males from February 2001 to December 2001

Taï guenon social system. An additional male was frequently seen in the group for another five months. Similarly, Hill (1994) recorded a second male associating with a group of Diana monkeys for five months.

The stable all-male groups found in Campbell's monkeys are also found in Mona monkeys in Benin and Grenada (Glenn 1996, 1997,

Table 2.7. *Number of observed (expected) agonistic bouts between age/sex classes of (a)* C. diana*, (b)* C. campbelli*, (c)* C. petaurista*, and (d)* C. nictitans

Marginal totals are for observed bouts; for each species the total number of bouts is in bold. To calculate the expected values, the marginal totals of the actor and recipient were each divided by the total number of bouts and then multiplied together; this product was then multiplied by the total number of bouts (see Methods). The differences between observed and expected bouts were insignificant in all cases (see Results).

	Victim					
Aggressor	Adult male	Adult female	Sub-adult	Juvenile	Unknown	Marginal totals
(a) *C. diana*						
Adult male	—	0 (2)	2 (0)	1 (1)	—	3
Adult female	0 (0)	23 (18)	4 (5)	7 (11)	—	34
Sub-adult	0 (0)	1 (3)	1 (1)	4 (2)	—	6
Juvenile	0 (0)	0 (1)	0 (0)	2 (1)	—	2
Marginal totals	0	24	7	14	—	**45**
(b) *C. campbelli*						
Adult male	—	0 (0)	0 (0)	0 (0)	—	0
Adult female	0 (0)	3 (2)	0 (0)	2 (3)	—	5
Sub-adult	0 (0)	0 (0)	0 (0)	0 (0)	—	0
Juvenile	0 (0)	0 (1)	0 (0)	2 (1)	—	2
Marginal totals	0 (0)	3	0	4	—	**7**
(c) *C. petaurista*						
Adult male	0 (0)[a]	0 (0)	1 (0)	0 (1)	—	1
Adult female	0 (0)	3 (1)	0 (0)	0 (2)	—	3
Sub-adult	0 (0)	0 (0)	0 (0)	0 (0)	—	0
Juvenile	0 (0)	0 (2)	0 (1)	5 (3)	—	5
Marginal totals	0 (0)	3	1	5	—	**9**
(d) *C. nictitans*						
Adult male	—	0 (0)	0 (0)	0 (0)	0 (0)	0
Adult female	0 (0)	4 (2)	0 (1)	0 (2)	1 (1)	5
Sub-adult	0 (0)	0 (1)	2 (0)	0 (1)	0 (0)	2
Juvenile	0 (0)	2 (3)	0 (1)	5 (2)	0 (1)	7
Unknown	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	1
Marginal totals	0 (0)	6	2	5	2	**15**

[a] In *C. petaurista*, adult male interaction with other adult males in the group was possible since PET1 frequently contained 2 adult males from February 2001 to December 2001

Glenn *et al*. 2002) as well as the Lowe's subspecies of Campbell's monkeys (*C. campbelli lowei*, Bourlière *et al*. 1970). Because these monkeys are all members of the *mona* superspecies (Butynski 2002), the presence of all-male Campbell's monkey groups in Taï forest suggests that this form of grouping may be a hallmark of the *mona* superspecies social system

(Glenn *et al*. 2002). Among the other forest guenons, all-male groups have also been reported in blue monkeys (Tsingalia & Rowell 1984, Macleod 2000) and de Brazza's guenons (*C. neglectus*, Chism & Cords 1998), but these males tend to move in loose associations, and grooming is rare (Glenn *et al*. 2002, Cords, personal communication). Struhsaker (1969) suggested that the formation of all-male groups is an adaptation against ground predators, perhaps because terrestrial species are more vulnerable to predation (Clutton-Brock & Harvey 1977, van Schaik & van Noordwijk 1985 but see Zuberbühler & Jenny 2002). Consistent with Struhsaker's prediction Campbell's and Mona monkeys frequently forage on the ground and in lower forest strata (McGraw 1996, Glenn *et al*. 2002, Buzzard 2004). All-male groups are also common in other terrestrial species such as Japanese macaques (*Macaca fuscata*) and patas monkeys (*Erythrocebus patas*). Further research on the presence of all-male groups in crowned monkeys (*C. pogonias*) would be valuable since this species is a member of the *mona* superspecies but uses higher forest strata (Gautier-Hion 1988) than the other members.

Population densities

Diana monkeys, Campbell's monkeys, and lesser spot-nosed monkeys were found at similar group densities, whereas putty-nosed monkeys were much more rare (see Table 2.2, Höner *et al*. 1997, Eckardt & Zuberbühler 2004). At Tiwai Island, densities of Diana monkeys, Campbell's monkeys, and lesser spot-nosed monkeys were similar (Oates *et al*. 1990, Fimbel 1994). Putty-nosed monkeys (*C. n. nictitans* and *C. n. martini*) are normally much more common than what we found at Taï (*C. n. stampflii*), however. For example, in Gabon (White 1994) and Cameroon (Mitani 1991), putty-nosed monkeys can reach densities of 2.0 groups/km^2 and are over three times more populous than sympatric moustached guenons (*C. cephus*) and crowned guenons. The low density at Taï is most likely because of competition with the other guenons, especially the Diana monkeys. Putty-nosed monkeys most likely originated in central Africa (Kingdon 1997) and it has been suggested that putty-nosed monkeys are later arrivals to the Taï Forest and have not been able to establish themselves as well there (Oates 1988, Eckardt & Zuberbühler 2004).

Inter-group encounters

Jolly (1985 p. 152) defined a territory as "a geographical area, defended by the owners, or exclusively used by the owners, or both." According to this definition, Taï Diana monkeys, Campbell's monkeys and spot-nosed monkeys can be classified as territorial as are Diana monkeys at

Tiwai Island (Oates & Whitesides 1990, Hill 1994). Inter-group encounters were often aggressive, and we never observed affiliative interactions between neighbors as described, for example, by Lawes and Henzi (1995) for blue monkeys. Diana monkeys were involved in more inter-group encounters than the other species with similar group densities, perhaps the result of the greater population density of this species (see Table 2.3). In blue monkeys, higher population density was related to higher rates of aggressive inter-group interactions (Butynski 1990). At Kakamega Forest (Kenya) the density of blue monkey groups was almost twice as high as in Taï and aggressive encounters were much more common occurring every other day on average (Rowell *et al.* 1991, Cords 2002a). Diana monkeys rely on large fruit trees (> 50 cm DBH) more extensively than Campbell's monkeys and lesser spot-nosed monkeys (Buzzard 2006), and the more clumped distribution of these larger trees may be responsible for the 3 to 10 times higher inter-group encounter rates seen in Diana monkeys. However, our data also showed that the percentage of aggressive encounters in Diana monkeys was not exceptional (see Table 2.4). Alternatively, it is possible that part of the species difference could be attributed to observer presence. The home ranges of our Campbell's and spot-nosed monkey study groups bordered on those of neighboring groups that were less habituated to human presence than the neighbors of our Diana monkey study groups, suggesting that inter-group encounters might be much more common, particularly for Campbell's monkeys (Buzzard unpublished data).

Intra-group interactions: affiliative and agonistic behavior

Since we did not use focal animal sampling our data on rates of affiliative and agonistic interactions are not directly comparable with other studies. Agonistic interactions in these monkeys are usually very brief, indicating that the scan sampling method is likely to generate underestimated values concerning the frequency of agonistic behavior. Nevertheless, rates of affiliative and agonistic behaviors of forest guenons in Taï appeared to be considerably lower compared to what is normally reported from many other non-guenon primate species in the wild (Seyfarth 1976, Barton 1993, Barton *et al.* 1996, Sterck & Steenbeek 1997).

Adult females were mainly responsible for observed grooming bouts, and grooming rates were similar in most species (see Table 2.6). The higher grooming rate in putty-nosed monkeys could reflect tighter group cohesion in this species (Chism & Rogers 2002). Males of all species did not normally groom other individuals, but they were sometimes groomed by others, with the exception of the Diana monkey males. Male Diana monkeys appear to be much less integrated into the group than other guenon males, corroborating earlier findings on captive Diana monkeys (Byrne *et al*. 1983) and free-ranging Campbell's monkeys (Hunkeler *et al*. 1972). The lower number of male-female interactions in Diana monkeys compared to the other species may reflect the low willingness of the Diana male to play an active role during inter-group encounters. In blue monkeys, male-female interactions are also rare, and blue monkey males also rarely play an active role during inter-group encounters (Pazol 2001).

Diana monkeys and putty-nosed monkeys exhibited considerably more agonistic interactions (threats, chases, and avoids) than Campbell's monkeys and lesser spot-nosed monkeys. Diana monkeys live in larger groups than Campbell's monkeys and lesser spot-nosed monkeys, suggesting that increased feeding competition could explain higher rates of agonistic interactions (van Schaik & van Hoof 1983, Wrangham *et al*. 1993, Janson & Goldsmith 1995). The putty-nosed monkey group was often associated with Diana monkeys and the two groups frequently foraged on the same large fruit trees (Eckardt & Zuberbühler 2004). Perhaps individuals found it more difficult to maintain comfortable inter-individual distances on these spatially restricted patches, leading to higher rates of agonistic behavior (Clutton-Brock & Harvey 1977, van Schaik 1989). Campbell's monkeys and spot-nosed monkeys foraged more dispersed than Diana monkeys leading to lower rates of agonistic interactions, which supports previous data from Campbell's monkeys (Bourlière *et al*. 1970, Hunkeler *et al*. 1972).

Theoretical implications

Although the low density of putty-nosed monkeys in Taï precluded comparisons of inter- and intra-group competition, our data showed clear differences in the relative importance of both types of competition in the other Taï guenons. In Campbell's monkeys and spot-nosed monkeys, within-group competition appeared to be low, while inter-group encounters were often aggressive suggesting that their social systems can best be classified as "resident-egalitarian" (Sterck *et al*. 1997). For Diana monkeys, however, both intra- and inter-group competition were high, as evidenced by the high rates of agonistic interactions among group members and the high encounter rates with neighboring groups, suggesting that the Diana monkeys may deviate from other guenons and that their social system may be better classified as "resident-nepotistic-tolerant." Additionally, female Diana monkeys engaged in mountings and coalition formation, behaviors often considered aspects of nepotistic societies (e.g. Smuts *et al*. 1987, Chadwick-Jones 1989, Srivastava *et al*. 1991). Finally, McGraw *et al*. (2002) reported a fatal attack of several

Diana monkey females on another one, further suggesting that the label "resident-egalitarian" is not suitable for Diana monkeys. Our data and the results from work on blue monkeys (Cords 2002a) suggest that the resident-egalitarian social system is not a hallmark of guenon social systems.

Conclusions

1. Diana monkeys, Campbell's monkeys, and lesser spot-nosed monkeys were found at similar group densities in the Taï forest, although Diana monkeys lived in consistently larger groups. Putty-nosed monkey groups were much more rare.
2. Study groups consisted of one single adult male and several adult females with their offspring. One lesser spot-nosed monkey group had two adult males during a five-month period following a male take-over. Some extra-group Campbell's monkey males formed stable all-male groups.
3. All species had low levels of social interactions in comparison to macaques and baboons.
4. All species had relatively equal rates of grooming while Diana monkeys showed higher rates of inter-group aggression and intra-group agonistic behavior in relation to the other species. In addition, Diana females formed coalitions and mounted each other, suggesting that their social system was "resident-nepotistic-tolerant," using a recent classification scheme (Sterck *et al*. 1997). Campbell's monkeys and lesser spot-nosed monkeys showed high levels of inter-group aggression, but low levels of intra-group agonistic behavior, suggesting that their social system was a "resident-egalitarian" one. Putty-nosed monkeys could not be classified because they did not have neighboring groups to interact with. High rates of grooming and agonistic acts in putty-nosed monkeys compared to the other species suggest that putty-nosed relationships may be differentiated, however.

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3 How small-scale differences in food competition lead to different social systems in three closely related sympatric colobines

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Introduction

As an essential aspect of life, food can evoke strong competition among individuals and shape a species' social system. Through a pathway of relationships we can link the competitive regime that food evokes in a population to such seemingly loosely related traits as social relationships within and between groups, ranging patterns and dispersal patterns. Food most strongly determines female relationships in many mammals because female reproductive success is mainly constrained by food acquisition. Male success, on the other hand, largely depends on access to mating partners (Trivers 1972, Emlen & Oring 1977). The competitive regime among females can be predicted based on the contestability or usurpability of their food (Wrangham 1980, van Schaik & van Hooff 1983, van Schaik 1989, 1996, Isbell 1991, Sterck *et al.* 1997). In most primates, food competition increases with group size (Clutton-Brock & Harvey 1977, Wrangham *et al.* 1993). However, folivores do not always fit into the general patterns found in such studies (Clutton-Brock & Harvey 1977, Isbell 1991, Janson & Goldsmith 1995). A comparative test of the effect of diet on social systems *within* a largely folivorous genus can solve some of these controversies. Since dietary category is only a proxy for a whole suite of traits that together determines the contestability of a species' food we need to look at each of these traits to investigate differences within a dietary specialization. Among these traits we find: caloric content and digestibility of food item(s), the size, abundance and distribution of

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

a food patch and how it is distributed in the larger space, as well as its abundance, the time it takes to get to the edible part of the food item, and the time that is spent at a food patch (Wrangham 1980, Whitten 1983, van Schaik 1989, Janson 1990, Isbell 1991, Isbell *et al*. 1998, Mathy & Isbell 2001). Considering the number of variables to be evaluated, it is not surprising that few studies have managed to plot the general diet of a species onto this continuum of contestability, as well as test the implications for specific levels of competition on the social organization of a species (van Schaik & van Noordwijk 1988, Borries 1993, Cords 2000, Koenig 2000). Furthermore, because the level of competition in one species or population is only meaningful when compared to that of another species or population, comparative studies produce the most convincing support for the proposed effects that food competition has on a species' social system (e.g. Mitchell *et al*. 1991, Barton *et al*. 1996, Sterck & Steenbeek 1997, Isbell & Pruetz 1998, Isbell *et al*. 1998, 1999, Thierry *et al*. 2000).

We use a unique natural experiment, the coexistence of three closely related colobines (western red colobus: *Pilio-/or Procolobus badius badius;* western black-and-white colobus: *Colobus polykomos polykomos*; olive colobus: *Procolobus verus*), to compare the impact of food on social systems. The enormous advantage of this set-up is that we control for the confounding effects of phylogeny, predation and seasonality of the forest simultaneously. We will discuss the suite of traits that determine the contestability of the foods chosen by these three folivorous species and test whether the differences in contestability can explain the differences in social relationships within and between groups as predicted by current socio-ecological theory.

Although the details and the categorization of social systems that different socio-ecological models produce vary (Isbell & Young 2002, Isbell 2004) the general basis of the theory behind them is very similar. The level of competition is determined by food available per individual at a certain food source (Clutton-Brock & Harvey 1979, Janson & Goldsmith 1995). The predominant mode of competition, either contest or scramble competition, depends on the distribution and size of food sources relative to the number of individuals using the source (e.g. Wrangham 1980, Janson 1988, van Schaik 1989, Milinski & Parker 1991, van Hooff & van Schaik 1992). Patchily distributed food sources that can be monopolized by one individual or a coalition evoke contest competition. Small and equally distributed food sources that are difficult to monopolize result in scramble competition. However, a group of primates does not exist in a vacuum and therefore, in order to understand a social system we have to investigate both competition within a group and competition between groups. The third level, competition between species will not be discussed here. The competitive regime between groups depends on the same variables as competition within groups, but it occurs at different levels: intra-group competition depends on distribution of food within a food source on which several group members feed, and inter-group food competition depends on distribution of food sources over the area that different groups use.

Based on general socio-ecological theory (Alexander 1974, Emlen & Oring 1977, Wrangham 1980, van Schaik 1983, 1989, van Schaik & van Hooff 1983, Dunbar 1988, Isbell 1991, 2004, Janson & Goldsmith 1995, Sterck *et al.* 1997, Isbell & Young 2002) we formulated a set of predictions for the social system of a species, as based on the characteristics of its food (see Table 3.1). The levels of within-group and between-group contest competition are expected to be positively correlated to the quality of food since only high quality food will make food defense worth the effort. Food quality is determined by the energy content, digestibility, and size of food items. Colobines tend to select foods especially on the basis of the levels of protein and fiber (Davies & Bennett 1988, Dasilva 1994, Waterman & Kool 1994, Brugière *et al.* 2002, Chapman *et al.* 2003, Wasserman & Chapman 2003). High quality items are young leaves, fruits, flowers, and seeds, while mature leaves are low quality. Contest competition within a group is also more likely to occur when foods are patchily distributed in a tree and relatively rare. High quality food, such as fruits, tends to be less common and more patchily distributed than low quality food, such as leaves (Clutton-Brock & Harvey 1979). Long processing time and a long time spent at a patch is also predicted to increase the levels of agonistic interactions an individual endures per unit time (Isbell 1991). A long handling time means that the quality of the food item increases with time until it has been processed completely. Frugivores and folivores do not generally spend much time processing their food but swallow most food items whole. Granivores, on the other hand, may take some time to get to the seeds, especially when these are encased in a wooden husk (e.g. Korstjens *et al.* 2002). The time spent at a patch increases the risk of being attacked by others. Several species have solved this problem by the use of cheek pouches: stuffing the cheek pouch reduces the time an individual spends at a food patch. It is noteworthy that cheek pouches are not found in colobines but they are in their closest frugivorous relatives the cercopithecines (Oates & Davies 1994) which supports the idea that fruits are more contestable than leaves. Finally, within a large tree, within-group

Table 3.1. *General predicted effect that various food traits and social traits have on each other based on socio-ecological theory and as investigated in this chapter*

	Effect	
Contestability of food at within-group (WG) level	Increases with:	Percentage fruit in diet Processing time Patchiness of food items within trees Food spot residence time
	Decreases with:	Percentage mature leaves in diet Density of items in tree Tree size relative to number of individuals
Contestability of food at between-group (BG) level	Increases with:	Percentage fruit in diet Processing time Patchiness of food trees Tree size relative to group size
	Decreases with:	Percentage mature leaves in diet Density of trees
Within-group F-F aggression	Increases with:	Contestability of food at WG-level
	Decreases with:	Contestability of food at BG-level
Between-group F-F aggression	Increases with:	Contestability of food at BG-level
Within-group F-F cooperation	Strength increases with:	WG F-F aggression if food items are shareable
Group-level cooperation	Strength increases with:	BG F-F aggression
F-F affiliation	Increases with:	WG & BG F-F aggression
Home range size	Increases with:	Group size Percentage fruit in diet Spatio-temporal patchiness of food trees
	Decreases with:	Density of food trees
Day-Journey Length	Increases with:	Group size Percentage fruit in diet Spatial patchiness of food trees Percentage time in association with frugivores
	Decreases with:	Density of food trees Food tree size relative to group size Food digestion and processing time
Territoriality	Increases with:	BG competition Small home range relative to day-journey length
	Decreases with:	Home range size
Female philopatry	Increases with:	Cooperation Patchiness and rarity of food trees Predation risk during transfer
	Decreases with:	Inbreeding risk e.g. few males per group

competition will be less than in a small tree because there is enough food to share.

Contest competition between groups is expected to be high when food trees are patchily distributed and occur at low densities. Fruit bearing trees generally follow these patterns more than leaf-bearing trees due to seasonal availability of food items (Harvey & Clutton-Brock 1981). Food source density is negatively correlated with competition as it removes any incentive to compete over food. Finally, the larger the tree that animals feed in relative to the number of individuals in the group, the more likely it is that they will spend a long time at each tree as it depletes more slowly than a small tree (Janson 1990, Isbell *et al.* 1998). Inter-group competition will be especially strong if large, patchily distributed and rare food sources are regularly used.

Although highly contestable food sources should lead to high levels of agonistic interactions between groups (Wrangham 1980), the level of territoriality of a species depends on more variables than contestability of food sources alone. The size of the home range relative to the distance travelled per day, should determine whether territories or individual patches are defended (Mitani & Rodman 1979, Lowen & Dunbar 1994). When home ranges are largely relative to day journey length, not territories but individual patches will be defended depending on the contestability of the patch at which two groups meet. Day journey length and home range size themselves correlate to the biomass of a group and food characteristics, such as its density, quality, and temporal and spatial distribution (Clutton-Brock & Harvey 1977, Harvey & Clutton-Brock 1981, Janson & van Schaik 1988, Wrangham *et al.* 1993, Janson & Goldsmith 1995, Gillespie & Chapman 2001). Because a large patch depletes less fast, day journey length is expected to decrease with patch size. Furthermore, because the animals have more energy and require less time for digestion, the species with the highest quality food is expected to travel the farthest each day. Finally, patchily distributed rare food sources would result in relatively long distances travelled between food sources and a generally large home range.

The levels of contest competition within and between groups affect the affiliative relationships within groups. Cooperation among individuals increases each partner's resource holding potential when contest competition prevails and resources can be shared (Wrangham 1980, Walters & Seyfarth 1987, Scheel & Packer 1991, Hawkes 1992, van Hooff & van Schaik 1992). Such cooperative relationships are often stronger and may require less maintenance if formed between kin than between non-kin.

This difference is reflected in more stable relationships over time and has been explained as a result of inclusive fitness benefits (Hamilton 1964a, 1964b, Trivers 1972). To maintain long-term cooperative relationships, partners often have regular affiliative interactions, such as allogrooming, embracing, and sitting close together (Dunbar 1991). With high levels of inter-group competition we expect strong affiliative relationships within the group to maintain a group-level coalition. Furthermore, if group-level alliances are important, within-group contest competition may be relaxed because the dominants depend on the subordinates to assist in inter-group conflicts (Sterck *et al.* 1997). Not only kinship, but also reciprocity or the pursuit of a common goal can form the basis for cooperation (Harcourt 1989, Noë *et al.* 1991, Noë 1992).

The importance of cooperation in a group may affect dispersal decisions of individuals. Female-biased philopatry is predicted when females depend heavily on cooperation in food competition (Wrangham 1980, van Schaik 1989, Sterck *et al.* 1997). As a result of the importance of cooperation, females may be especially reluctant to migrate when food is contestable. However, dispersal patterns are determined by a multitude of costs and benefits to leaving and staying in an area or social unit (Greenwood 1980, Moore 1988, Clutton-Brock 1989, Isbell & van Vuren 1996, Sterck & Korstjens 2000, Isbell 2004). It is generally assumed that any individual would rather stay in a familiar environment and thus not disperse away from its natal group and/or range. This is especially true if leaving the natal range means immigrating into an unknown area. Moving to or through an unknown area is especially costly if food sources are not easily detected, for example because they are patchily distributed and occur at low densities, and if predation risk depends on knowledge of safe havens. However, inbreeding avoidance or high levels of intra-group food competition may force a female to migrate.

We tested the suggested relationship between diet and social system of three folivores in the Taï National Park. Despite their close relatedness and the fact that they share the same forest areas, there is little overlap in dietary preferences (Bergmann 1998) and social systems (Korstjens 2001, Korstjens *et al.* 2002). We are not trying to fit the different species into different categories of the various models. Rather, we expect them to largely fit into the same general category: low levels of contest competition with an egalitarian type of dominance relationships and weakly defined affiliative relationships among females, leading to the potential for female dispersal. We are interested in testing if current socio-ecological theory is strong enough to predict subtle differences between the social systems of species that are using relatively similar food sources. We will address the following questions:

1. Does the species with more contestable food items have higher levels of agonistic interactions and stronger affiliative or cooperative relationships than the species with less contestable food items?
2. Does the species with more contestable food patches have more inter-group competition over food and stronger group-level cooperation?
3. Does the species with the strongest need for female-female cooperation within the group have a higher degree of female philopatry than the others?

Methods

The study groups

All individuals in the black-and-white and olive colobus study groups were individually recognized. In red colobus, most adults were individually recognized. Data on social behavior was only collected on individuals that were individually recognized. Recognition of individuals was based on characteristics of face, tail, and coloring of skin or fur. Individuals in the study groups were classified into the following age-sex categories: "sub-adults" were slightly smaller than adults and presumably sexually mature. Sub-adult females were nulli-parous, had smaller nipples and, in the case of red colobus, smaller swellings than adult females. Red and olive colobus males were classified as sub-adult as soon as their testes started to descend and for red colobus when their faces started to broaden. Black-and-white colobus sub-adult males were as large as adult females and they produced an incomplete version of the male roar (loud-call). "Adults" were sexually active individuals with fully developed secondary sex characteristics. Throughout the chapter we used the following abbreviations for these age-sex classes: AM = adult male, AF = adult female, SM = sub-adult male, SF = sub-adult female.

Red colobus. The two study-groups of red colobus, Bad1 and Bad2, were followed from 1992–9. Each of these groups consisted of over 90 individuals in 1997. The groups each started to split up into two sister-fractions between 1994–8 (Bshary 1995, van Oirschot 1999, 2000). In June 1999 all groups were counted based on individual recognition of adults and sub-adults (see Table 3.2). The two sister fractions of each group shared the same home range for 2–3 years during and after the splitting process.

Table 3.2. *Summary of social and ecological variables for red colobus (groups Bad1 and Bad2), black-and-white colobus (groups Pol1 and Pol3), and olive colobus (Ver1 and Ver3)*

	Bad1[a]	Bad2[a]	Pol1	Pol3	Ver1	Ver3
Group size[a]	A 41[b] B 64[b]	A 60[b] B 44[b]	12–16	16–18	3–7	3–4
Adults: [a] males/females	A 6/14[b] B 15/22[b]	A 12/22[b] B 9/15[b]	1–2/4–6	1/6	1–2/1–3	1/1–2
% Fruit average[c]	29.7 ± 13.31	29.7 ± 19.1	45.1 ± 27.5	–	7.5 ± 7.2	–
Monthly averages	16.7, 36.9, 31.3	21.6, 40.1, 24.7	37.2, 48.4	8.1	7.5	17.0
Yearly averages	36.1, 32.5	21.6, 40.1, 24.7	46.6, 49.9	–	8.6	–
Tree size median	55	51	44	56	10	44
Tree biomass[d]	5197 ± 2771	6735 ± 2201	2530 ± 1262	5897 ± 2375	6440 ± 2344	5299 ± 2938
Yearly HR size[e] average ± SD	65.7 ± 8.5	50.3 ± 5.8	83.3 ± 10.5	71.5 ± 4.9	53.5 ± 4.9	57.7 ± 7.1
DJL average ± SD *(# days)*[f]	922 ± 214 *(16)*	822 ± 235 *(54)*	677 ± 216 *(54)*	637 ± 2.5 *(25)*	1202 ± 297 *(12)*	1222 ± 589 *(7)*
Rodman & Mitani Index D[g]	1.01	1.03	0.71	0.65	1.46	1.43
HR overlap ± SD[h] (% of HR size)	5.7 ± 2.1	7.0 ± 3.6	20.5 ± 12.0	21.5 ± 7.8	14.0 ± 5.7	14.0 ± 8.5

[a] For Bad1 and Bad2 we provide the values for the two sister groups (A = group A and B = group B) separately if data were collected for the groups separately.

[b] In June 1999 we individually distinguished all adult and sub-adult individuals per group, we added an estimate of the number of immatures per group based on the average number of females with infant or juvenile in each group.

[c] Average percentage of fruit in the diet was calculated in multiple ways since we had several years of data. The top values give the annual monthly average. It was calculated by first taking the average per month of the values from 1996, 1997, and 1998. Then the average and standard deviation of these average months was calculated and presented. The second value provides the monthly average of each year in which data were collected during every month. The third value provides the total percentage of fruits consumed during a particular year for years (1996–8 only) in which data were collected during every month.

[d] Monthly average, see Table 3.3 for comments.

[e] HR=Annual home range size was averaged over two years, ± SD.

[f] DJL=average distance travelled from one night's sleeping spot to the next night's sleeping place.

[g] Defensibility index D (Rodman & Mitani index): territory defense is expected when D > 1.

[h] HR overlap: overlap in yearly home ranges of two neighboring groups measured as average ± SD per cent of the home range of study group for two consecutive years.

The smaller sister fractions slowly moved out of the main home-range area. Kin relationships within the study groups were not known.

Black-and-white colobus. We followed two black-and-white colobus study groups and all individuals in the groups were individually recognized (see Table 3.2). Pol1 was followed from 1992–9 and the mothers of one of the sub-adult females, all juveniles and all infants were known (Korstjens *et al*. 2002). Pol3 was followed from 1998–9 so no kin relationships were known in Pol3 except for mother-infant relationships.

Olive colobus. Four groups, Ver1 to Ver4, were studied: Ver1 from 1994–7; Ver2 (4–7 individuals: one AM and 1–4 AFs) from 1997–9; Ver3 from 1997–9; and Ver4 (4–10 individuals: 2–3 AMs and 2–5 AFs) from 1997–8 (details on group dynamics in Korstjens & Schippers 2003, Korstjens & Noë 2004). Kin relationships were known for mother-infant pairs only.

Group compositions and group sizes of study groups were representative for the population (Galat & Galat-Luong 1985, Korstjens 2001). Study-groups Bad2, Pol1, and Ver1 formed a cluster in the sense that their home ranges overlapped greatly or entirely. Bad1, Pol3, and Ver3 formed a similar cluster in an adjacent area of the study-site. This meant that ecological parameters were completely identical for the members of such clusters and, therefore, any differences in food choice were not a result of differences in availability of food but in species-specific preferences.

Data collection and analyses

Most data were collected during day-follows from 7:00–17:30 hrs. The same methods were used for all species (following Altmann 1974, Martin & Bateson 1993) unless mentioned otherwise. Data that were collected by various observers are used only when inter-observer reliability was at least 90 per cent (for details on number of observers for different data sets see Korstjens 2001 and references cited with results). Dietary and behavioral data were collected from adult and sub-adult individuals using scan sampling, focal sampling and ad libitum sampling. Throughout the day we collected ad libitum data on social interactions within and between groups.

Scan samples were taken every hour and lasted for a maximum of 25 minutes. The observer assured that no single individual was sampled twice using individual recognition and location in the group. For each scanned individual observers noted: age-sex class, identity, activity (lasting for at least 5 seconds), item consumed, diameter at breast height (DBH) if not feeding in a liana, and species of the tree or liana in which the animal fed (if applicable), and number, sex, and distance to neighbors.

Scan samples were used to determine diets, food tree size, and proximity to neighbors.

The diet is expressed as the percentage of scans in which a certain food item was consumed. Food items were categorized as: fruits, leaves, flowers, insects, or termite matter. Termite matter consisted of termite earth and/or termites. The category "fruits" contains all fruits, irrespective of whether fruit pulp, whole fruits or only seeds were consumed. Food tree size is obtained from the median of the DBH of trees used during scan samples. A "neighbor" was an adult or sub-adult individual located within two meters of the scanned individual. The time spent with neighbors was defined as the percentage of scans of a certain individual in which it had at least one neighbor. Wilcoxon matched pairs signed ranks tests and Mann Whitney U tests were performed using scans from individually recognized animals only, with the individual animal as the sampling unit. The neighbor data are presented in two ways: (1) as the percentage of the total number of scan samples of an individual in which it had a neighbor (the uncorrected percentage); and (2) as this percentage corrected for the sex ratio in the group (the corrected percentage). The corrected percentage was calculated by multiplying the uncorrected percentage of scans spent with a female neighbor by the sex ratio in the study-group: 0.5 for Bad2A, 0.17 for Pol1 and 0.5 for Ver1. Only data of A. H. Korstjens (AHK) on red and black-and-white colobus were used for statistical tests (AHK did not collect these data on olive colobus). The neighbor scans presented for Ver1 were collected by F. Bélé, who had been trained by AHK for this type of data collection.

Focal animal samples were collected on individually recognized females and lasted from three to ten minutes. Consecutive focal samples of the same individual were separated by at least one hour. The number of focals was distributed approximately equally among individuals (Korstjens 2001). During a focal animal sample all social interactions involving the focal individual were recorded continuously. We collected 21.3 hours of focal observations on 16 females of Bad2A and 129.9 hours of focal observation on 9 females of Pol1 between 1997 and 1998. No focal data of olive colobus were used because there were many different observers who did not always use the same protocols. Focals were used for calculating rates of social interactions as well as handling time and food patch residence time.

For calculating handling time of food items, we recorded the number of times per minute that an individual moved its arm in order to pick a food item during each focal sample. We used the average value for each focal sample as one sampling unit. Mann Whitney U tests were used to compare arm movements between red and black-and-white colobus. These tests were also used to compare arm movements per minute for different food items within the black-and-white colobus sample.

The "food spot residence time" was defined as the number of full minutes with no movements or only movements in which an animal moved with a food item in hand. Some of the food spot residence periods were truncated ("censored" data) when the focal ended but the individual still fed at the same spot. We used Kaplan Meijer tests of survival, in the loglinear analysis setting (SPSS 7.5 for Windows) to compare food spot residence time between the species.

Rates of agonistic or affiliative interactions were calculated from focal animal samples. During a focal sample, we counted the number of interactions of the focal animal with any other individual that was within two meters distance. Only very few agonistic interactions (threats) occurred at a greater distance. Agonistic interactions included all instances of submissive and/or aggressive behavior. Submission was recorded when one individual yielded to, fled from, or crouched in front of another individual. Aggressive actions included threatening, pushing, biting, hitting, chasing, and stealing food from an individual. Nearly all of the aggressive acts produced a submissive response. When several agonistic or submissive acts occurred in the same context within three minutes of each other, all of the events were considered to be part of a single interaction. When the individual that was approached or attacked was feeding or manipulating a food item, the context was labelled as "food."

For calculating the rate of grooming interactions, we counted the number of grooming bouts per minute focal sampling. A single grooming bout was defined as a series of grooming episodes between the same individuals with interruptions of less than three minutes. When two individuals groomed alternately this was recorded as one interaction for each individual, irrespective of how often the grooming direction switched during the grooming bout. Cooperation among individuals was recorded when two individuals simultaneously threatened or chased a third individual.

Ranging data were derived from hourly samples of the location of the center of mass of the group in relation to a painted grid system with 100 by 100 m cells. The day journey length (DJL) was the summed distances travelled between the hourly data points during the day, plus the distance from the last observation of the day to the first observation on the consecutive day. The home range was the sum of all one hectare cells entered by the groups during the sampling period. The Mitani and Rodman index (Mitani & Rodman 1979) was used to determine whether home range size and day journey length allowed for territory defense. The similar Lowen and Dunbar index (Lowen & Dunbar 1994) requires an estimate of visibility that would differ greatly between the species and between situations and was, therefore, not used here (Korstjens 2001). Ranging data for red colobus were collected in the years before observers noted the identity of the sister groups they followed. As a result data collection was biased towards the larger and more conspicuous fractions.

Inter-group interactions were recorded ad libitum every time that individuals of different conspecific groups approached each other to within 50 meters (the distance over which an observer was likely to notice the presence of neighboring groups, following Oates 1977, Stanford 1991, Steenbeek 1999, Fashing 2001b). Agonistic inter-group encounters were defined as those encounters in which threat displays, aggressive physical contact or chasing occurred between individuals of different groups. This category combines display and aggressive inter-group encounters as defined in Korstjens *et al*. 2005. Non-aggressive inter-group encounters were those in which no obvious interactions occurred between individuals of the different groups.

Food tree density and biomass

Three line transects (north–south) of 1 km long and 25 m wide were laid out through the middle of the home ranges of the two study group clusters. Each transect was divided into quadrants of 25 by 25 m. For every tree (girth >20 cm) or liana (girth of the largest stem >10 cm) in each quadrant the girth at breast height (translated into diameters at breast height, DBH) and species name was recorded. In total 98.5 per cent of the trees and lianas on the two transects were identified at the species level.

A tree or liana was defined as a food-tree when the species made up at least 5 per cent of the feeding scans recorded in a specific calendar month (diet was taken from all scan samples collected between 1996 and 1997). Korstjens (2001) presents more details and slightly different analyses of food biomass.

Spatial distribution of food trees was measured with the coefficient of distribution: CD = variance/mean (following Chapman *et al*. 1995). The CD was calculated per transect for the number of trees per unit. Two consecutive quadrants (i.e. 25 by 50 meters) were taken as one unit. We used two quadrants because the average spread of the colobine groups was >25 m (Korstjens unpubl data). The DBH's of all food-trees were summed as a measurement of food biomass (cm DBH/ha) (see Chapman *et al*. 1995). In the Kruskal-Wallis tests (Siegel & Castellan 1988) on monthly collected variables the months were taken as independent units.

Although monthly values cannot be completely independent this method allowed us to incorporate the great differences between months due to changes in the diets. Furthermore, comparing dietary details between species during matched months allowed us to identify the real differences in food selection between the species because they all had the same food to choose from.

General data analyses

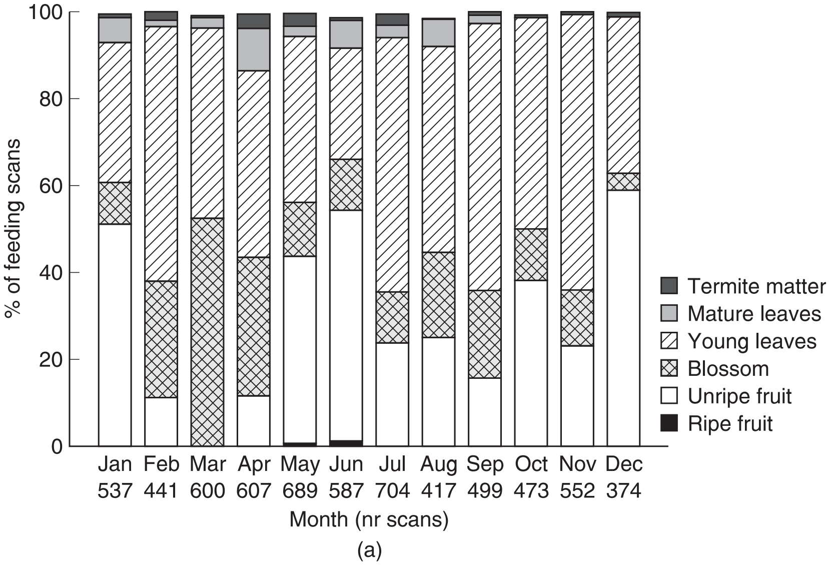
Statistical comparisons between the three colobus species were limited to comparisons within the cluster of Bad2, Pol1, and Ver1. Data on Pol3 and Ver3 were insufficient for statistical comparisons in the Bad1, Pol3, and Ver3 cluster. Non-parametric statistics were used (Siegel & Castellan 1988). All tests were two-tailed and α was set at 0.05. An α'-value was calculated, using a sharper Bonferroni correction (Hochberg 1988) when multiple tests were performed with the same dataset. Statistical tests were conducted with SPSS for Windows.

Results

Contestability of food

All three colobus species consumed mainly unripe fruits and young leaves (diets from January 1996 – April 1998; see Figures 3.1a, 3.1b, and 3.1c; see Table 3.2). Of the three species, olive colobus females consumed the least fruits ($N = 14$ months; Ver1-Bad2: $Z = -3.04$, $p = 0.002$; Ver1-Pol1: $Z = -2.86$, $p = 0.0043$) and red colobus females fed less on fruits than did black-and-white colobus females ($N = 28$ months: $Z = -2.53$, $p = 0.011$). Similar results were found for adult males (Pol1-Bad2: $N = 28$ months, $Z = -2.32$, $p = 0.020$; Pol1-Ver1: $N = 14$ months, $Z = -2.35$, $p = 0.019$; Bad2-Ver1: $N = 14$ months, $Z = -1.60$, $p = 0.109$; see Figure 3.1). Fruit consumed by red and olive colobus consisted mainly of fleshy fruits that were eaten as a whole, while black-and-white colobus more often ate seeds of woody fruits without fruit flesh (tree species lists in Korstjens 2001). Handling time and food spot residence time were significantly longer for black-and-white colobus than for red colobus (Korstjens *et al.* 2002). Such data were not available for olive colobus.

Red colobus selected the largest trees, while olive colobus selected the smallest trees (Mann Whitney U tests: Bad2-Pol1: $Z = -14.6$, $p < 0.0001$; Bad2-Ver1: $Z = -28.9$, $p < 0.0001$; Bad2-Ver1: $Z = -20.6$, $p < 0.0001$; $\alpha' = 0.05$; see Table 3.3). We compared the total biomass per ha (see Table 3.3) and the distribution (measured as coefficient of distribution) of the trees from which each species selected their food using Wilcoxon Signed Ranks Matched Pairs tests that paired matching months



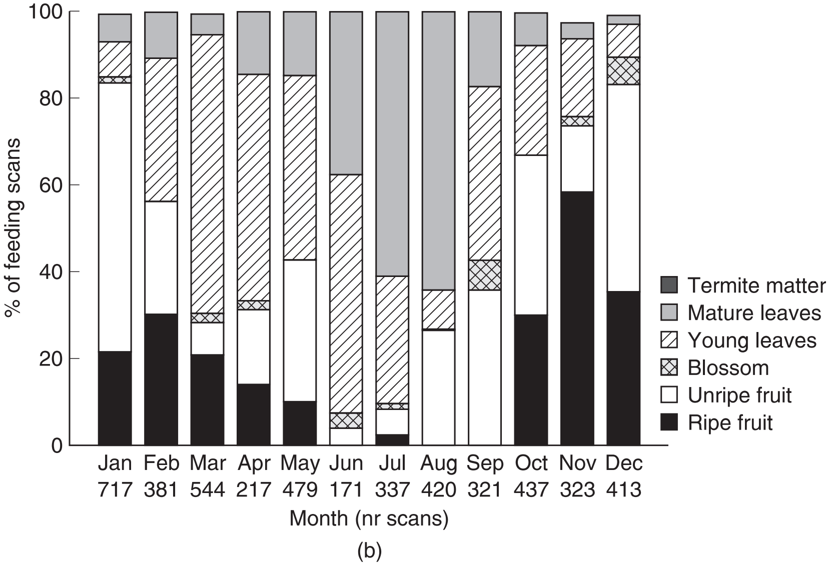


Figure 3.1. Monthly diet of: (a) red colobus; (b) black-and-white colobus.

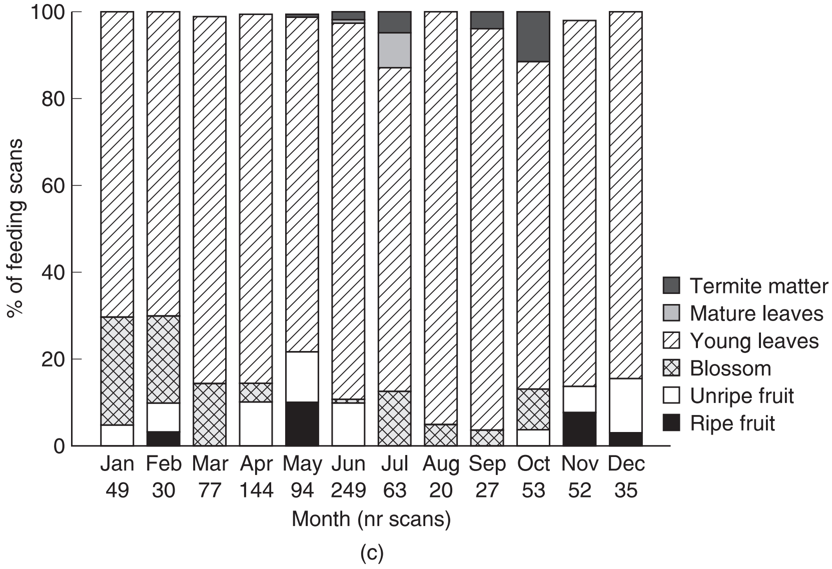


Figure 3.1. The monthly diet, separated into the major food categories, (measured as a percentage of feeding-scans of adults and sub-adults) of red colobus (for Jan 1996–Apr 1998; Figure 3.1a), black-and-white colobus (for Jan 1996–Apr 1998; Figure 3.1b), and olive colobus (for Jun 1996–May 1997; Figure 3.1c); "Termite matter" = material obtained from termite hills and from termite earth attached to tree branches.

together for the three transects combined and dietary data from 1996 to 1997 (maximum 24 months). Olive colobus and red colobus selected food from more abundant food sources (i.e. number of trees per ha) than black-and-white colobus (Bad2-Pol1: $N = 23$ months, $Z = -3.7$, $p = 0.0002$; Pol1-Ver1: $N = 17$ months, $Z = -3.6$, $p = 0.0004$; Bad2-Ver1: $N = 17$ months, $Z = -2.4$, $p = 0.017$; $\alpha' = 0.025$). Similarly, the biomass of food sources selected by red and olive colobus differed little but was higher than that for the black-and-white colobus (Bad2-Pol1: $N = 23$ months, $Z = -4.2$, $p < 0.0001$; Pol1-Ver1: $N = 17$ months, $Z = -3.6$, $p = 0.0004$; Bad2-Ver1: $N = 17$ months, $Z = -0.02$, $p = 0.98$; $\alpha' = 0.025$; see Figure 3.2). These results are the same if we use the trees that represented at least 10 per cent of the diet except that the biomass did not differ significantly between red and black-and-white colobus ($p = 0.09$). Note that the biomass of 5 and 10 per cent trees in the annual diet is higher for black-and-white colobus groups than for red colobus groups while this is not true for the monthly averages. This is the result of a more diverse diet for red colobus, e.g. red colobus consumed food from 77 tree/liana species while black-and-white colobus consumed food from 51 species

Table 3.3. *The diameter (DBH in cm) of food trees and the biomass of food trees used by the study groups (cm DBH/ha)*

					Food biomass (cm DBH/ha)			
	Food tree size				Monthly average		Annual diet	
Group	N	25%	Median	75%	5%	10%	5% trees	10% trees
Bad1	3535	44	55	71	5197	3469	4838; 4942	2798; 2798[a]
Bad2	2997	41	51	71	6735	3375	3266; 4063	2798; 2798[a]
Pol1	2390	23	44	69	2530	1858	5403; 6921	1521; 1748
(Pol3	274	45	56	117	5897	2866	4475	2798)
Ver1	430	6	10	21	6440	4227	6570; 5611	6570; 4098
(Ver3	59	36	44	58	5299	2314	5589; 2226	4311; 798)

The median and quartiles of the size of food trees selected by the three species were obtained from all scan samples (N = number of scans) in which the DBH of the tree was measured. Data stem from scan data collected in 1996 and 1997 for Bad1, Bad2, Pol1, and Ver1, in some months of 1997 and 1998 for Ver3 and March–December 1998 for Pol3. Tree biomass is given for two consecutive years of dietary data. Tree biomass was measured as the summed cm DBH per ha for all trees that represented either ≥ 5 per cent or ≥10 per cent of the annual diet. Data for Pol3, Ver3, and Ver1 are to be considered preliminary due to the small sample of dietary data. Bad = red colobus, Pol = black-and-white colobus, Ver = olive colobus, the numbers refer to the different study groups

[a] The biomass for the 10 per cent trees are the same for both red colobus groups in both years because only the tree species *Scytopetaleum tieghemii* occurred more than 10 per cent of the time in all situations in the annual diet

in the 1996 annual diet. This means that red colobus had fewer tree species that represented > 5 or > 10 per cent of their annual diet than did black-and-white colobus. The differences between the primates in the index of dispersion were less straightforward (see Figure 3.3). Further studies should be performed using a larger set of transects to conclude anything about the differences in the patchiness of food. The variation between months in the abundance of food trees tended to be higher for black-and-white colobus than for red colobus (Kremer 1999, Korstjens 2001 pp. 86–118). The results for olive colobus need to be considered with caution due to the small sample sizes for monthly diet.

Thus, based on the percentage of fruits, handling time, food spot residence time, and food density, black-and-white colobus food was more contestable than that of red and olive colobus at both the within- and between-group level. Considering the higher percentage of fruit in the red colobus diet their food may be slightly more contestable than olive colobus food. Both the percentage of fruits and the abundance and size of food

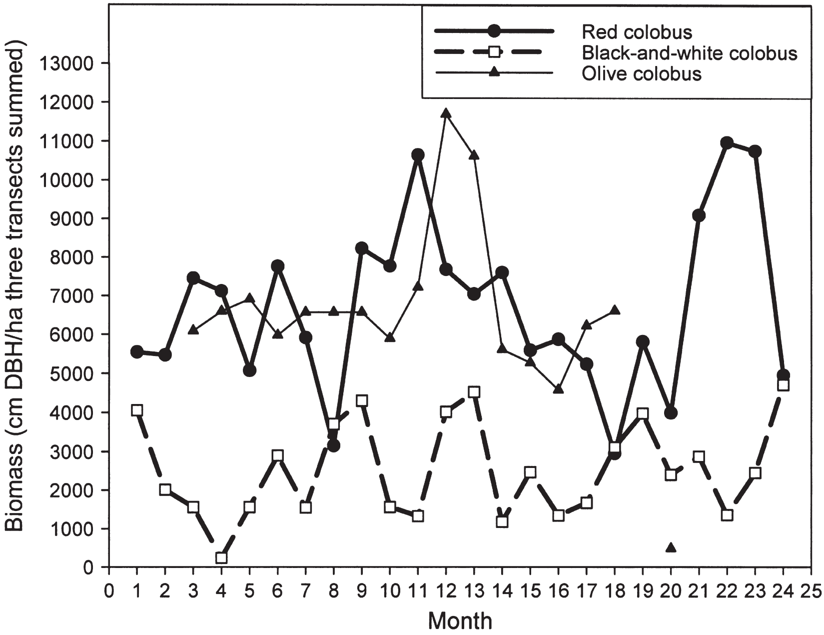


Figure 3.2. Biomass of food trees and lianas (cm DBH/ha) that occurred for at least 5 per cent of the monthly diet for the three primate species, values represent the sum of the three transects plotted against the months between January 1996 (1) through December 1997 (24) for the study groups Bad2, Pol1, and Ver1.

sources suggest that at the between-group level olive colobus' food might be less contestable than red colobus food.

Intra-group food competition

Indirect competition can be measured from the relationship between group size and the distance a group travels per day (DJL) or the size of the area (home range = HR) that the species uses. The black-and-white colobus study groups had the largest HR and shortest DJL of the three species. Red colobus had relatively small HR and intermediately long DJL. Olive colobus HR were slightly larger than those of the red colobus and DJL was the longest of the three species (see Table 3.2). The DJL and the HR of the olive colobus were almost entirely determined by those of the Diana monkey group with which the olive colobus travel. Therefore, DJL differences suggest that indirect competition is slightly more influential in the large red colobus group than in the black-and-white colobus group. Black-and-white colobus, however, required a larger HR per individual than red colobus. The dependence of black-and-white colobus on less

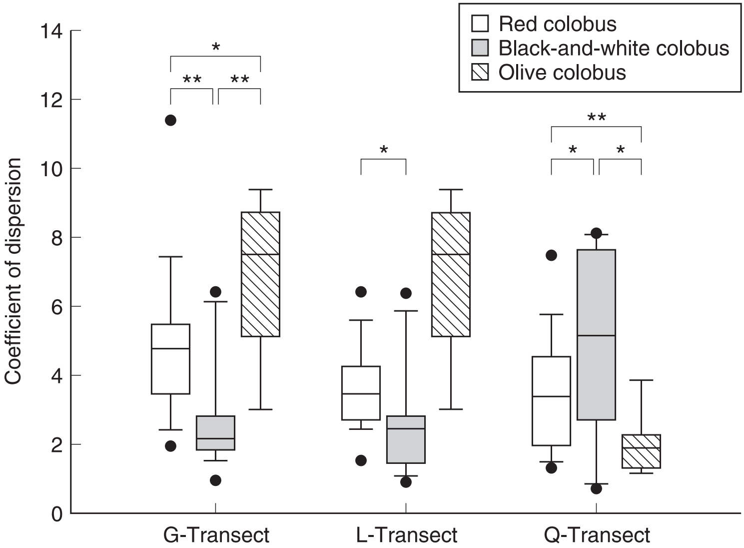


Figure 3.3. Summary of the coefficient of dispersion of the number of trees per 25 by 50 m section of the three transect lines for monthly values (taken from the 1996–1997 diets) of trees and lianas that represented at least 5 per cent of the monthly diet; a CD of 1 indicates a random distribution, CD > 1 indicates a clumped distribution, and a CD < 1 indicates an equal distribution (line through the boxes is the median, boxes represent the 25 and 75 percentiles and the dots depict the 5 per cent and 95 per cent percentiles) for the study groups from cluster 1 (uncorrected p-values from Wilcoxon matched pairs tests are depicted; $^{*}p < 0.05$ level, $^{**}p < 0.01$).

abundant and seasonally more variable food sources than those of red colobus, explains this discrepancy.

As predicted, agonistic interactions among red colobus females, rate 0.19 interactions/focal observation hour (21.3 hours), and among olive colobus females, n = 5 in 250 ad libitum observation hours (Deschner 1996) and N = 2 in 162 ad libitum observation hours (Krebs 1998) were less common than those among black-and-white colobus females, rate 0.60 interactions/focal observation hour (data from AHK, 21.7 hours; for combined E. C. Nijssen [ECN] and AHK dataset the value is 0.84 over 129.9 focal hours). In each species agonistic interactions among females were especially frequent during feeding (focal and ad libitum observations combined): in red colobus 5 of the 8 agonistic interactions and in black-and-white colobus 107 of 176 interactions concerned food (data of ECN & AHK). In olive colobus for all agonistic interactions by males and females combined: 14 out of 18 and 5 out of 8 agonistic interactions concerned food (Deschner 1996, Krebs 1998).

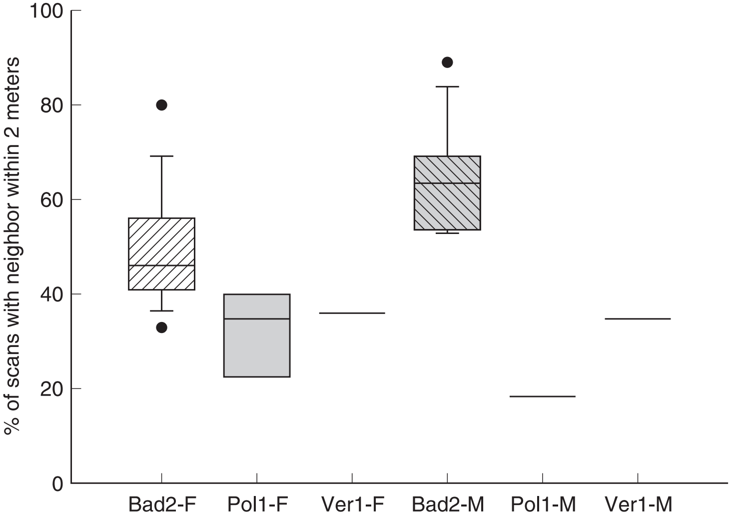


Figure 3.4. The percentage of scans that individuals spent with an adult or subadult neighbor of any sex; boxplots represent the quartiles (25 & 75 per cent) and the dots are outliers; red colobus data from 15 females (Bad2-F) and 14 males (Bad2-M), black-and-white colobus data from 6 females (Pol1-F) and 1 male (Pol1-M), olive colobus data from 2 females (Ver1-F) and 1 male (Ver1-M).

In black-and-white colobus agonistic interactions occurred more often when females fed on items that required long handling times and for which food spot residence time was long, namely seeds, than when they fed on soft fruits or on leaves for which handling time and food spot residence time was short (Korstjens *et al.* 2002). Thus, the differences in contest competition can be explained by differences in food choice: the more patchily distributed food items (fruits) with longer handling time (seeds) evoked the strongest contest competition.

Intra-group affiliation

The higher levels of food competition within and between groups in black-and-white colobus compared to red and olive colobus leads to the prediction that there are higher levels of within-group cooperation and affiliation among black-and-white colobus females than red and olive colobus females. Compared to black-and-white colobus females (N = 6), red colobus females (N = 15) spent a higher percentage of scans with a neighbor (adult or sub-adult) but an equal percentage with a female neighbor (Mann Whitney U tests: unsexed neighbor: U = 10, p = 0.006; male neighbor: U = 4, p = 0.001; female neighbor: U = 38, p = 0.56; see Figures 3.4 and 3.5). Red colobus females spent as much absolute

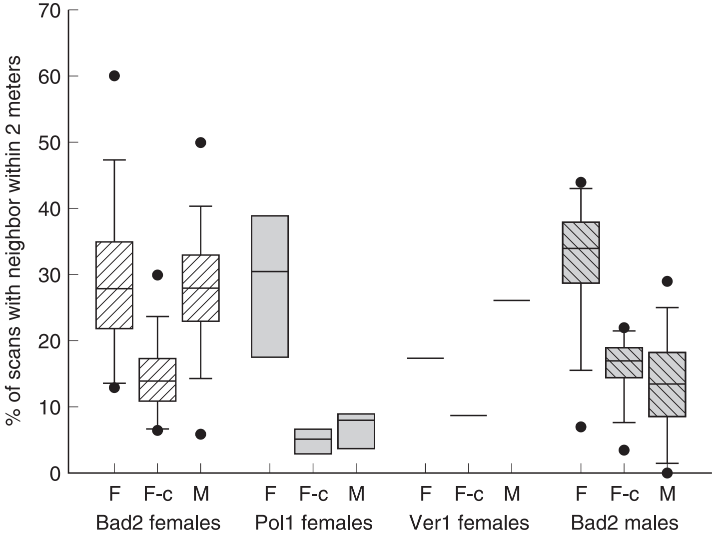


Figure 3.5. The percentage of scans that individuals spent with an adult or sub-adult female (F = uncorrected per cent, F-c = corrected per cent) or male (M) neighbor; boxplots represent the quartiles (25 and 75 per cent) and the dots are outliers; red colobus data from 15 females (Bad2 females) and 14 males (Bad2 males), black-and-white colobus data from 6 females (Pol1 females), olive colobus data from 2 females (Ver1 females), black-and-white and olive colobus males are not depicted because there was only 1 per group, thus, the time spent with a neighbor of any sex (Figure 3.4) corresponds to the time spent with females.

time with males as with females (Wilcoxon matched pair signed ranks test, $Z = -0.126$, $p = 0.90$) but less time with females if we corrected for group composition ($Z = -2.954$, $p = 0.003$; $\alpha' = 0.025$; Figure 3.5). Red colobus males spent more time near others than did females ($N = 14$; unsexed neighbor: $U = 31$, $p = 0.0013$; male neighbor: $U = 21$, $p = 0.0002$; female neighbor: $U = 66$, $p = 0.092$; see Figures 3.4 and 3.5). Red colobus males spent slightly more time with females than with males if we corrected for group composition (uncorrected: $Z = -1.014$, $p = 0.310$, corrected: $Z = -2.971$, $p = 0.003$; see Figure 3.5). Black-and-white colobus females spent more time with females than with the male if we did not correct for group composition ($N = 6$; uncorrected percentages: $Z = -2.00$, $p = 0.046$; corrected percentages: $Z = -0.54$, $p = 0.6$; Figures 3.4 and 3.5). Similar results were found when we investigated grooming interactions (Korstjens 2001, Korstjens *et al.* 2002). In olive colobus groups the male spent more time with others (Figure 3.4) and he groomed other adults more than he did the females (Deschner 1996, Deffernez 1999, Schippers 1999, Krebs 1998). The number of females in Ver1 ($N = 2$)

was too low for statistical comparisons of olive colobus with the other two species.

A coalition was formed in one of the eight agonistic interactions observed among red colobus females. A male supported another male in 13 of 100 agonistic interactions in which a male had a dispute with a female or another male of the group. We never observed a male to support an adult that was under attack. Rather, they always supported the attacker in an intra-group dispute. In 176 agonistic interactions among black-and-white colobus females we observed no coalitions. The only supportive behavior we saw was when a daughter aided her mother by carrying away an infant sibling during a sexual dispute between the mother and the adult male. In nine agonistic intra-group interactions among olive colobus, individuals were never seen to form a coalition.

Affiliative relationships among females and the tendency to form coalitions appeared weak in all three species. This was predicted for red and olive colobus. Black-and-white colobus females may be relatively unsocial despite high levels of contest competition because the most contestable food item (seeds) was not shareable. An individual could take over 15 minutes to open one pod, which it did not then share voluntarily with another individual.

Cooperation against intruders

Several types of intruders were recorded: conspecifics of another group, individuals of other primates species, human observers and predators. Due to the descriptive quality of the data on intruder defense we lumped data for different intruder types together in the descriptions below.

Red colobus males cooperatively attacked, mobbed or threatened intruders. Cooperation among males was often preceded by an embracing ritual that resembled a mount. It never occurred among females or between males and females. A similar ritualistic embrace or mount was described for Eastern red colobus (Struhsaker 1975). Red colobus females gave alarm calls but did not attack or form coalitions against intruders. R. Bshary and B. Beerlage performed two experiments in which the study groups (each group was tried once) were presented with an eagle dummy. Males attacked the dummy in twos or threes after elaborate embracing. During the experiments the females rarely entered the tree that contained the dummy. In black-and-white colobus females and males jointly threatened, mobbed, and alarm called when threatened by humans or predators but only males attacked such intruders. In olive colobus groups, males would face intruders and females would hide away (generally out of sight in large tall trees). In multi-male groups the males jointly attacked, mobbed or threatened (Schippers 1999, Korstjens & Noë 2004).

Inter-group food competition

Based on the contestability of food sources, black-and-white colobus females were predicted to compete most strongly and olive colobus least strongly. The Mitani and Rodman indices (Mitani & Rodman 1979) for the three colobus species suggest that olive and red colobus groups, in contrast to black-and-white colobus groups, could defend territories (see Table 3.2). Thus, the combination of food contestability and defensibility of the home range would predict that red and olive colobus *females* do not get involved much in inter-group disputes but red and olive colobus *groups* might defend territories. Black-and-white colobus females, on the other hand, are predicted to compete with females from other groups over individual food sources.

Indeed, concerning territory defense, we found that overlap between two neighboring groups was largest for black-and-white colobus, intermediate for olive colobus and smallest for red colobus (see Table 3.2). Furthermore, red colobus non-sister groups rarely encountered each other: once every 30 days (group Bad1, 122 observation days) and once every 21 days (group Bad2, 63 observation days). Agonistic interactions occurred in 50 per cent (Bad1) and 33 per cent (Bad2) of these encounters. Female red colobus were not observed to threaten members of non-sister groups (Korstjens *et al.* 2002). In black-and-white colobus, inter-group interactions occurred once every five days (99 observation days in 1997–8). Agonistic acts occurred in 76 per cent of encounters between entire groups (N = 83 in 1994–9) and females actively attacked members of conspecific groups in 68 per cent of the 62 agonistic inter-group encounters (Korstjens *et al.* 2002, Korstjens *et al.* 2005). However, when a single male attacked the group only the adult male would chase the intruder away and females ran from this male. Olive colobus inter-group encounters occurred when their partner Diana monkey groups met. During a well-monitored period this entailed an inter-group encounter once every 3 days (Ver3, 36.5 observation days). Females were not observed to attack members of other groups (Korstjens & Schippers 2003, Korstjens & Noë 2004).

Thus, in support of the predictions, red and olive colobus had relatively clearly demarcated territories, which were defended by males but not females. On the other hand, female and male black-and-white colobus defended locations but not territories. Korstjens *et al.* (2005) showed that female aggression was more common during the time that

Pentaclethra macrophylla fruits (that had long handling time) constituted a major portion of the animals' diet. However, clear proof that black-and-white colobus females fought over individual food sources is lacking.

Dispersal

Based on competitive relationships in the groups, we would only predict the strongest reluctance of females to disperse in black-and-white colobus. Furthermore, our black-and-white colobus study groups used the most widely distributed and unpredictable food sources, which suggests that knowledge of the home range was important. The number of males in the groups leads to the prediction that inbreeding avoidance is only a problem for maturing olive and black-and-white colobus females. However, red colobus are known for male philopatry (Struhsaker 1975, Stanford 1998) and potentially, some level of inbreeding could still occur. We predict, therefore, that females of all three species could disperse but that black-and-white colobus females may be least likely to migrate due to a stronger need for cooperation and knowledge of food sources.

Dispersal in red colobus

Dispersal patterns in red colobus were difficult to observe because we could not distinguish between male and female juveniles and we recognized only a few, older juveniles. We observed one female immigrating into Bad1 and one nulliparous female transferring from Bad2A to Bad2B (after the group composition of the sister-groups had become stable). Group membership was relatively stable for breeding females (0 disappearances for 20 well-recognized parous red colobus females between February 1997 and August 1999). The three nulliparous females that were individually recognized disappeared before they reproduced but after they had experienced their first few receptive cycles with sexual swelling (during which they mated with many males). Adult male group membership was stable over long periods of time in red colobus groups, normally only changing due to deaths and new recruitment from the sub-adult age class. One adult red colobus male transferred permanently from Bad3 into Bad1A, at a time when Bad1A had three males left (van Oirschot 1999). Another male of Bad3 joined him in Bad1A during his first two months there before disappearing again. Thus, we could confirm only two immigrations of females and one immigration of a male and suspected three emigrations of nulliparous females. More female immigrations were suspected on the basis of the shyness of several females in the study groups.

In addition, we regularly observed extra-group red colobus individuals either alone or in pairs of flexible composition, but always mingled with black-and-white colobus. Due to the difficulties in determining the sex of these individuals, we followed 12 of them for several days. Of these 12 individuals, three were most likely nulliparous females, eight were sub-adult males (testes were observed), and one was an adult male (December 1996–January 1999). In addition, one solitary juvenile male (recognizable because of a deformity) returned as a sub-adult to his natal group (Bad1) after an exile of about nine months. We saw the extra-group males generally over a period of several months, whereas, extra-group females were encountered only over periods of less than a week. Although this suggests that males migrated more than females, we suspect that these were males that were temporary or permanent exiles from their natal group who were not able to immigrate into a new group. This is supported by the fact that they remained in the area for longer periods of time than females. This scenario is based on the one well-documented case in Taï and observations on other red colobus populations (Struhsaker 1975, Starin 1994, Starin 2001). Not all sub-adult males spent time in exile: at least five natal red colobus males matured in Bad2A (1997–9).

Dispersal in black-and-white colobus

In Pol1, between 1992 and 1999, two parous females immigrated and three of four sub-adult females disappeared in healthy condition simultaneously from the group (Nijssen 1999, Korstjens *et al.* 2002). Support for the possibility that they emigrated rather than fell victim to predators or poachers comes from the intra-group relationships in this group. Aggression within the group was more common during the three months before their disappearance, 1.1 interactions/hour (in 58.6 focal hours), than during the 6 months before that, 0.62 interactions/hour (in 62.5 focal hours), and after their disappearance, 0.34 interactions/hour (in 8.85 focal hours). The three females that disappeared were harassed disproportionately during the period before their disappearance (Nijssen 1999). Two males disappeared simultaneously at the beginning of our study; one was a sub-adult and the other an adult. At least one female bred in the group in which she matured. Coincidentally, this was the female that had immigrated into the group with her mother when she was a juvenile. No males bred in their natal group. Three adult females and the adult male remained in Pol1 throughout the study.

Dispersal in olive colobus

In olive colobus, group composition changed regularly (Krebs 1998, Schippers 1999, Korstjens & Schippers 2003). Olive colobus individuals of all age-sex classes dispersed in groups or alone. Of the 12 observed juveniles at least 11 disappeared or dispersed before reproduction while the twelfth individual was still a juvenile at the end of this study. Olive colobus females seemed to spend only a short period of their breeding life with a particular group. Olive colobus males, on the other hand, seemed to spend most of their reproductive life in one particular group (Korstjens & Schippers 2003, Korstjens & Noë 2004).

Discussion

We investigated the links between the contestability of food and the social organization of three closely related folivorous primate species. The comparison of the species confirmed the idea that the contestability of food can be measured only if we incorporate a complete set of characteristics of the food. Based on differences in the contestability of food we could explain differences in social systems following the general logic of socio-ecological theory. In support of our predictions, contest competition was stronger in black-and-white colobus, who had the most contestable food items, than in red and olive colobus. Indeed, food competition among black-and-white colobus females was highest when they ate their most contestable food item: *Pentaclethra macrophylla* seeds. The seeds of this legume are contestable because they have a high protein to fiber ratio and high oil content (Dasilva 1994, Sicotte & MacIntosh 2004), they require a long processing time (Korstjens *et al*. 2002), and they are relatively few and unevenly distributed within the tree. Furthermore, black-and-white colobus food sources were more contestable than red and olive colobus food sources (based on temporal distribution, abundance, and relative size of trees). In addition, based on the Mitani and Rodman index we predicted that black-and-white colobus would not be able to defend territories. In support of our predictions, females more often interacted aggressively in inter-group encounters in black-and-white colobus than in the other two species but they did not defend territories. Although, red and olive colobus could be considered to be territorial, this territory defense was a male business.

Affiliative relationships among females were weak in all three species although, in support of the predictions, only black-and-white colobus females appeared to not favor males over females for affiliation. Female cooperation in defending food items from other group members did not occur regularly in any of the species. Thus, despite the contestability of black-and-white colobus food items, they did not cooperate to defend them. This is not surprising considering that the most contestable food of black-and-white colobus was not shareable. Black-and-white colobus females did defend food sources as a group. Considering the strong contest competition between females from different groups, socio-ecological theory would predict female philopatry in black-and-white colobus. Although, our observations can only be considered preliminary, at least some female dispersal occurred in all three species (see further discussion below).

Within a group, even if contest competition is low, scramble competition (measured as an increase in DJL and HR with group size) as a result of the mere presence of competitors is still expected to have an effect. Red colobus, with the largest groups, had longer day journey lengths than black-and-white colobus but not a larger home range. We can explain this discrepancy by incorporating the effect of food distribution and density. The relatively rare and unpredictable food sources used by black-and-white colobus require a relatively large annual home range.

Olive colobus had the largest range area per individual group member and travelled the farthest each day, despite having small food sources that occurred at high densities and the smallest groups. The ranging behavior of olive colobus is explained by their constant association with a particular Diana monkey partner group. We suggest that the selective foraging of olive colobus for high quality young leaves from abundantly available small trees, allowed them to keep up with these guenons.

In general, frugivores tend to have longer day journey lengths than folivores as a result of the more patchy and less dense distribution of fruiting trees compared to trees bearing leaves, and the readily digested high energy source that fruits present. In contrast to this pattern, black-and-white colobus had a shorter day journey length than the more folivorous red and olive colobus. To understand this result it is essential to know more about the digestive system of colobines. Colobines digest their food in much the same way as do ruminants and have an enlarged sacculated forestomach for microbial fermentation. This system allows them to get nutrients from leaves and seeds but digestion takes more time than digesting ripe fruits or insects (Kay & Davies 1994, Chivers 1994, Milton 1998). As a result of their gastro-intestinal adaptations, colobines are less able to digest ripe fruits with high sugar contents (Kay & Davies 1994). Therefore, when eating fruits, colobines extract seeds of unripe fruits, consume unripe fleshy fruits or fleshy fruits with low sugar contents. Hence, a higher percentage of fruit in the diet leads to longer daily travel distances (Clutton-Brock & Harvey 1977), unless digestively challenging seeds are consumed from those fruits.

The large number of subspecies and species (further referred to as populations) of red and black-and-white colobus offer an ideal opportunity for inter-population comparisons (Fashing 2007, Korstjens & Dunbar in press). This is not possible for the olive colobus, who is endemic to sub-Saharan West Africa and is becoming very rare. It has been studied at one other site, Sierra Leone, and the results from that study strongly resemble those from this study (Oates 1988, 1994, Oates & Korstjens in press).

African colobine populations vary widely in group size and group compositions, but black-and-white colobus groups are on average smaller than red colobus groups (Oates 1994, Fashing 2007, Korstjens & Dunbar in press). Colobines are typically expected to experience scramble but not contest competition over food within groups because of the generally even distribution of their food (van Schaik 1989). Three studies tested the importance of scramble competition within groups but found no correlation between group size and day journey length (*C. guereza* Fashing 2001a, *P. kirkii* Siex 2003, *P. tephrosceles* Struhsaker & Leland 1987). In unusually large groups, however, scramble competition may become more important (Fashing 2001a, Teichroeb *et al.* 2003). This direct test of intra-group food competition does not incorporate differences in food distribution and density, and such a correction is needed to really know the importance of scramble competition. When correcting for food density, red colobus, *P. tephrosceles*, do appear to experience increased scramble competition with increased group size (Gillespie & Chapman 2001). The generally smaller group sizes in combination with shorter day journey lengths in black-and-white colobus compared to red colobus (Fashing 2007, Korstjens & Dunbar in press) do indicate that red colobus may need to travel further than black-and-white colobus as a result of living in larger groups. In support of the idea that contest competition should be low in African colobines, most researchers report very low levels of aggression among females (Struhsaker & Leland 1979, Dunbar 1987, Fashing 2001a) the presented study on black-and-white colobus at Taï being an exception. We suggested that the high rates of aggression among black-and-white colobus females in Taï (Korstjens 2001, Korstjens *et al.* 2002) are explained by the high percentage of seeds consumed by *C. polykomos* (Korstjens & Galat-Luong in press). If this is true, we would expect the same for black colobus, *C. satanas*, at Douala-Edea, who have an even higher percentage of seeds in their diet (McKey & Waterman 1982).

Affiliative interactions are relatively rare in colobines, but have been studied in greater detail than agonistic interactions. In red colobus, the general trend is relatively little grooming among females: for *P. tephrosceles*, at Kibale and *P. pennantii* at Gbanraun grooming was most common among males, and females were more likely to groom males than other females (Struhsaker 1975, Struhsaker & Leland 1979, Werre 2000);

at Taï, *P. badius badius*, Abuko, *P. badius temminckii*, and Jozani, *P. kirkii*, males rarely groomed each other, and females more readily groomed males than other females (Starin 1991, Korstjens 2001, Korstjens *et al.* 2002, Siex 2003). In Taï, males do, however, associate together and cooperate regularly. Struhsaker and Leland suggested that the strong affiliative relationships among red colobus males were related to male philopatry. In black-and-white colobus the general trend is relatively more grooming among females than between the sexes or among males (Oates 1977, Dasilva 1989, Korstjens 2001, Fashing 2007).

Based on the generally evenly distributed food, socio-ecological theory predicts that females of different groups should rarely get aggressive in colobines. Indeed, in all African colobines studied to date, males are the more active aggressors during inter-group conflicts (reviewed in Fashing 2001b, 2007): in 17 of 18 populations males exhibited inter-group aggression, while 11 had female aggression. When information was available, male aggression was furthermore, more common than female aggression ($N = 6$ populations summarized by Fashing 2007). Females are only regularly involved in inter-group aggression in Abuko, *Procolobus badius temminckii* (Starin 1991), *Colobus polykomos polykomos* in Taï (Korstjens *et al.* 2005), and shamba-dwelling *P. kirkii* on Zanzibar (Siex 2003).

Socio-ecological models have always placed an important link on the connection between female involvement during inter-group aggression, as a sign of strong inter-group food competition, and female bonding. However, recent studies suggest that some of the generalizations need to be reconsidered. Either because males take on the role of food defense (reviewed in Fashing 2001b, 2007) or because strong inter-group contest competition is not associated with female philopatry and strong bonds among females (Starin 1991, Glander 1992, Strier *et al.* 1993, Pope 2000, Koenig 2002, Korstjens *et al.* 2002, Korstjens *et al.* 2005).

Although dispersal patterns have not been studied in many species, red colobus are known for their female-biased dispersal (Struhsaker 1975, Marsh 1979, Starin 1991, Decker 1994). The extra-group red colobus males in some populations do not necessarily indicate male dispersal but could reflect a surplus of males in a male-bonded society. Immigration may be very difficult for these males, and some are known to have returned to their natal group eventually (*P. tephrosceles*: Struhsaker 1975, *P. temminckii*: Starin 1994). The most intriguing exception is the *P. kirkii* population inhabiting the shambas of Jozani (Zanzibar). They differ from their neighbors in the forest in many aspects of their social organization of which male transfer is just one (Siex & Struhsaker 1999, Siex 2003). In support of socio-ecological theory, this switch to male dispersal may have resulted from the high levels of inter-group aggression among females in the shambas (Siex 2003).

Although males appear to disperse more than females in black-and-white colobus, at least some female dispersal occurs as well (Dasilva 1989, Oates 1994, Korstjens *et al.* 2002, 2005, Sicotte & MacIntosh 2004, Fashing 2007). The three females that disappeared from our study group would have benefited from emigrating through inbreeding avoidance. As predicted on the basis of their need for cooperation at the group level and the unpredictability of their food, these females seemed reluctant to leave (as measured from the increase in aggression they received before their disappearance).

In olive colobus, females and males appeared to leave quite readily and regularly even after breeding in a group (Oates 1994, Korstjens & Schippers 2003). Although the low contestability of their food, the high availability of food in the area and their ability to remain in poly-specific associations during transfer suggest that the costs of dispersal are relatively low, individuals would still need to benefit from dispersal. Korstjens and Schippers (2003) showed a preference of females for small groups, but further study is needed. Thus, in general, African colobines support the idea that a lack of contestable food allows for female dispersal.

We showed how small scale differences in the contestability of food can explain large scale differences in social organization as long as contestability is measured at various levels. The simple dichotomy between fruits and leaves is not sufficient to classify food items as contestable or not. Furthermore, it is not just differences in dietary items but also in digestive adaptations that need to be considered when testing socio-ecological theory. To determine whether food will evoke contest or scramble competition it is essential to have an independent measure of the contestability of food. Appropriate measures are handling time of food items and food patch residence time (Isbell 1991) in combination with food distribution and density (Gillespie & Chapman 2001). Furthermore, we emphasize that the differences between species should be seen as occurring on a continuum, not in classes. Lastly, future socio-ecological considerations need to incorporate the costs and benefits of dispersal that are not related to food competition (Strier 1999, Isbell & Young 2002, Isbell 2004) without ignoring the strong empirical support for the general logic behind the relationships between food traits and social organizations.

Conclusion

1. Intra-group contest competition over food was highest in black-and-white colobus. This was also the species that selected the most contestable food items as measured from handling time, food spot residence time, percentage fruit in the diet, and food density. Thus, our results support the notion that contestable food items evoke contest competition in groups.
2. The most frugivorous of the species, the black-and-white colobus, used less abundant and more variable food sources than the more folivorous red and olive colobus. As predicted based on their food distribution and density, but not on the relative size of their group, the black-and-white colobus had the largest home range. The relatively short day journey lengths for black-and-white colobus could be explained by their group size and food choice if we consider that the seeds they consumed required long processing and digesting times. The relatively long day journey lengths for the olive colobus were explained by their permanent membership in a poly-specific group that contains the frugivorous Diana monkeys.
3. Intra-group ties were not very strong in any of the species. Dispersal costs appeared highest for black-and-white colobus based on their higher levels of contest competition between groups and their use of less predictable food sources. Still, females seemed to disperse at least occasionally in red and black-and-white colobus, and regularly in olive colobus. This supports the idea that females have weak affiliative relationships and may disperse when food competition is relatively relaxed. The exception may be the occasional dispersal of black-and-white colobus females despite strong inter-group contest competition that requires cooperation at the group-level.

Acknowledgments

We thank T. Deschner, A. Schaaff, A. Moresco, J. Béné, A. Bitty, S. Kruppa, and especially C. Kremer and the Taï Monkey Project field assistants for their help in the data collection. The research was financially supported by the Max-Planck Institut für Verhaltensphysiologie, the Deutsche Forschungsgemeinschaft, the University of Utrecht, the Lucie Burgers Foundation for Comparative Behaviour Research, the Dr. J. L. Dobberke Foundation, and the Dr. Christine Buisman Foundation. A. H. Korstjens thanks E. H. M. Sterck and H. de Vries for their support and advice on many occasions. A. H. Korstjens extends special thanks to Jan van Hooff, who has been an enormous source of inspiration and support throughout her career.

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4 *The structure of social relationships among sooty mangabeys in Taï*

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Introduction

Living in groups has both advantages and disadvantages. Being in a social group may decrease vulnerability to predation or increase acquisition of certain resources, but it may also increase intra-group competition for food, mates, and sleeping sites and lead to a higher risk of disease or infanticide (reviewed in Krebs & Davies 1993). The optimal size and structure of social groups is generally thought to be a balance between the costs and benefits associated with sociality.

The evolution of sociality may be directly relevant to the evolution of cognitive skills. Recent research suggests that the primate brain evolved as an adaptation to cope with the social complexity that results from competition within a framework of kinship networks, friendships, dominance hierarchies, and triadic alliances (the ‘‘social brain hypothesis’’). As group size increases, the number of triadic relations explodes and the need for triadic knowledge to choose the best behavioral strategies places high demands on individuals, which could in itself offer an explanation for the large primate brain (Seyfarth & Cheney 2001).

Sooty mangabeys live in large groups (over 100 animals), are terrestrial and forest dwelling and form-differentiated relationships among group members. All of these features make them ideal subjects with which to test the ‘‘social brain’’ hypothesis. However, before we consider the social intelligence of sooty mangabeys, we need to understand how dominance rank, competition, affiliation, and migration shape the pattern of interactions among females and males. In this chapter, we present the first results of our work on the social system of sooty mangabeys in their natural environment. These results form the basis for our further research on cognitive skills in this species.

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

Hypotheses and predictions

1. Several observations of sooty mangabeys in Taï, and of other *Cercocebus* species at the Tana River and in Cameroon suggest that female mangabeys are philopatric, whereas males leave their natal group and immigrate into new groups (Homewood 1976, Mitani 1989, Range & Noë 2002). As a result, when we began our study we predicted that mangabey females would be closely related to each other, and that mangabey social structure would be organized around a number of ranked matrilines as reported for other related species with the same migration patterns (e.g. baboons, vervets).
2. We examined whether sooty mangabeys form defined and unidirectional dominance relationships and if they can be ranked into a linear dominance hierarchy.
3. We assumed that if dominance relationships were established some advantages would be connected to having a high rank in the dominance hierarchy. Females' reproductive success is thought to be mainly limited by food and safety, whereas for males, competition for mates is hypothesized to be the most important factor affecting reproductive success (Trivers 1972). Thus, for the females, we predicted that rank would be correlated with acquisition of food and/or a safe position in the group, while high-ranking males should have better access to receptive females.
4. Finally, based on theoretical considerations and empirical evidence, we predicted that if dominance has an important effect on access to resources, females would form well-differentiated relationships, with preferred female partners as defined by frequent association, grooming, and the formation of alliances. Moreover, females could try to get access to important resources by forming "friendships" with adult males, for example in "exchange" for copulations.

Methods

Claudia Rutte and Ralph Bergmueller started to habituate our study group in 1996. Since then, the group has been under constant observation by at least one observer. After the first year of observation, most animals were well enough habituated that observers could follow them within a distance of five meters, allowing for the collection of detailed data on social behavior. Mangabeys are relatively easy to recognize individually, but their large group size (over 100 animals) and fragmentation into subgroups makes individual recognition difficult and time consuming. All adult animals have been known since 1998; all juveniles and sub-adults since 2001.

Data collection

The group is followed every day from dawn till dusk by at least one observer, who maintains detailed data on demographic events such as births, immigrations, disappearances, and notes the reproductive state of females (sexual swelling or lactating) on a daily basis. Swellings were rated on a four-point scale where 1 was flat and 4 maximum tumescence observed in any female.

Data on social behavior of individuals is collected by focal animal sampling in which an observer follows a selected animal for a certain amount of time and records its activity patterns and all social interactions with other individuals in the group (Altmann 1974). All focal samples are 15 minutes long with at least 60 minutes between consecutive samples of the same individual to ensure that samples are independent from each other.

During sampling we record the activity (see Table 4.1), the position of the focal animal relative to others, and the identity of the nearest adult female and male within five meters of the focal animal every minute [instantaneous sampling (Altmann 1974)]. The focal animal can be in three different kinds of positions relative to other animals. Positions are designated by the presence of other individuals in a circular area with a radius of 10 meters surrounding the focal animal. If there are other individuals on all sides, the focal is in the center position (c), if other individuals are only on one side, the focal is considered to be in a border position (b), whereas if no other group member is within 10 meters, the focal is scored to be in the periphery (p) (Figure 4.1).

If individuals are searching or feeding, we note whether or not they are inside or outside the border of a food patch. We recognize two types of food patches (1) areas of up to 10 meters in diameter on the forest floor with either mushrooms or termites (*Macrotermes spec.*), and (2) larger circular patches of seeds or fruits on the forest floor around the trunks of food trees (radius up to 10 meters).

Social interactions are recorded continuously. For definitions of the behavioral categories see Table 4.1.

When an observer is not occupied with following a certain individual, all observed agonistic interactions, grooming interactions, and copulations between identified individuals are recorded ad libitum (Altmann 1974).

Table 4.1. *Ethogram (Range & Noë 2002)*

Activity	Definition
Maintenance activities	
Feeding	Animal sits or stands at one place and puts objects in its mouth continuously, moving its jaws, emptying its cheek pouches.
Searching	Animal moves slowly forward while visually scanning the forest floor, occasionally putting objects in its mouth.
Travelling	Animal walks steadily forward without visually scanning the forest floor.
Resting	Animal is grooming, playing, sitting, or sleeping.
Social behavior	
Crouch	The belly is close to the ground. The crouch may occur during a severe physical attack, signalling complete submission.
Stare	The actor raises the eyebrows and forehead while staring directly at a target animal; the head can be rapidly lowered and raised while exhibiting the stare.
Stare and lunge	After the stare the actor darts rapidly towards the recipient, but stops before reaching the recipient at which time the actor lowers its shoulders as in preparation to jump forward.
Fighting	Any hard aggressive contact: biting, hitting, gripping, and fighting.
Taking place	The actor takes the place of the recipient after the recipient is threatened or pushed away.
Supplant	The actor approaches another individual who is occupying a resource and replaces that individual without overt aggression.
Grooming	The actor cleans the fur of the recipient with the mouth and/or hands (Altmann 1962).
Invite groom	The actor can use various behaviors to illicit grooming from another individual: the actor presents and/or exposes a part of his body to reactor while standing or sitting stiffly (Hinde & Rowell 1962).
Ventral-hug	The actor approaches a seated animal and lifts its leg onto the shoulder of the seated reactor. It moves its head towards the genital area of the seated reactor.
Hugging	The actor places the arm on the recipient's shoulder. One or both animals may rise onto two legs or remain seated and place both arms around the other's ventrum.
Touch	The actor lightly places one of its hands on the reactor.
Approach	The actor moves into the reactor's space ($r < 2m$).
Agonistic support	An intervention of a third individual in an agonistic dyad on behalf of one individual, directed against its opponent.
Coalition	The combined agonistic interaction of two animals against one opponent.

Data analysis

Dominance relationships

We defined dominance rank according to the direction of supplants for adult males and females. Several measures were used to describe characteristics of the dominance hierarchy, such as the degree

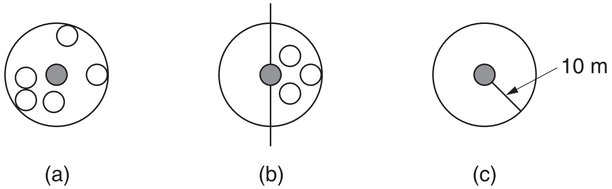

Figure 4.1. Possible positions of a focal animal. The black dot describes the position of the focal animal in relation to other group members of the group. a) center position, b) border position, and c) periphery.

of uni-directionality (van Hooff & Wensing 1987) and the degree of linearity (de Vries 1995). When no clear dominance relationship between two animals could be detected, an average rank was assigned to both of them.

Benefits of high-ranking animals

1. Competition for food

We predicted that high-ranking females would have better access to food patches than low ranking females. Moreover, high-ranking females were expected to be less disturbed than low-ranking individuals during foraging. We quantified the degree of disturbance for each individual with the "foraging efficiency coefficient," defined as the ratio feeding time/searching time (for definitions see Table 4.1). Time in a food patch, as well as feeding and searching time, for each female was defined as the percentages of instantaneous samples during focal animal observation the focal spent within a food patch, feeding, or searching respectively.

2. Competition for safety

We predicted that high-ranking females would more often be in a safe position than would low-ranking females. Safety was measured as a function of the distribution and number of neighbors surrounding the focal animal. The safest position was assumed to be if the focal was in the center of several other animals and thus was "protected" from all sides. The time in the center position for each female was defined as the percentage of instantaneous samples during focal animal observation the focal was surrounded by other animals (c – position).

3. Competition for mates

We predicted that high-ranking males would have better access to estrous females and be able to copulate more often than low-ranking males. Female sooty mangabeys exhibit sexual swellings with peak tumescence indicating ovulation, which we used as measurement for receptivity. We compared the number of copulations with adult females during peak swelling between males of different dominance rank.

Relationship patterns among group members

1. Nearest neighbor analysis

We calculated association indices for individual dyads to analyze proximity among individuals. We predicted that if animals have preferred partners they would spend more time with these individuals than one would expect by chance alone. To calculate the probability of a chance distribution compared to the observed distribution we used permutation tests (for details see Box 4.1). We excluded samples, including grooming interactions from this analysis, which were analyzed separately to test whether differences between close associates and grooming partners existed.

2. Affiliative relationships

We calculated hourly rates of interaction for each dyad by dividing the number of total interactions between A and B by the sum of the total

Box 4.1 Nearest neighbor analysis (Range & Noë 2002)

We calculate association indices using the simple ratio association index: ratio of the number of minutes two individuals are nearest neighbors, divided by the sum of the number of minutes each is observed without the other and the number of minutes they are neighbors (Cairns & Schwager 1987). Association indices can vary from 1 (nearest neighbor present all the time) to 0 (never nearest neighbor). To test whether adult females have preferred companions or if each individual associates with others by chance alone, we use a permutation test in the SOCPROG software. The tests are based on the Monte Carlo procedure and have been modified by Whitehead (Whitehead & Dufault 1999) (software is available at http:/www.dal.ca/~hwhitehe/social.htm). The test compares the observed association indices with the results of a random set of data generated by 20,000 permutations of the original data set. To generate permutations, the total numbers of observations for each individual and the total number of association partners per individual are drawn from the matrix of actual observations. The 20,000 permutations are used as the null-hypothesis against which observed values are tested. We use the mean, the standard deviation, and a p-value to compare the two matrices with each other.

observation time (h) that A and B were observed. The duration of grooming bouts was recorded to the nearest minute during focal sampling. The total amount of time spent grooming was estimated for each dyad as the proportion of all sample intervals during which grooming occurred. Minutes per hour were calculated for each female dyad.

To test whether the distribution of grooming among female sooty mangabeys differed from the expected distribution, we used the permutation test in the SOCPROG software (see Box 4.1).

Statistics

Statistical analyses were performed with the SPSS (Version 7.5.1) statistical program for Windows 2000, SOCPROG (Version 1.3), and with MATMAN (Version 1.0, Noldus Technologies). Spearman's test of correlation between ranks was used to test for a correlation between foraging efficiency and the rank order, between position and rank order as well as number of copulations and rank order. These tests were one-tailed, as the predictions were directional. The results were considered significant when $p < 0.05$. (Alpha was set at 0.05 unless we corrected for multiple tests with the same data set.)

Results

Birth and mating season

During the three years of sooty mangabey observation in the Taï National Park, births were recorded from October through March, with a peak in the months December through February (Figure 4.2). The peak coincides with the dry season in Taï, which starts in the beginning of December and lasts until the end of February. Of the 52 infants that were born during three birth seasons, two infants (3.8 per cent) died within the first month, three others (5.8 per cent) survived for two months only. One infant was neglected by its nulliparous mother. Although the mother still nursed her infant, she ceased carrying it and it was instead carried by sub-adult females. After about two weeks the infant vanished. Another infant died after what seemed to be a disease because no injuries could be detected. Another infant was observed with a large wound on its back the day before it vanished. The distribution of births per female and the seasonality of births, suggest an interbirth interval of approximately 2 years.

In accordance with birth seasonality, we have found that mangabeys in Taï exhibit a mating season beginning in June and lasting till October. The mating season is defined by the occurrence of sexual swellings, which was highly correlated with copulations and mate guarding of adult males.

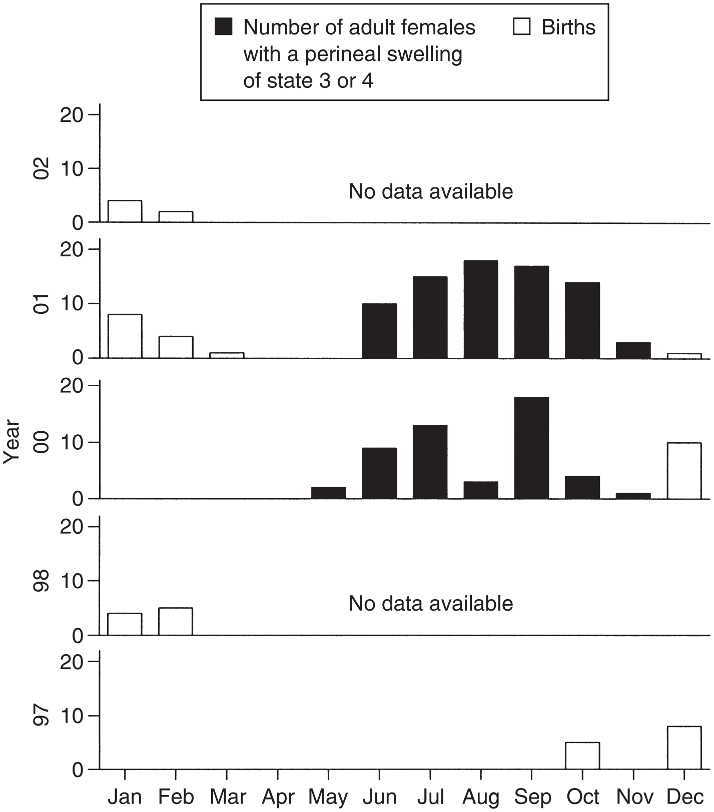

Figure 4.2. Birth and mating seasons of sooty mangabeys. Data were collected from 1997 until 2002 in the Taï National Park. Sexual swellings of adult females can vary between 1 (flat) and 4 (maximal tumescence).

Dispersal patterns and group membership

Dispersal is usually difficult to observe, since we often know only that an animal has vanished, and not where it has gone or whether it is still alive. Moreover, unhabituated animals from other groups are often afraid of human observers and will not transfer into groups where humans are present. In Taï, several groups of mangabeys are used to human observers so migration events can be observed more easily. Several observations suggest that males are the dispersing sex in sooty mangabeys. First, several known sub-adult females (10) have stayed in their natal group and have started to reproduce. Second, nine sub-adult males were observed to transfer into the group, while six males vanished; one of them was seen in another group. We have never observed new females joining the study

Actor (→ ascending dominance)

	Mul	Pis	Ven	Oul	Fal	Fer	Sam	Mar	Sim	Ste	Alf	Total
Mul		2	3	2	2		2	3		1		15
Pis			16	19	21	7	17	10	7	20	18	135
Ven		1		5	8	30	19	23	10	10	12	118
Oul			1		3		12	3	7	8	16	50
Fal						15	16	17	5	10	26	89
Fer			4		1		33	20	8	23	10	99
Sam						2		18	11	10	27	68
Mar						1			15	11	13	40
Sim						1		3		14	20	38
Ste						1					28	29
Alf							1	1				2
Total		3	24	26	35	57	100	98	63	107	170	683

Figure 4.3. Matrix based on 683 interactions among adult males in 2000 and 2001 involving submissive behaviors (avoid and yield) recorded during both focal animal and ad libitum sampling. Individuals are noted by three-letter codes and the order is chosen by minimizing the circular triads.

group, although several old females disappeared. Third, lone males are frequently encountered in the home range of the study group, but never lone females.

Male mangabeys exhibit at least three different patterns of group membership. Some males stayed in the group for long periods of time (>6 months). Other males joined a group for one to four months then vanished for good or at least for several weeks to months. Sometimes these males were subsequently observed in neighboring groups. Finally, other males remained in the group only for a few hours or days and stayed mainly in the periphery. Whereas the third behavior was mainly observed during the mating season, the second was observed all year round. The fluidity of male group membership further supports the hypothesis that male mangabeys transfer between groups.

Dominance hierarchy

Adult males and adult females can be arranged in a linear dominance hierarchy (Figures 4.3 and 4.4). Based on 683 submissive interactions between adult males, we could determine the dominance relationships in 40 of 55 possible adult male dyads (72.73 per cent). For adult females present in 2000 and 2001, we observed 1199 submissive interactions and could define 250 of 300 possible dominance relationships (83.33 per cent). In the female hierarchy one circular triadic relationship (Va-Ti-Bi) was observed (Figure 4.4). Three female dyads (Co-Vi; Ka-Gi; Fu-Di) were

Actor (⟶ ascending dominance)

	Co	Vi	Ro	So	Ka	Gi	Fa	St	Cl	Si	Ol	Po	Va	Ti	Bi	Ma	Lu	Em	Ri	Fu	Di	Hi	Lo	Fe	Sa	Total
Co			3	3	5	7	6	1	2	1	9	5	3	4	9	2	3	8	13	4	4	5	4	3	2	16
Vi			9	18	1	6	6	4	6	12	8	6	1	4	4	5	7	1	2		1	1	1	1	3	17
Ro				1	6	5	3	1	6	2	3	5	5	6	3	2	1	3	2	5		4		1	2	66
So					3	5	1	4	3	4	5	4	1	7	4		4	3	1		1	2	1	2	3	58
Ka			1			1	6	4	6	11	6	6	3	5			3	3	4	1	1	3	2	3	3	72
Gi				1	1		2	6	3	1	2	16	4	1	5	5		1		2	1	6	2		5	64
Fa					1			1	1	5	3	4	1	3	1	1	3	5	6	1	4	2	4			46
St									8	7	3		4	9	2	5		4		1	5	1	5		2	56
Cl		1			1					3	2	3	1			3	1		2	1	1	1	1			21
Si			1	1				1			4	1	3	2	5	1	4	3	1	4	1	1	5		1	39
Ol				1		1				1		9	3	4	2		3	7	1	5	3	5	2	1	1	49
Po														3	6	5	7	5	3	4	1	7	1		6	48
Va				1						1				5	$\underline{1}$	2	3	3	1	3	5	1	5		2	33
Ti															3	1	3	3	5	4	5	4	4	1		33
Bi													$\underline{2}$	1		13	8	4	4	6	3	4	11	4	4	64
Ma																	3	1	5	2	1	4			1	17
Lu																		5	5	5	7	6	5	2	4	39
Em								1											21	12	8	8	9	5	9	73
Ri																				19	9	17	12	4	12	73
Fu																					1	18	15	4	1	39
Di																				1		9	9	4	1	24
Hi																				1			15	6	14	36
Lo																				1				7	14	22
Fe																									14	14
Sa (1.rang)																										
Total		1	14	26	18	25	24	23	35	48	45	59	31	54	45	45	53	59	76	82	62	19	113	48	14	1199

Figure 4.4. Matrix based on 1,199 interactions among adult females present in 2000 and 2001 involving submissive behaviors (avoid and yield) recorded during both focal animal and ad libitum sampling. Individuals are noted by two-letter codes and the order is chosen by minimizing the circular triads. Fe is a subadult female in 2000 but already often involved in agonistic interactions and thus included in this table.

assigned equal rank in this rank order, because no interactions or an equal number of submissive interactions were observed between them.

The degree of uni-directionality of dominance relationships for adult males and females is high ($DC = 0.95$ and $DC = 0.97$ respectively). The degree of linearity is slightly higher in males ($h' = 0.83$) than females ($h' = 0.77$). The probability that the observed linearity results from a random process is $p < 0.001$ for males and females. Relative ranks of at least 14 females were stable from the first study conducted in 1997 till 2001. For the other females, data from the first study were not sufficient to construct a well-defined dominance hierarchy that would allow a comparison between the relative ranks of these females for the entire study periods. For males no comparative data over a longer period of time are currently available.

Benefits of rank

1. Competition for food

Female sooty mangabeys attribute the majority of their time to activities related to foraging – on average over 74 per cent of the observation time.

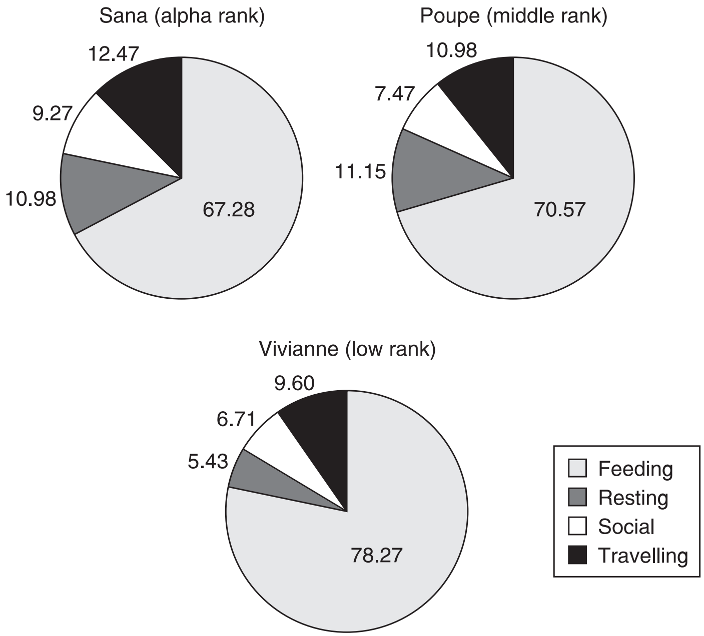

Figure 4.5. Activity budgets of a high, middle, and a low-ranking adult female.

The other time they spend mostly resting and grooming other individuals (Figure 4.5). High-ranking females spend significantly more time in food patches than low-ranking females (Spearman rank correlation: $r_s = -0.6$, $N = 24$, $p < 0.001$). Moreover, the foraging efficiency coefficient (ratio feeding/searching) is correlated with rank (Spearman rank correlation: $r_s = -0.634$, $N = 24$, $p < 0.01$). The highest-ranking females have the highest scores for foraging efficiency (Range & Noë 2002).

2. Competition for safety

High-ranking females spend significantly more time surrounded by other animals than low ranking females (Spearman rank correlation: $r_s = 0.773$, $p < 0.001$) (Figure 4.6). Low ranking individuals are often in a border position or in the periphery.

3. Competition for mates

High-ranking males copulate significantly more often with estrous females (swelling 4) than low ranking males (Spearman rank correlation: $r_s = 0.833$, $p < 0.01$). The male Mul was excluded from this analysis since no data were available for him during the mating season.

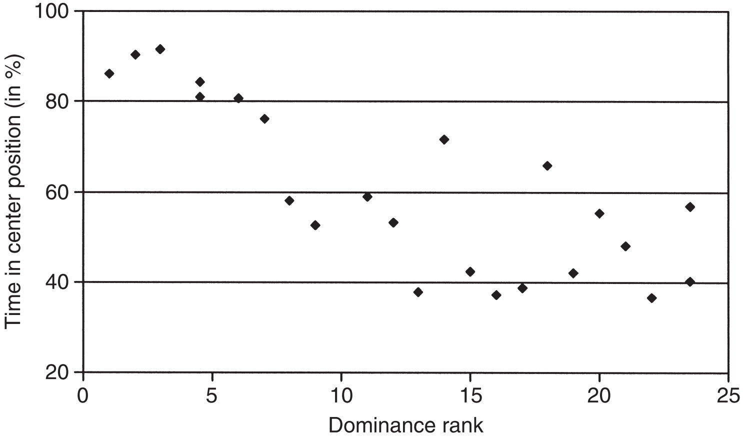

Figure 4.6. Relationship between position and rank. We defined the time in the center position for each female as the percentage of instantaneous samples during focal animal observation the focal was surrounded by other animals. Spearman's rank coefficient: r_s = Spearman's rho = 0.773, $p < 0.001$.

Relationships between group members

1. Nearest neighbor analysis

Figures 4.7 and 4.8 summarize the most frequent associations among adult male and among adult female sooty mangabeys in 2000–2001. Adult males associated mainly with two other partners except the α-male, who associated with four other males. The highest association rate was observed between the α- and β-male (Figure 4.7). Lower-ranking males that showed no high association indices with high-ranking individuals (Ven, Pis, and Mul) were all natal, slightly younger individuals. Fer, who did not associate much with other males either, was a male of type 2 (see above), who joined the group several times for up to two months but in between these stays vanished for weeks at a time.

Adult females exhibit a different association pattern. The seven highest-ranking females associated more often with each other than with any other lower-ranking females in the group (Figure 4.8) (Range & Noë 2002). However, no clear pattern can be observed between middle and low-ranking individuals. Figure 4.9 shows association indices between adult males and females, which indicate that high-ranking males associated mainly with high-ranking females. The α-female had the highest association index with the α-male. However, while the α-male associated as well with other high-ranking females, the α-female had no other

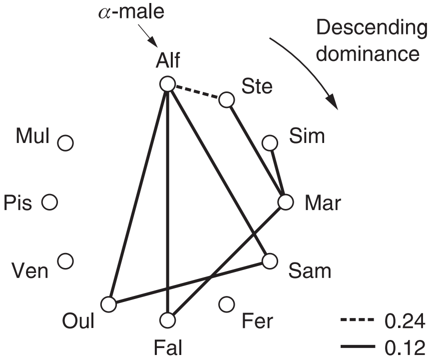

Figure 4.7. Association among adult males. The simple ratio association index was used to calculate associations between two males A and B using frequencies of the total observation time of A and B that A and B were nearest neighbors. Association indices could vary from 1 (nearest neighbor all the time) to 0 (never nearest neighbor). Only association indices, which are higher than 0.10, are represented. Ranks decline in clockwise direction (Alf has the highest rank).

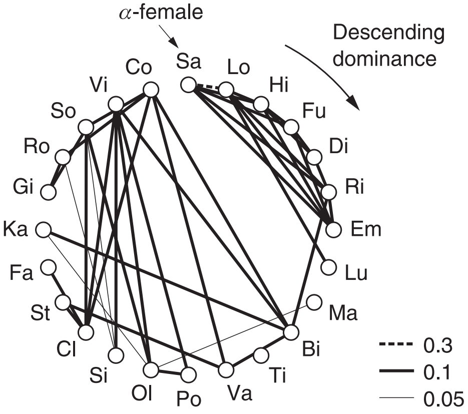

Figure 4.8. Association among adult females. The simple ratio association index was used to calculate associations between two females A and B using frequencies of the total observation time of A and B that A and B were nearest neighbors. Association indices could vary from 1 (nearest neighbor all the time) to 0 (never nearest neighbor). Only association indices, which are higher than 0.05, are represented. Ranks decline in clockwise direction (Sa has the highest rank).

male associates. Several high-ranking females, especially Di and Fu, were frequently observed with different high-ranking males. In contrast to the high-ranking females, hardly any association was observed between low-ranking females and adult males.

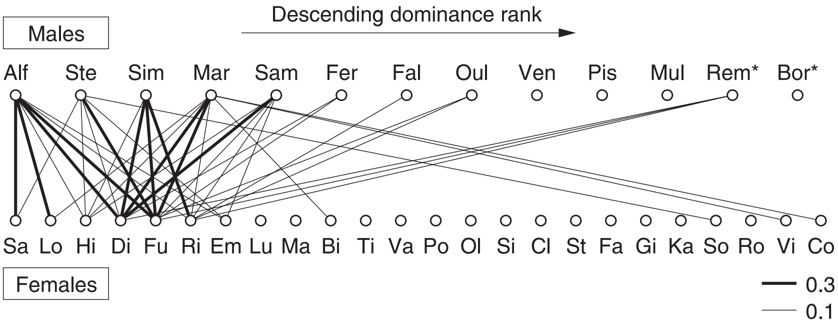

Figure 4.9. Association between adult males and females. Males and females are ordered according to their dominance rank. (*Bor and Rem left the group before their dominance rank could be determined.) The simple ratio association index was used to calculate associations between two individuals, male A and female B using frequencies of the total observation time of A and B that A and B were nearest neighbors. Association indices could vary from 1 (nearest neighbor all the time) to 0 (never nearest neighbor). Only association indices, which are higher than 0.10, are represented.

To test whether these association patterns (**m**ale-**m**ale, **f**emale-**f**emale, and **m**ale-**f**emale) differ significantly from what would be expected if each individual associated with other individuals at random, we generated several random sets of data and conducted permutation tests (see Box 4.1). We found that there were significant differences in the mean association indices for dyads between the observed matrices and the generated matrices (**mm**: 0.07 versus 0.075, $p < 0.000$; **ff**: 0.079 versus 0.081, $p < 0.01$; **mf**: 0.021 versus 0.022, $p < 0.001$), indicating that individual dyads associated less than expected. Moreover, the standard deviation for dyads was significantly lower for the random than for the observed matrices (**mm**: 0.056 versus 0.058, $p < 0.05$; **ff**: 0.035 versus 0.056, $p < 0.001$; **mf**: 0.029 versus 0.036, $p < 0.001$), suggesting that the observed data contain some very high and some very low values. We would expect this result if animals chose to associate with certain individuals, and avoid others.

2. Affiliative relationships among females

Grooming among adult females was not evenly distributed. Most females tended to restrict their grooming to preferred partners. In 2000, 11 females devoted 50 per cent or more of their grooming bouts towards a single female partner. Figure 4.10 summarizes the distribution of grooming among adult females in 2000 (from Range & Noë 2002). We tested if the observed distribution differs significantly from a chance distribution by generating

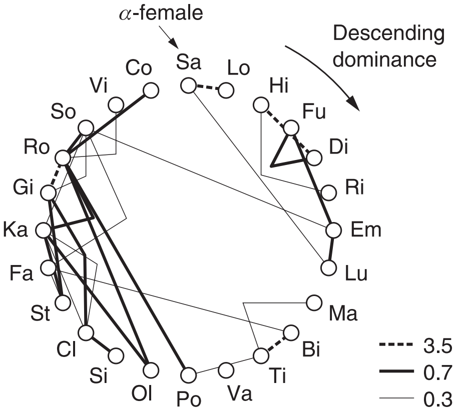

Figure 4.10. Grooming network among adult female sooty mangabeys. Presented here is the grooming duration calculated as rates per hour. Rates lower than 0.3 are not shown. Females are shown in decreasing rank order reading clockwise from the top (Range & Noë 2002).

a random data set as described above and comparing it with the observed grooming matrix (from Range & Noë 2002). We found a significant difference between the mean as well as the variance for dyads between the observed and the generated matrix (mean = 0.024, STD = 0.083 versus mean = 0.23, STD = 0.043; $p < 0.01$) indicating that grooming was not equally distributed among group members. Female sooty mangabeys groomed less than expected (lower mean in observed matrix), but the higher standard deviation in observed matrix compared to the generated matrix suggest that they had preferred female grooming partners.

3. Coalitions among adult females

Forty-six coalitions between adult females were recorded using ad libitum and focal animal data (Figure 4.11). Most coalitions were observed between the eight highest-ranking females, especially between the two highest-ranking females, Sa and Lo. Agonistic support was mainly given from Sa to Lo (six times), while Lo supported Sa only once in a conflict. Interestingly, we observed several coalitions between these two highest-ranking females as early as 1997/98, when Lo was still a sub-adult female suggesting that these two animals are mother and daughter. Another dyad that was observed to support each other in conflicts frequently was Fu and Di. Fu supported Di twice, while Di helped her three times in agonistic encounters. However, it was not clear who is the higher-ranking female in this dyad (see Figure 4.4). Among most other dyads, coalitions were

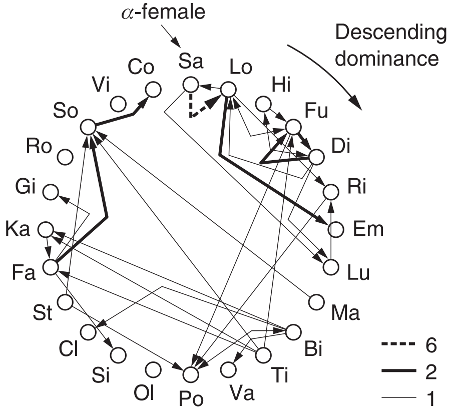

Figure 4.11. Agonistic support given and received among adult female sooty mangabeys. Presented is the total number of agonistic supports for each female recorded during focal and ad libitum sampling in 2000 and 2001.

observed only once or twice. Most agonistic support (37) was given when the receiver was higher-ranking than the supporter.

Discussion

Many species of Old World Monkeys such as baboons, vervets, and macaques show a similar pattern of social organization. In these species, males transfer from their natal groups into new groups, high intra-sexual competition for mates results in linear hierarchies and males often form friendships with adult females. On the other hand, females are philopatric and form well differentiated relationships often based on relatedness. The support of relatives in coalitions usually results in matrilineal-based, stable, and linear dominance hierarchies. The results of our study on the social behavior of sooty mangabeys in their natural environment suggest that they resemble these other old world primate species that live in multi-male multi-female groups.

Seasonality, group membership, and transfer pattern

Our observations of male group transfer support the hypothesis that males are the dispersing sex and that female are philopatric, which is likely to have implications on female relatedness. In theory, females in these groups should be more closely related to each other than males facilitating the formation of a matrilineal-based social system among female sooty mangabeys. However, so far no DNA-analysis has been conducted to test this hypothesis.

Sooty mangabeys in Taï exhibit a mating and birth season, which is likely to have profound consequences on the social behavior of adult males. If estrus in adult females is synchronized it will be impossible for a single high-ranking male to monopolize mating allowing the development of alternative strategies for lower-ranking males. The different types of group memberships that males engage in imply these alternative strategies. Some males stay with a group for long periods of time, form close relationships with females and males, while others join the group for weeks at a time, never fully integrating (no association with other males). And then during the mating season, we observe a third strategy: males only come for hours or days at a time. Interestingly, these "visitors" have been observed to copulate with estrus females that were mate guarded by constant group males. Currently, we are trying to understand the characteristics of these different strategies and the benefits for the males.

Dominance and benefits of rank

We found that all adult females could be ranked in a linear dominance hierarchy that has remained stable for several years. But are there advantages correlated with a high dominance rank? The diet of mangabeys in Taï mainly consists of fruits and seeds (68 per cent) and invertebrates (26 per cent) (Bergmüller 1998). Especially in the summer, the seeds of *Sacoglottis gabonensis* represent the dominant food resource, occurring in large circular patches around trees. These food patches are very large, but still cannot provide space for all group members (~120 animals). Our study showed that high-ranking females are more often in food patches than low-ranking females. Foraging efficiency was also positively correlated with rank (Range & Noë 2002); a further indication that high-ranking females have better access to food resources, which could have consequences for their reproductive success.

Safety from predators has been argued to be an important factor influencing survival in adult females and especially the position within a group has been shown to be an important predictor of predation risk (Ron *et al.* 1996). Predation pressure in Taï is relatively high (Chapters 10 & 11) and both eagles and leopards are known to prey upon mangabeys. Although it is difficult to observe predation events and highly risky to allocate the vanishing of a female to predation, it is theoretically safer in a position surrounded by other animals than being at the border or in the periphery of the group. High-ranking females in our study group were more often surrounded by group members than low-ranking females presumably decreasing their risk of predation.

Adult males form linear dominance hierarchies as well and access to estrous females is rank-dependent. Interestingly, even the male that joined the group only for a few months at a time and was not considered a long-term resident male, had access to estrous females. However, until paternity tests have been conducted it will not be possible to really evaluate the influence of rank on reproductive success in sooty mangabeys. Moreover, more studies have to be conducted to elucidate the role of visiting males and other short-term group members to conclude about costs and benefits of different male strategies.

Affiliative relationships

Female sooty mangabeys had well differentiated social relationships in regard to association, grooming as well as coalition partners. Moreover, we showed in another study that females not only groomed their association partners, but especially females with positions close in rank (Range & Noë 2002) which suggests a matrilineal based social system. However, we cannot test the hypothesis that female bonds are based on relatedness with behavioral data alone, but need to conduct a genetic analysis (currently under way). Theoretically, the observed interaction patterns could be predicted even without underlying nepotistic mechanisms if females were attracted to high-ranking females (Seyfarth 1977), or to females of similar rank (de Waal & Luttrell 1986).

In Taï, association pattern of adult males differed according to their age and the duration of their group memberships. Young males had no close associates among high-ranking males, neither had the male (Fer) who stayed with the group only a limited amount of time. Grooming was never observed between adult males (personal observations) and so far, no detailed data are available on the formation of coalitions among adult males. However, coalitions have been observed frequently especially during the mating season and could explain the association patterns observed among males. Young males leave the group, thus investing in the formation of relationships in their natal group might not be a good strategy, which could explain the absences of associations with high-ranking males. Long-term group members, in contrast, associated with only a few other males indicating differentiated relationships. Further research will elucidate if these associations are correlated with agonistic support in conflicts against other group males or intruders.

High-ranking females associated closely especially with high-ranking males in the group. Grooming and several coalitions have been observed within the same dyads (personal observations). Moreover, adult males often tolerate high-ranking females in food patches, while low-ranking females are chased away (personal observation). "Friendships" with adult males could have several advantages for the adult females, but adult males could also benefit from these relationships if it increases their probability of siring the females' offspring. We are currently studying this hypothesis in Taï.

Current and future research

Research on sooty mangabeys in their natural environment provides us with the background knowledge to investigate questions concerning cognitive skills of sooty mangabeys. To date, several experimental studies show that primates engage in a number of complex interactions that demonstrate an understanding of third-party relationships implying some kind of triadic knowledge. For example, (1) in conflicts with higher-ranking individuals, animals solicit help from group members higher ranking than the opponent (Silk 1992, 1999a), (2) redirect aggression preferentially toward the kin of their former opponent (Cheney & Seyfarth 1986, 1989, Aureli & Schaik 1991a), (3) react differently compared to controls if dominant individuals behave submissively towards lower-ranking individuals (Cheney *et al.* 1995). Evidence from field studies on vervets and baboons and captive studies on macaques suggest that primates understand categories of third-party relationships and that they can make inferences about the behavior of other pairs of individuals (e.g. Cheney & Seyfarth 1980, 1986, 1999, Dasser 1988a, 1988b, Cheney *et al.* 1995, Silk 1999b). Considering the size of our study group (~120 animals) compared to baboons (~80 animals) and vervets (~25 animals), the question of what sooty mangabeys know about each other's dominance and kin relationships becomes intriguing. After all, they would have to know over 180,000 triadic relationships, twice as much as a baboon. Moreover, sooty mangabeys live in a forest habitat, where an animal is hardly ever able to see many interactions between others. Considering these circumstances, it seems an almost impossible task to learn to differentiate relationships between all other group members. Thus, do sooty mangabeys really know all these relations or do they use other, simpler strategies to achieve their goals? Currently, we are investigating this question with observational data such as the pattern of solicitation of agonistic support in conflicts and the pattern of supplant of grooming partners between females. Moreover, we conduct playback experiments to investigate experimentally if sooty mangabeys know third-party relationships.

Conclusions

1. Observations of male group transfer in the absence of female dispersal in Taï imply that female mangabeys are philopatric, whereas males leave their natal group and transfer into new groups.
2. Adult male and female sooty mangabeys form linear dominance hierarchies, based on the direction of approach-retreat interactions. Relative ranks of several females remained stable over the entire study period.
3. Several benefits of high rank have been shown for females as well as for males. High-ranking females have better access to food patches as well as a higher foraging efficiency. Moreover, they occupy more often positions surrounded by other group members, implying lower predation risk. Both access to food as well as to safe positions are thought to be closely linked with reproductive success in primate females. Males' access to estrous females was rank-dependent as well as hinting towards higher reproductive success of high-ranking males compared to low-ranking males.
4. Finally, females and males formed well-differentiated relationships with preferred partners. Females especially had a limited number of partners with whom they frequently associated, groomed, and in conflicts against others supported. Moreover, high-ranking females formed close associations with high-ranking males, however, no data are available yet on the function of the relationships between the sexes.

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II *Anti-predation strategies*

5 Interaction between leopard and monkeys

K. Zuberbühler and D. Jenny

Introduction

Although predation is clearly a crucial factor in the evolution of primates its actual effects as a selective force are not well understood. Predation is thought to have affected various traits such as body size, group size and composition, vigilance, ecological niche, as well as vocal and reproductive behavior (van Schaik 1983, Cheney & Wrangham 1987, Cords 1990, Hill & Dunbar 1998, Stanford 1998, Uster & Zuberbühler 2001). However, there are reasons to remain cautious about many of the proposed relationships. In particular, little is known about the hunting pressure exerted by the various primate predators and the selective pressure they impose on a primate community. Nevertheless, predation is often treated as a homogeneous evolutionary force even though predators differ considerably in their hunting behavior. For instance in the Taï forest, monkeys are hunted by chimpanzees *Pan troglodytes*, crowned eagles *Stephanoaetus coronatus*, and leopards *Panthera pardus*. Predatory chimpanzees locate monkey groups by acoustic cues and hunt for individuals in the high canopy (Boesch & Boesch-Achermann 2000). Not surprisingly, the presence of chimpanzees reliably elicits cryptic behavior in nearby monkeys (Zuberbühler *et al*. 1999). Crowned eagles, in contrast, hunt by sweeping through the canopy to surprise their prey (Gautier-Hion & Tutin 1988, Shultz 2001) and their discovery typically elicits loud and conspicuous alarm calling and sometimes even mobbing behavior (Zuberbühler 2000b). Because they differ fundamentally in their hunting strategies, the selective force of chimpanzees, leopards, and eagles – as predators – is not homogeneous. Predation, in other words, is a heterogeneous selective force.

In this chapter, we review studies on the hunting behavior of the first Taï predator: the leopard. Leopards occur in a wide variety of habitats ranging from open savannah to closed rainforests (Kitchener 1991). To date, most information on leopard ecology and behavior has been

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

Figure 5.1. The adult male Cosmos passing a photo-trap (Photo: D. Jenny).

collected from individuals living in the African savannah (Hamilton 1981, Bailey 1993), and little is known about forest leopards (Hart *et al*. 1996). As the largest carnivore predator, leopards are a key component in the forest ecosystem and are likely to play an important role in the evolution of primates and other animal groups.

The hunting behavior of the Taï leopards

To investigate the behavior and ecology of forest leopards, four adult individuals were captured with a cable snare and sedated with a mixture of Domitor/Ketamine administered with a syringe fired from a carbon-dioxide gun (Jenny 1996, Dind *et al*. 1996). The animals were then fitted with a radio-collar, anti-sedated, and liberated back into the forest (Jenny 1996, Figure 5.1, Table 5.1).

In this chapter, we mainly review data collected from two of the study animals (Cosmos, Adele) that were monitored from three different platforms installed in the high forest canopy. This permitted monitoring activity patterns as a function of time of day, month, and amount of rain (Jenny & Zuberbühler 2005). Readings were taken every 15 minutes both during the day and at night. Activity was scored as either ‘‘moving’’ or ‘‘resting,’’ depending on whether the impulses of the received signal were fluctuating or stable. Both radio-tracked individuals were significantly

Table 5.1. *Morphometric data on the study animals (Jenny 1996)*

Individual	Capture date	Sex	Age (years)	Weight (kg)
Cosmos	5 Feb 93	Male	3–5	56
Adele	16 Aug 93	Female	3–5	34
Cora	16 Jun 94	Female	2–3	32
Arthur[a]	11 Oct 94	Male	3–4	49

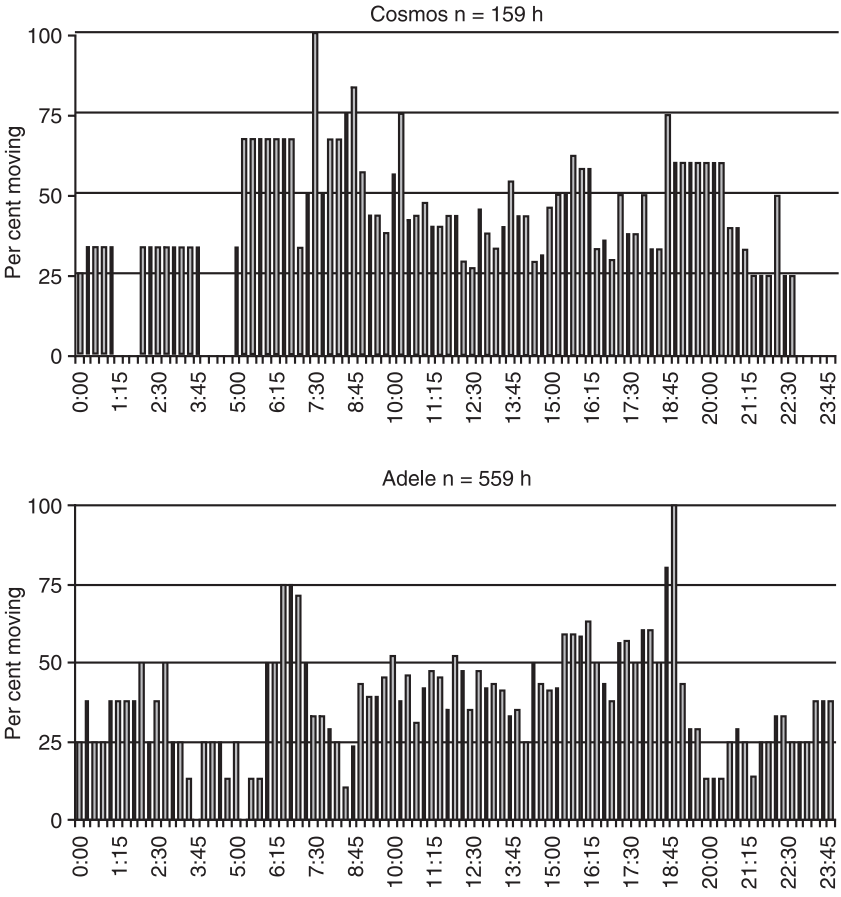
[a] Dind *et al.* (1996), Dind, F. (1995) (unpublished M.Sc. thesis, University of Lausanne)

more active during the day than during the night (Adele: $\text{mean}_{\text{day}} = 46.9$ per cent, $N = 53$, $\text{mean}_{\text{night}} = 26.3$ per cent, $N = 43$, $z = 6.34$, $p < 0.001$; Cosmos: $\text{mean}_{\text{day}} = 49.3$ per cent, $N = 53$, $\text{mean}_{\text{night}} = 30.3$ per cent, $N = 43$, $z = 4.384$, $p < 0.001$; Mann-Whitney U-tests, two-tailed; Zuberbühler & Jenny 2002; see Figure 5.2).

At night, two distinct activity patterns could be distinguished. Either the individuals remained completely inactive throughout the night or they moved continuously, often traveling great distances. Daytime activity was more evenly distributed and inactive periods during the day never lasted more than five hours. This pattern was comparable to that observed in Asian forest leopards (Karanth & Sunquist 1995, 2000), but contrasted strongly with savannah leopards that were reported to be predominantly nocturnal (e.g. Bailey 1993), suggesting that habitat type determine circadian activity patterns.

Overall moving activity was significantly correlated with season. We found that the lowest monthly moving rates were observed during the main rainy season in October, whereas the highest moving rates were recorded during the dry season in January (see Figure 5.3). Per cent moving activity per month was significantly negatively correlated with amount of rainfall (Spearman-Rank correlation, $N = 11$, $r_s = -0.718$, $z = -2.271$, $p < 0.03$). During heavy rains, it may be more difficult for prey to detect an approaching or hiding leopard which likely leads to greater hunting success and decreased traveling time during the rainy season (Jenny 1996).

Although direct observations of leopards was not possible in the forest, two individuals (Cosmos and Adele) were also followed on a regular basis at a close distance ranging from 30 to 150 meters. Focal animal follows of Adele and Cosmos were conducted between February 1993 and August 1994 for 15 and 11 months, respectively (Jenny 1996). The other two collared animals, Cora and Arthur, were subjects of a follow-up study (Dind *et al.* 1996) and are not included here (Table 5.1).


Cosmos n = 159 h

Adele n = 559 h

Figure 5.2. Circadian activity patterns of two study animals. (Data from Jenny & Zuberbühler 2005.)

Once a focal animal was located from platforms by triangulation, one observer moved quickly to the area and began following the animal. These indirect follows revealed additional information about leopard hunting behavior.

Forest leopards are thought to be ambush predators that hide and attack their prey by surprise. Our study supports this view. On one occasion, we were able to observe a successful attack by Adele on a *C. atys* after a prolonged period of hiding. After making this kill, she remained active in the same area for a few consecutive days. In general we noted that Adele appeared to approach monkey groups selectively. Once close to a group,

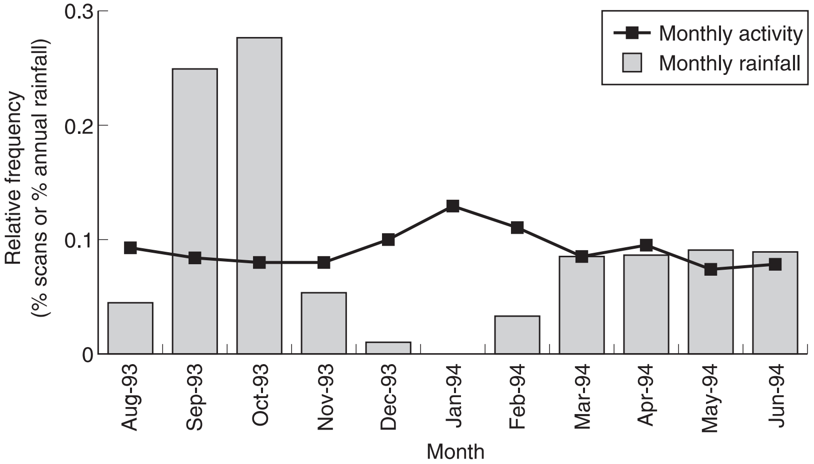


Figure 5.3. The relationship between average monthly activity and the amount of rainfall in the adult female Adele. Monthly rates of moving were significantly negatively correlated with amount of rainfall. (Data from Jenny & Zuberbühler 2005.)

she hid in dense understory on or near the ground, presumably waiting for monkeys to descend. In two out of nine direct sightings, Adele was observed sitting in the lower canopy on the lower branches of a tree, but never in the high canopy. All eight species of monkeys occasionally come to the ground to forage or play (McGraw 1998). To determine whether Adele selectively approached monkey groups, Jenny and Zuberbühler (2005) analyzed whether at least one monkey group could be located within 50 m from Adele's various hiding locations. This occurred approximately four times as often as when the observer David Jenny (DJ) was sitting alone at randomly selected points throughout the study area. In 60 out of 97 hiding bouts (7.4 per cent; N = 7821 min) a monkey group came within 50 meters of the hiding leopard. In contrast, when sitting at one of 10 different observation points throughout the study area, monkeys came within 50 meters only four times (1.9 per cent; N = 5940 min), a statistically significant difference ($z = -3.092$; $p < 0.01$; binomial test; two-tailed, Jenny & Zuberbühler 2005). This finding suggested that Adele selectively chose her hiding spots close to monkey groups. In contrast, Adele clearly avoided chimpanzee parties. After the occurrence of drumming or screaming from nearby chimpanzee parties, she inevitably altered her course in the opposite direction if already moving. We never observed her approaching chimpanzee parties (Zuberbühler & Jenny 2002).

Table 5.2. *Home range sizes*

	Study period 1[a] (February 1993–August 1994)		Study period 2[b] (January 1995–June 1995)	
Individual	N	Estimated home range size (km^2)	N	Estimated home range size (km^2)
Cosmos	159	85.6	93	41.5
Adele	342	28.5	161	25.3
Cora	53	22.2	79	22.4
Arthur	–	–	136	35.4
Total/mean	554	45.4	469	31.2

N = number of independent triangulations; [a] Jenny (1996); [b] Dind *et al.* (1996)

Leopard encounters and predation risk

Predation pressure can be measured at two different levels, predation rate and predation risk (e.g. Dunbar 1988, Janson 1998). Predation risk represents the animals' own perception of the likelihood of being attacked by a predator, regardless of whether the attack is successful (Hill & Dunbar 1998). This risk can be operationalized by the likelihood of a group encountering a predator (Hill & Dunbar 1998). Encounter rates between leopards and the different primate species will depend on factors such as density, home range, and daily travel distance of both predator and prey. Additional factors, such as the predators' prey preference and searching abilities as well as the preys' ability to predict and avoid the predator will also play a role, but they are more difficult to quantify. It is beyond the scope of this chapter to provide an accurate assessment of the predation pressure exerted by the Taï leopards. Nevertheless, a rough estimate is possible due to information available concerning the home range size of four radio-collared animals (Jenny 1996, Dind *et al.* 1996). Home range size was determined by two observers sitting on platforms in the high canopy simultaneously locating the focal individuals by triangulation (location accuracy ± 0.01 km^2). Distance was determined by the strength of the signal using a reference table (see Table 5.2).

The analysis provides important information on ranging behavior. First, male home ranges overlapped strongly with female home ranges while the ranges of same-sex individuals showed little overlap (Dind *et al.* 1996). Second, the home range size of the adult male Cosmos decreased dramatically between 1994 and 1995, most likely due to the appearance of a new male, Arthur, who began to occupy much of Cosmos' home range. Third, the actual density of leopards is likely to be higher because information collected from the photo traps suggests that at least three more individuals frequented the roughly 100 km^2 study area. The addition of these individuals yields a density estimate of 7–11 individuals per 100 km^2 (Jenny 1996). As a consequence, a particular primate group will encounter not only the 1–2 resident leopards, but also occasional trespassers or newly settled individuals. Assuming a home range size of 22 km^2 for female and 86 km^2 for male leopards (Jenny 1996), the average monkey group is likely to have one of the two resident leopards within its own home range once every 15–30 days.

Leopard prey spectrum and predation rates

In contrast to predation risk, predation rate refers to the successful predation events a predator can actually achieve. To determine the predation rates of leopards on the Taï monkeys we review two studies that have analyzed leopard feces in the Taï forest (Hoppe-Dominik 1984, Zuberbühler & Jenny 2002). In the second study, a total of 200 fecal scat samples were collected systematically along trails and throughout the study area. Samples were collected regularly between June 1992 and June 1994. We assumed that each fecal sample corresponded to one predation event. A day's search rarely led to the recovery of more than one fecal sample. All samples were inspected for the presence of hairs, bones, teeth, nails, and other remains. Hairs were identified using a reference collection and reference photographs (Hoppe-Dominik 1984, Bodendorfer 1994).

Roughly 140 mammal species are known to be present in the park and at least 12 of them are endemic. Table 5.3 illustrates the wide variety of prey species found in leopard feces, most of them mammals weighing less than 10 kg. The 200 feces analyzed contain remains of at least 23 different prey species. The large proportion of monkeys and duikers is particularly noteworthy, which reflects the species diversity of the rainforest habitat. Our results are comparable to those of an earlier study (Hoppe-Dominik 1984) in which a large number of samples were collected from the eastern side of the park where disturbed secondary forest prevailed and poaching pressure was much more intense. Still, the prey profiles are not equivalent. For example, *Colobus polykomos* and *Procolobus badius* were under-represented in the 1984 study, perhaps as the result of lower population densities of these two species in the eastern side of the park due to high poaching pressure.

Table 5.3. *Prey spectrum of Taï leopards*

Scientific name	Common name	Zuberbühler & Jenny (2002)	Hoppe-Dominik (1984)
Procolobus badius	Red colobus	21	8
Colobus polykomos	Black-white colobus	16	5
Procolobus verus	Olive colobus	1	0
Cercopithecus diana	Diana monkey	5	17
Cercopithecus petaurista	White-nosed monkey	1	5
Cercopithecus campbelli	Campbell's monkey	3	4
Cercopithecus nictitans	Putty-nosed monkey	0	0
Cercocebus atys	Sooty mangabey	6	9
Cercopithecidae	Unknown monkeys	10	3
Pan troglodytes	Chimpanzee	1	0
Perodicticus potto	Potto	0	1
Primates total		**64**	**61**
Cephalophus spp total	Duikers	82	82
Manis spp.	Pangolins	43	10
Sciuridae (undet.)	Squirrels	8	9
Panthera pardus	Leopards	6	6
Other Mammals	Other mammals	18	62
Mammalia (undet.)	Unknown mammals	6	26
Non-primates total		**163**	**195**
Aves total		**2**	**2**

Are leopards opportunistic or selective hunters?

Leopards are generally described as opportunistic predators, implying that they hunt prey species in proportion to abundance. Much of the evidence supporting this contention comes from open savannah habitats, however a study conducted in the Congolese Ituri Forest suggested that leopards are selective hunters with a particular bias towards l'hoest's guenons, *Cercopithecus lhoesti* (Hart *et al.* 1996). Moreover, studies using fecal data routinely average over a large number of individuals to calculate the prey spectra that masks the effects of individual differences (e.g. Zuberbühler & Jenny 2002). If the difference between savannah and forest leopards is real, then this could be the outcome of decreased competition from other predators in the forest habitat (Ray & Sunquist 2001). Similarly, because of the spatial overlap in home ranges, individuals are likely to develop individual prey preferences to reduce competition with more dominant competitors with whom they share a home range.

Opportunistic and selective predators are likely to differ in the evolutionary pressure they exert on a prey population. Selective hunters tend to increase species diversity in an ecosystem, particularly if their preference is directed towards a competitively dominant prey (Begon *et al.* 1996, p. 809). Furthermore, selective predators are predicted to increase the behavioral flexibility in prey. If predators develop individual preferences for certain species, then members of different species are forced to compete with each other to avoid preference formation. Individual or kin based anti-predator strategies thus might not be sufficient to avoid preference formation, because individuals should be interested in avoiding predation on any conspecific group members, regardless of the degree of relatedness. However, individuals responding to a generalist predator that does not develop preferences should be mainly concerned about their own survival and that of close relatives. Living in large groups provides a good strategy against opportunistic predators because individuals can benefit from a dilution effect where costs are shared among unrelated conspecifics. In sum, selective predators are expected to favor the evolution of flexible and cooperative defense behaviors, whereas generalist predators are expected to favor the evolution of simple selfish or kin selected defense strategies.

Considering the potential implications of selective hunting for the evolution of prey defense strategies, we attempted to determine whether Taï leopards are best classified as selective or generalist hunters. In a recent study (Jenny & Zuberbühler 2005) we compared the overall prey spectrum of Taï leopards (see Table 5.3) with the prey spectrum using three sets of data. First, local variations in prey spectra were used as an indicator of individual differences in prey selectivity. Second, an infrared-triggered photo-trap was installed along one trail that was frequently used by leopards, allowing us to assign a large number of feces to particular individuals. This was possible when individuals were photographed by the photo-trap, identified, and when its spoor could be followed to a fresh fecal sample. Third, while following a radio-collared individual it was possible to assign a further set of fecal samples to identified individuals.

Pangolin remains were frequently found in leopard feces throughout the 100 km^2 study area (see Table 5.3) but frequencies varied both regionally and temporarily, suggesting individual differences in the hunting behavior of the various leopards (Jenny & Zuberbühler 2005). In the southeast part of the study area, 40 per cent of feces contained pangolin remains. In the northwest part the number was lower: between June 1992 and March 1993 33 per cent of all feces contained pangolin remains. This rate dropped to less than 5 per cent between March 1993 and June 1994. No changes in the percentage of feces containing pangolins were observed in the southeast part during the same time periods. Interestingly, the sudden drop in feces containing pangolin remains in the northwest coincided with the death of a resident leopard, perhaps a specialized pangolin hunter, in early March.

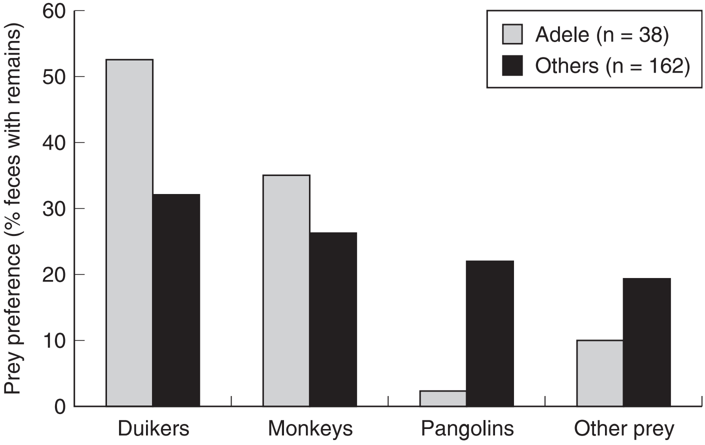


Figure 5.4. Prey selectivity of the focal animal Adele compared to other leopards in the Taï forest. (Data from Jenny & Zuberbühler 2005.)

In contrast, Adele, whose home range was also in the northwest part, did not usually hunt pangolins. With the aid of a photo-trap it was possible to assign a large number of feces to Adele, only one (3.6 per cent) of which contained pangolin scales. This is in comparison to 26.7 per cent for the other leopards contributing to the whole sample (see Table 5.3). Adele preferred to hunt duikers and monkeys significantly more often than other leopards (see Figure 5.4).

In sum, the different rates of pangolin predation in geographically distinct areas, the sudden change of these rates following the death of a resident leopard and the difference between Adele's prey spectrum and that of the rest of the leopard population strongly suggest that forest leopards developed highly idiosyncratic prey preferences among the large spectrum of possible prey species. In an earlier study, Boesch (1991) suggested that one individual specialized in preying on his chimpanzee study group, causing unusually high mortality rates during some time. In the two studies reviewed in this chapter chimpanzee remains were only found exceptionally, suggesting that preference formation for chimpanzees is an exception.

Primate anti-predator strategies

Recent molecular studies estimate the origin of modern leopards occurred approximately 500,000 years ago (Uphyrkina *et al.* 2001), suggesting that leopards have been a significant factor in the recent evolutionary history of non-human primates. To assess the potential impact of leopards on primates, we compared rates of leopard predation on the Taï monkeys with a number of behavioral, demographic, and morphological traits that are commonly viewed as anti-predation adaptations: body size, group size, group composition, female reproductive rate, and use of forest strata. The general prediction was that if a trait had evolved as an adaptation to leopard predation, there would be a negative relationship between the expression of the trait and the individual's vulnerability to leopard predation.

It has been suggested that large body size is an adaptation to predation (e.g. Isbell 1994). If true, then the larger Taï primates should be underrepresented in the leopards' prey spectrum compared to the smaller ones. Similarly, it has been suggested that individuals living in large groups are less susceptible to predation than individuals living in a small group, due to dilution effect and increased vigilance (e.g. van Schaik 1983). Taï primates that live in larger groups should thus be less susceptible to predation and therefore underrepresented in the leopard's prey spectrum. It has also been argued that the formation of groups containing several adult males is an adaptation to predation pressure, particularly in species where males engage in cooperative defense against predators (Stanford 1998). According to this hypothesis, Taï primates living in multi-male groups should be better protected against predation and therefore underrepresented in the leopard's prey spectrum relative to single-male groups. Another hypothesis states that natural selection can lead females to accept higher levels of predation if their potential reproductive rate is high enough to compensate for the losses incurred from predation (Hill & Dunbar 1998). In that case, rather than evolving predator-specific defense mechanisms, natural selection favors females who shorten their inter-birth intervals to increase their lifetime reproductive success. Species with short inter-birth intervals should thus be overrepresented in the leopards' prey spectrum. Finally, Taï primates show species-specific preferences for particular forest strata (McGraw 1998), presumably as a result of interspecies competition. Hence species living in the lower forest strata should be more exposed to ground predators (Dunbar 1988, Plavcan & van Schaik 1992) and should therefore be overrepresented in the leopards' prey spectrum. We should note that since the different primate species in the Taï forest vary dramatically in their population density this variable might be important in explaining variation in leopard hunting success. To assess how the various primate traits affected leopard hunting success, we compiled a data set for the Taï primate species, using several sources of information (see Table 5.4).

Table 5.4. *Data on population density, group size, body weight, strata use, number of males per group, birth rate, and usage of the lower forest strata for the Taï primates (Data from Zuberbühler & Jenny 2002)*

Species	Density	Body size	Group size	N males	Reproduction	Habitat
Cercopithecus diana	48.2	3.9	20.2	1	0.62	6.1
C. campbelli	24.4	2.7	10.8	1	0.63	36.8
C. petaurista	29.3	2.9	17.5	1	0.52	9.9
C. nictitans	2.1	4.2	10.5	1	0.50	0.7
Procolobus badius	123.8	8.2	52.9	10.1	0.42	0.4
Colobus polykomos	35.5	8.3	15.4	1.42	0.59	1.3
Procolobus verus	17.3	4.2	6.7	1.43	0.61	13.2
Cercocebus atys	11.9	6.2	69.7	9.0	0.40	88.9
Pan troglodytes	2.6	47.5	61.1	6.7	0.23	85.0

Density: estimated number of individuals per square kilometer
Body size: adult female body weight in kg (from Oates *et al.* 1990)
Group size: average number of individuals per group
N males: average number of adult males per group
Reproductive rate: average number of infants per adult female per year
Habitat: per cent time observed in lower forest strata (Data from McGraw 1998, 2000, Eckardt 2002.)

Data were natural log transformed [$y = \text{LN}\,(x + 1)$] to ensure normality before performing linear regression analyses (Hill and Dunbar 1998). Univariate analyses of the six variables using data of the eight monkey species showed that predation rate was significantly related to population density ($r^2 = 0.583$, $F_{1,6} = 8.383$, $p = 0.028$) and body size ($r^2 = 0.572$, $F_{1,6} = 8.011$, $p = 0.030$, Figure 5.5). However, contrary to predictions, body size and predation rates were positively related because the larger monkey species were preyed upon more often than smaller ones. The relationships between predation rate and group size and the number of adult males per group were also positive (group size: $r^2 = 0.390$, $F_{1,6} = 3.836$, $p = 0.098$; number of males: $r^2 = 0.353$, $F_{1,6} = 3.277$, $p = 0.120$), although they did not reach statistical significance. Predation rates were unrelated to the reproductive rate of adult females ($r^2 = 0.054$, $F_{1,6} = 0.340$, $p = 0.581$) and to a species' use of the lower forest strata ($r^2 = 0.030$, $F_{1,6} = 0.188$, $p = 0.680$). A stepwise multiple regression analysis using all six variables indicated that population density and body size combined accounted for a significant proportion of the overall variance of the leopard predation rate ($F_{2,5} = 18.347$, $p = 0.006$). Figure 5.5 summarizes the main findings.

These data show that leopard predation was most reliably associated with density, suggesting that leopards hunt primates according

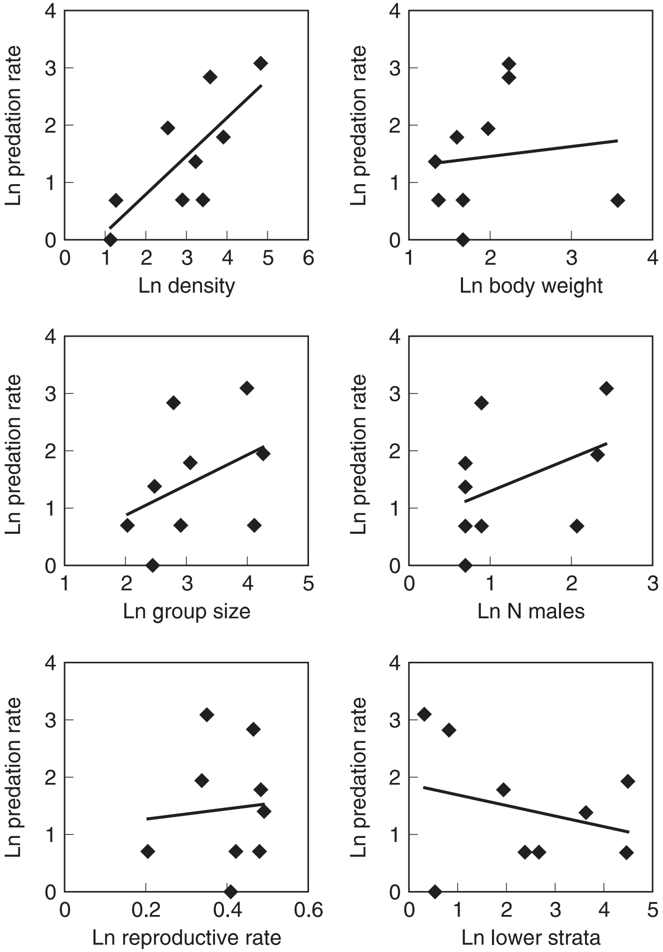


Figure 5.5. The relationship between leopard predation rates and various primate traits commonly interpreted as anti-predator adaptations. (Data from Zuberbühler & Jenny 2002.) Predation rate has been estimated by using the natural logarithm of the number of feces that contained remains of a particular species in a sample of 200 leopard feces collected over a period of two years from a 100 km^2 study area. *Density*: estimated number of individuals per square kilometer; *Body size*: adult female body weight in kg (from Oates *et al*. 1990); *Group size*: average number of individuals per group; *N males*: average number of adult males per group; *Reproductive rate*: average number of infants per adult female per year; *Habitat*: per cent time observed in lower forest strata. (Data from McGraw 1998, 2000, Eckardt 2002.)

to abundance. Contrary to predictions, leopard predation rates increased significantly with body size and was positively related to group size and the number of males per group, suggesting that predation by leopards did not drive the evolution of these traits in the predicted way.

In the next section we discuss these findings in light of some recent experimental data and suggest that the principal effect of leopard predation may have been on primates' cognitive evolution.

Interactions between leopards and monkeys

To investigate the primates' responses to the presence of leopards, one of us (DJ) collected data on the monkeys' responses to detection of a leopard's presence while following the radio-tagged leopard. Monkeys reacted strongly when detecting a leopard by giving a myriad of alarm calls and by approaching the predator in the lower canopy. Anti-predator behavior of this kind appeared to have striking effects on the leopard's hunting behavior: individuals typically gave up their hiding positions and moved on to find another group. To investigate this empirically, we performed two kinds of analyses using focal data collected from the adult female Adele (Zuberbühler *et al*. 1999). First, we tested whether detection had an effect on Adele's hiding behavior by comparing the duration of hiding before and after detection by the monkeys. Between August 1993 and June 1994, Adele was followed on 27 days (310 h) at a distance of 30 to 150 m. We scored the following variables based on changes in the strength and constancy of the received signal: encounter, detection, departure, leopard resting, leopard movement. An "encounter" between the leopard and a group of monkeys started when the leopard came to rest within about 50 m of a monkey group. The observer (DJ) then identified the monkey species present according to their vocalizations and remained concealed at a distance of 50–100 m from the leopard and monkeys. As long as a constant signal was received, the leopard was scored to be "resting," presumably hiding from the monkeys. A changing signal indicated "movement," which could be anything from body movements to changing the hiding spot. Movement that increased the distance from the monkey group beyond the 50 m radius was scored as "departure," which ended an encounter. The observer monitored the vocal behavior of the monkey group. As soon as the monkeys started to give loud and conspicuous vocalizations at high rates, it was assumed that the group had noticed the leopard and "detection" was scored.

We witnessed 24 different encounters between the leopard and a mono- or polyspecific monkey group (Zuberbühler *et al*. 1999). In 18 cases we were able to determine the encounter's exact duration (median: 61 min,

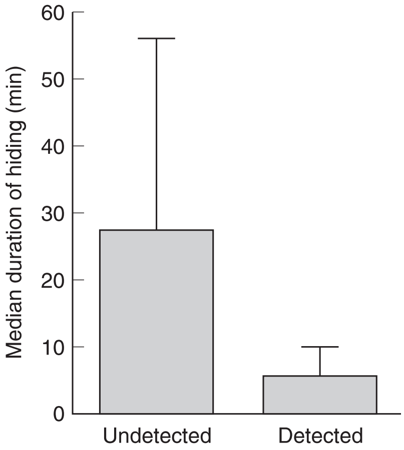


Figure 5.6. Median duration of hiding behavior in minutes of the focal animal before and after detection by a group of monkeys. (Data from Zuberbühler *et al*. 1999.)

range: 7–285 min). In all cases the monkeys detected the leopard at some point and subsequently vocalized at high rates. This affected the hunting behavior of the leopard. Detection by a group of monkeys appeared to terminate hunting behavior by the leopard because the time spent hiding underneath a monkey group was significantly shorter after detection than before (see Figure 5.6; Wilcoxon-test, one-tailed: $z = 2.112$, $n = 18$, $p < 0.02$). As mentioned before, one prolonged period of hiding led to a successful attack by Adele on a *C. atys*.

A qualitative analysis of the data suggested that the relationship between monkey alarm calls and the leopard's departure was causal because the leopard's stay after detection was short regardless of the time already spent hiding (see Figure 5.7). Adele not only gave up the hiding spot after detection but also was more likely to move on and leave the group.

Encounters with leopards generally led to extraordinarily high alarm call rates in all primate species. At first, this appears paradoxical because instead of remaining cryptic, individuals deliberately make their presence known to a highly dangerous predator. Conspicuous behavior in the presence of predators has been described in a number of species (e.g. skylarks, *Alauda arvensis*, Cresswell 1994). In these cases, it is typically argued that conspicuous behavior has evolved because predators rely on unaware prey for successful hunting; it is to the advantage of prey to signal detection and the futility of further hunting attempts

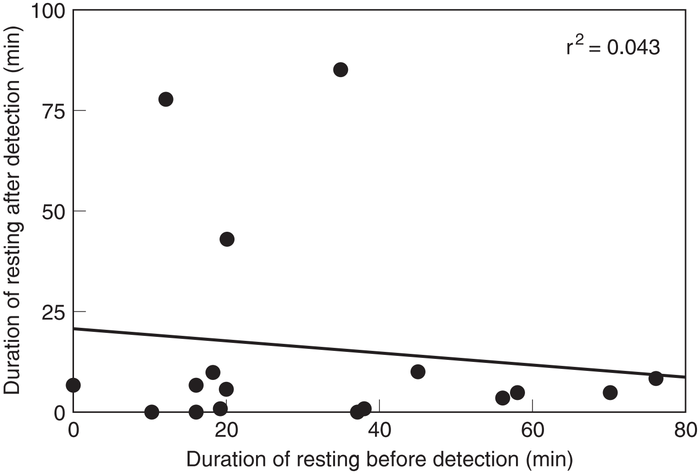


Figure 5.7. Relationship between the leopard's resting behavior in minutes close to a monkey group before and after detection (N = 18 encounters).

(the perception advertisement or detection-signalling hypothesis). Although the mechanism has been well described for some time, primate alarm calls have not been conceptualized this way. Instead, kin selection arguments have usually been put forward to explain why primates vocalize in the presence of predators (e.g. Cheney & Seyfarth 1981).

To investigate the alarm call behavior of Taï monkeys more systematically, predator presence was simulated by broadcasting typical vocalizations of the two major ground predators of Taï monkeys, leopards, and chimpanzees, from a concealed speaker (Zuberbühler *et al*. 1999). Various monkey groups were tested throughout the study area, but never more than once on each stimulus type. Once a group was located, usually by auditory cues, the speaker was hidden about 50 m away and a trial was conducted provided no monkey had detected the observer or part of the equipment and no predator alarm calls had occurred for at least 30 minutes. The focal group's vocal response was recorded on audiotape and it was determined whether the group had approached. All monkey species tested gave significantly higher rates of alarm calls to playbacks of leopard growls than to playbacks of chimpanzee pant hoots (see Figure 5.8). Groups occasionally approached the speaker after hearing playback stimuli, but only during playback of leopard growls and never after playback of chimpanzee pant hoots. The latter stimulus typically caused flight away from the speaker.

Among other things, our analyses show that monkey alarm calls affected Adele's hunting behavior because she tended to give up her hiding spot to

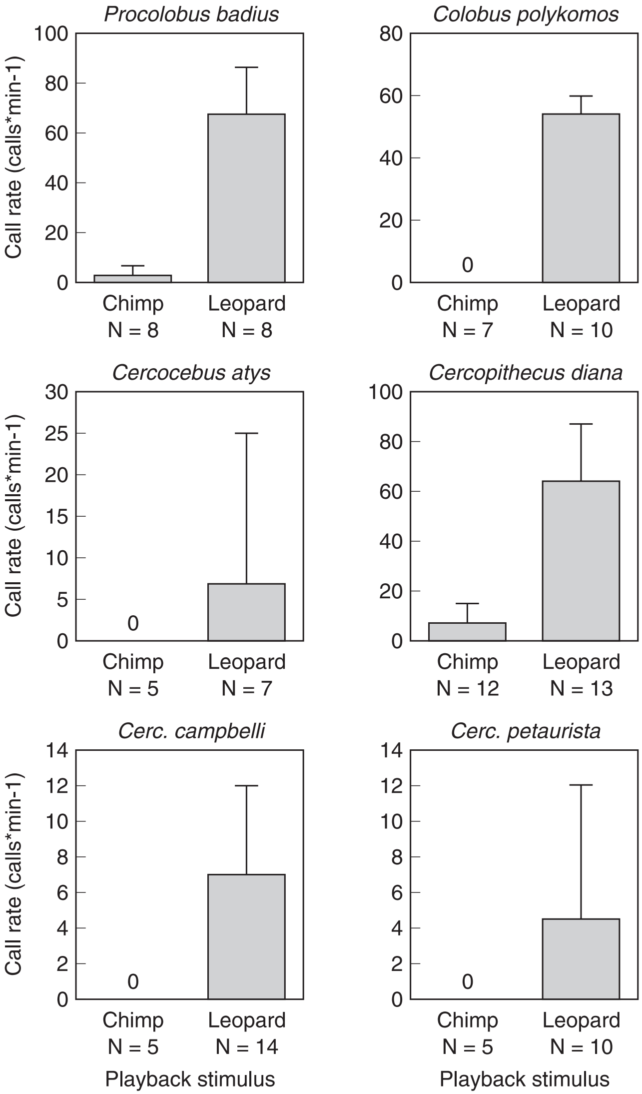


Figure 5.8. Alarm call behavior of six Taï monkeys in response to chimpanzee pant hoots and leopard growls. (Data from Zuberbühler *et al*. 1999.)

move on and leave the area (see Figure 5.6). Although no systematic data were collected, qualitative observations on the other three radio-tracked individuals revealed the same pattern, suggesting that Adele's behavior represented a general pattern of forest leopard hunting behavior.

In contrast, Taï chimpanzees are clearly not deterred by monkey vocalizations and they may even use them to locate a group (Boesch & Boesch 1989). Differences in predation pressure exerted by chimpanzees and leopards are unlikely to account for the differences in calling behavior since both predators prey upon the six species investigated in this study. In sum, data support the hypothesis that monkey alarm calls to leopards have a predator deterrence function because leopards, in contrast to chimpanzees, elicited conspicuously high alarm call rates, which drove the leopards away.

As discussed earlier, the fact that forest leopards can develop individual preferences may also explain why all monkey species engage in this cooperative form of acoustic anti-predator behavior. Successful predation on a conspecific is likely to increase preference formation, which will increase future predation pressure on the individual and its kin. Since leopards defend geographically stable home ranges (Jenny 1996, Dind *et al.* 1996), a particular monkey group will encounter the same few resident individuals repeatedly, perhaps even over several years, suggesting that preference formation can have fatal consequences for the affected individuals. Clearly, this hypothesis will require further and more rigorous testing. In particular, it needs to be demonstrated that individual leopards vary in their preference for different monkey species, and that this preference is the result of past hunting success.

The results presented in Figure 5.5 question the impact of leopards as a selection factor for the evolution of body size, group size, and other variables commonly thought to be anti-predator adaptations. Instead, we suggest that the main impact of leopard predation has been to enhance the primates' behavior flexibility to deal with this predator (Stoddard 1999). Support for this notion comes from at least four lines of evidence. First, several guenon species have evolved acoustically distinct alarm calls to warn each other about the presence of specific predators, including leopards (Seyfarth *et al.* 1980, Zuberbühler 2000a, 2001, Zuberbühler *et al.* 1997) and it is likely that similar findings will emerge from other species. Second, the suspected presence of a leopard appears to trigger complex cognitive processes (Zuberbühler 2000b, 2001, Zuberbühler *et al.* 1999). For example, Diana monkeys distinguish between chimpanzee screams given in a social setting and chimpanzee screams given to a leopard (Zuberbühler 2000d) suggesting that these calls are meaningful and inform the monkeys about the presence of a leopard. Diana monkey groups living near the periphery of a chimpanzee territory are less likely to understand variations in chimpanzee screams than groups living in the core area of a chimpanzee group, suggesting that meaning is individually acquired

(Zuberbühler 2000d). Third, meaning is not always rigidly attached to specific acoustic structures. Instead, it can be generated according to pragmatic information obtained from the environment (Zuberbühler 2000c). This is exemplified by the Diana monkeys' response to the alarm calls of crested Guinea fowl (*Guttera pulcheri*). Guinea fowl forage in large groups and when chased, produce conspicuously loud alarm calls that can be heard over long distances. Guinea fowl are not hunted by chimpanzees but may be taken by leopards and human poachers. Diana monkeys respond to recordings of Guinea fowl alarm calls as if a leopard were present. Playback experiments have shown that Diana monkeys are able to recognize that Guinea fowl alarm calls can be caused by both leopards and humans, and can also determine the most likely cause of the birds' alarm calls (Zuberbühler 2000c). Finally, recent research suggests that monkeys are able to alter the meaning of alarm calls by simple combinatorial rules in their vocal repertoire (Zuberbühler 2002). It is clear that the hypothesis that leopard predation has favored the cognitive evolution of primates, rather than body size or group composition, will require more rigorous testing using various empirical approaches. Nevertheless, we think that predation has generally been underestimated as a factor in primate cognitive evolution, a position that enjoys increasing support (e.g. Grimes 2002).

Conclusions

Although predation is believed to be an important driving force of natural selection its effects on primate evolution are still not well understood, mainly because little is known about the hunting behavior of the primates' various predators. A number of studies demonstrate that forest leopards primarily hunt for monkeys on the ground and during the day. The behavior of forest leopards differs in many aspects from that of individuals living in the savannah. Most strikingly, individuals are most active during the day and individuals show idiosyncratic prey preferences suggesting that at the individual level, leopards are better classified as selective hunters. Fecal analyses confirm that primates account for a large proportion of the leopards' diet and reveal in detail the predation pressure exerted on the eight different monkey species. Relating the species-specific predation rates to various morphological, behavioral, and demographic traits, usually considered adaptations to predation, reveal that leopard predation is most reliably associated with primate densities and body size although opposite the direction predicted. Body size, group size, and the number of males per group were all positively correlated to predation rates suggesting that predation by leopards does not drive the evolution of these traits in the manner predicted. At the same time, a variety of evidence shows that monkeys have evolved a number of behavioral strategies that appear to be based on complex cognitive capacities. In particular, all monkey species use their alarm call behavior to interfere with the leopards' hunting techniques. Signallers appear to gain fitness benefits in directly communicating to the predator by advertising perception and unprofitability. In these cases, leopards give up their hiding spot and leave the group significantly faster than expected by chance, suggesting that the high vocalization rates to leopards are part of an anti-predator strategy in primates that may have evolved to deter predators who depend on surprise. In light of the studies discussed, we conclude that leopard predation has acted as a major selection factor, enhancing individuals' ability to predict predator presence and behavior and to interfere with its hunting technique. Predation by leopards, it appears, has acted as a major natural selection factor in the evolution of primate intelligence.

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6 Interactions between red colobus monkeys and chimpanzees

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The question how red colobus monkeys try to avoid predation by chimpanzees was central from the start of the Taï monkey project. Boesch and Boesch (1989) had documented the hunting behavior of Taï chimpanzees and their prey spectrum. Their major results were that Taï chimpanzees: (1) hunt in a very cooperative coordinated way in which individuals play different roles, i.e. a "chaser" tries to chase monkeys out of their hiding trees into neighboring trees where "blockers" try to block the escape routes; (2) often decide to hunt before they have singled out a group of monkeys for attack and actively search for groups; (3) stalk monkey groups silently and only start screaming after being detected, probably to increase confusion; (4) mainly hunt red colobus and black and white colobus monkeys, while guenons and non-primate species are rarely caught; (5) hunt all age/sex classes of red colobus. Studying the anti-predation behavior of Taï red colobus thus offered a wonderful opportunity to study a predator-prey system where both predator and prey are primates that live in large permanent individualized social groups supposedly selecting for an enlargement of the neocortex (Dunbar 1992; note that data on red colobus neocortex size are lacking). We therefore hoped that the complexity of Taï chimpanzee hunting behavior reflected adaptations (genetic or learned) to complex red colobus counter adaptations (genetic or learned). This perspective was exciting because evidence that predator-prey systems can indeed evolve like an "arms race" (Dawkins & Krebs 1979) in which one adaptation by one side is matched by a counter adaptation and so on was scarce (Abrams 1986, Endler 1991). In particular, it was unclear whether this apparent scarcity reflected reality or whether it was due to the problem of showing its existence in systems where strategies are mostly one-dimensional (i.e. running as fast as possible). Futuyma (1986) had argued that predator-prey arms races might be rare because typically, several predator species with varying hunting

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

Box 6.1 Clarifying the terminology used in this chapter

The project's approach to red colobus-chimpanzee interactions was dealing with functional questions rather than asking how behavioral decisions are made. Studying mechanisms according to scientific laboratory standards under natural conditions is virtually impossible. We thus do not know the extent that the arms race between red colobus and chimpanzees reflects genetically determined or learned behavior. The underlying mechanisms, however, would be important for the correct terminology that should be used. I use the evolutionary terminology and write about strategies and coevolution, which implies that genetic components guide the behavior. I do not imply, however, that this is actually the case. The behavior of both chimpanzees and red colobus is likely to be shaped by learning, in which case one should use the term "tactics" rather than strategies.

strategies interact with several prey species with varying escape strategies. Under these circumstances, an adaptation to one opponent or strategy may decrease efficiency against another one. Taï red colobus have four main predators that partly differ in their hunting strategies. Chimpanzees and human poachers are pursuit hunters that may continue to hunt even after early detection. Leopards rely on surprise and attack from the forest floor, while eagles rely on surprise as well but attack through the canopy. Thus, if red colobus show specific strategies to each type of predator, Futuyma hypothesis can be disregarded.

Fortunately, we were not the only ones who started to study red colobus-chimpanzee interactions in more detail. Almost parallel to us but slightly ahead, Stanford and colleagues (Boesch 1994, Stanford *et al.* 1994a, 1994b, Stanford 1995) investigated similar questions at Gombe, Tanzania. Their results were strikingly different from our results for Taï (see below), allowing us to search for factors that may explain these differences (Bshary & Noë 1997b). At present, additional data on the interactions between chimpanzees and red colobus at Kibale/Uganda and Mahale/Tanzania have been studied in detail (Uehara 1997, Mitani & Watts 1999, 2001, Chapman & Chapman 2000). Here I incorporate this new information as a test of how well our original conclusions still stand up to the evidence. I first describe our major experimental results on the anti-predation behavior of Taï red colobus with respect to chimpanzees.

We tested the following predictions.

1. As chimpanzees actively search for monkey groups, red colobus should counter this strategy by becoming silent when chimpanzees are heard in the vicinity and move away from them, thereby reducing the probability of being detected.
2. The coordinated hunts of chimpanzees seem to be an adaptation to a prey that is superior in moving through the highest parts of the canopy where thin branches do not support the weight of chimpanzees. Therefore, we expected that red colobus move up into the highest parts during close encounters or hunts. In addition, each individual should hide so that the chimpanzee chasers might select another tree for their hunt.
3. The interspecific associations with Diana monkeys might be part of the red colobus anti-predation strategy with respect to chimpanzees. As Diana monkeys rarely fall victim to chimpanzees, the major advantage of being with them might be to receive an early warning.

Box 6.2 Methods

We conducted playback experiments that simulated the presence of chimpanzees and other predators, combined with presentations of control stimuli. The experiment that tested the behavior of red colobus when chimpanzees are almost underneath the group was conducted with our first red colobus study group. For all other playback experiments, nine different groups were chosen, and each group was tested only once with each stimulus presented. Most groups were unhabituated to the presence of humans and had to be followed out of sight. The playback design matched recommendations of the NATO life sciences symposium as closely as possible (McGregor 1992) to avoid variance caused by the experimental design (which would have worked in favor of the null-hypotheses). To find out how well different monkey species detect predators that stalk along the forest floor, I approached 48 different monkey groups of variable species composition and noted which species detected me first, the distance of the alarming individual at the moment of detection and the distances of the nearest individuals of all species present.

Avoidance behavior of red colobus monkeys during early stages of an encounter

Chimpanzees are usually noisy primates. Their pant hoots and drumming on tree buttresses can be heard over several hundred meters. Therefore, monkey groups are often informed about their presence. It is important to note that chimpanzees are rarely within the home range of each single monkey group. This is because the home range of chimpanzees comprises about 27 km^2 (Boesch & Boesch 1989), while there are about 2.4 red colobus groups per km^2 (Noë & Bshary 1997). Hearing chimpanzees thus tells the monkeys that the chance of being hunted by chimpanzees is much higher than on average. At such an early stage of an encounter where the monkeys are probably not even detected by the chimpanzees, the red colobus can reduce the chance of being detected by becoming silent. In addition, they can move away from the chimpanzees, thereby reducing the probability that the chimpanzees will move close by chance. To test this idea, we conducted playback experiments in which we used pant hoots of several chimpanzee males to simulate the presence of a potential hunting party within the home range of nine different red colobus monkey groups. Prior to the playbacks, we used the vocalizations of the monkeys and branch movements to locate the group's center of activity, i.e. where the highest concentration of individuals was. The speaker was placed approximately 100 m from the nearest individual(s) and the playback followed. Eight out of nine groups responded with movements, and the resulting vector of these movements was almost exactly in the opposite direction to the speaker (177 degree). Usually, group movements in red colobus are accompanied by an increase in vocalization rates. In their response to the playbacks, however, red colobus were almost completely silent during the 5 min interval following the playbacks, except for some initial calls. Similar data were obtained during natural encounters of our first two study groups and chimpanzees (Bshary & Noë 1997a). Thus, red colobus indeed reduce the probability of being detected either by vocalizations or by a chance approach when chimpanzees are nearby by falling silent and by moving away from the chimpanzees. This behavior of red colobus is specific to pursuit predators that approach over the forest floor, i.e. chimpanzees and humans. In contrast, playbacks of leopard growls lead to an increase in calling frequencies and groups do not move away from this stimulus (Bshary & Noë 1997a). Similar responses are elicited by eagle shrieks (personal observations).

Hiding behavior of red colobus when chimpanzees are (almost) underneath the group

In response to playbacks of a group of male chimpanzee pant hoots, individuals of our first study group moved up into the high canopy or emergent trees, fell silent and the exposure to the forest floor, when corrected for height, was lower than before playbacks. It became much more difficult for the observer to actually spot individuals after the chimpanzee playbacks (personal observation), indicating that the exposure of the monkeys to the forest floor was even more reduced than the data suggest. Individuals of all age/sex classes behaved in a similar way. This was expected as Taï chimpanzees hunt all age/sex classes (Boesch & Boesch 1989), so red colobus males that try to defend other group members would be at high risk of predation themselves. We obtained similar data during natural close encounters between chimpanzees and our first two study groups (Bshary & Noë 1997a). Again, this behavior of red colobus is specific to pursuit predators that approach over the forest floor, i.e. chimpanzees and humans. In contrast, placing a cloth with the color pattern of a leopard underneath the group or placing an artificial crowned eagle (*Stephanoaetus coronatus*) in a tree does not elicit movements away from the stimuli. On the contrary; on four occasions, groups of 4–5 red colobus males attacked the eagle model and continued to bite it after it fell to the forest floor (Bshary & Noë 1997a). Wrapping the leopard cloth around the body was an ideal way to film unhabituated red colobus monkeys because the monkeys were looking and shouting at the cloth (personal observation).

Interspecific associations with Diana monkeys

Observational evidence strongly suggested that red colobus seek the presence of Diana monkeys to reduce predation pressure from chimpanzees (Bshary & Noë 1997b, Noë & Bshary 1997). Most importantly, association rates peaked during September through November, the chimpanzee-hunting season (Boesch & Boesch 1989), due to the initiative of red colobus. Even more pronounced was the observation that association rates were particularly low between June and August, the time of the year when members of chimpanzee communities are dispersed. If chimpanzees are dispersed, that means that there is no group of males together that could start a cooperative hunt. Predation risk from chimpanzees should therefore be particularly low during this season. As the associations with Diana monkeys most likely reflect a balance between the benefits of reduced predation risk and the costs of deviation from an optimal foraging pattern, one would predict low association rates when predation risk is low. The only predator in Taï, which clearly has a seasonal pattern in hunting activity, is the chimpanzee. It could therefore be considered unlikely that the low association rates in June through August were caused by low predation risk from other predators. However, an alternative explanation was that the same environmental constraints that promote dispersed feeding of chimpanzees also constrain high association rates of red colobus and Diana monkeys.

The hypothesis that the low association rates in June to August were due to low predation pressure by chimpanzees was tested with playback experiments. Hearing pant hoots of several chimpanzee males would indicate to the monkeys that the momentary risk of being (successfully) attacked by chimpanzees is very high relative to the average risk in this season. Note that the playbacks merely simulated the presence of a nearby group of male chimpanzees (100–200 m from the group) rather than an actual hunting attempt. However, given that our playbacks successfully fooled the monkeys into believing that chimpanzee males are nearby, the monkeys should have some knowledge that if the chimpanzees decided to hunt at some point, it is likely that they would target the nearest red colobus group, i.e. them. If the associations with Diana monkeys indeed serve as a flexible strategy to reduce mortality due to chimpanzee predation, we had two predictions concerning the association pattern. (1) We predicted that associated groups should stay together for longer throughout the day after hearing a playback of chimpanzee calls in the morning than after other playback stimuli. (2) We predicted that red colobus-Diana monkey groups that were about to split up should reunite immediately in response to playbacks of chimpanzee calls but not in response to other playback stimuli.

The results were clearly in line with the hypothesis that the associations with Diana monkeys serve as a flexible strategy to reduce predation from chimpanzees (Noë & Bshary 1997). Six out of nine groups that were associated in the morning stayed together with their Diana monkey group until the end of observation at 17:00 following a short playback of male chimpanzee calls in the morning. The three groups that eventually split up did so only late in the afternoon. Red colobus-Diana monkey associations thus lasted significantly longer after playbacks of chimpanzee calls than after control playbacks of a generator engine or empty tape. Playbacks of leopard growls yielded intermediate results in that associations did not last significantly shorter than after chimp calls and not significantly longer than after control playbacks. The results for our second prediction were even more clear-cut. All nine red colobus groups that had a Diana monkey group nearby on the verge of moving away were intermingled with them again shortly after the playbacks of male chimpanzee calls. In most cases, the red colobus had made the more significant move towards the Diana monkeys though Diana monkeys contributed on two occasions and were fully responsible for the intermingling on one occasion. Intermingling after playbacks of chimpanzee calls was more likely than intermingling after both control stimuli (generator and empty tape) and intermingling after playbacks of leopard growls (Noë & Bshary 1997). In particular the response after leopard growls was strikingly different from the response following playbacks of chimpanzee calls as five out of nine groups split up further. In conclusion, the association pattern of red colobus and Diana monkeys was flexibly adjusted to perceived momentary predation pressure from chimpanzees. This adjustment is not a general strategy against perceived presence of predators, as leopard growls did not elicit an increase in association duration or rate compared to control stimuli. It is important to note that the absence of an influence of leopard growls on association patterns does not show that associations do not serve to reduce predation pressure from leopards. A major difference between chimpanzees and leopards is that chimpanzees are noisy unless they start searching for prey, while leopards are usually silent. Therefore, hearing or not hearing chimpanzees provides monkeys with some information about momentary predation risk with respect to these predators. Not hearing a leopard, however, does not offer any information about the whereabouts of these predators. Thus, even if associations serve to reduce predation pressure from leopards, monkeys cannot adjust their association rates to momentary predation risk with respect to leopards but have to base their decision to stay together or to split up on an average risk value. The only way to test this idea is to search for a site where leopards are the only predators of monkeys and see whether or not association rates are still above chance levels or not.

What is the advantage of being with Diana monkeys?

Until now, we have only shown that red colobus adjust the duration and frequency of associations with Diana monkeys according to momentary predation risk from chimpanzees; we have yet to show why this should be advantageous. Diana monkeys rarely fall victim to chimpanzees (Boesch & Boesch 1989), making dilution advantages for red colobus very unlikely. On the contrary, a major advantage for Diana monkeys with respect to predation by chimpanzees could be to be associated with a prey species that is preferred by the predators. For example, Grant's gazelles are often associated with Thompson's gazelles for apparently this reason: cheetahs mainly hunt the latter when attacking a mixed species association (FitzGibbon 1990). Thompson's gazelles benefit from the presence of Grant's gazelles because the latter are more vigilant and therefore more likely to spot a stalking cheetah in the first place (FitzGibbon 1990). We assumed that, as with the gazelles' system, Diana monkeys might provide red colobus with an early warning when chimpanzees stalk an associated group and try to surprise them. Diana monkeys use the lower strata more frequently than red colobus (Bshary & Noë 1997b), they move around more during foraging, searching for insects (McGraw 1996) and are more often at outer branches than red colobus (McGraw 1996). All these factors should facilitate detection of predators approaching over the forest floor, as chimpanzees, humans, and leopards do. To test this hypothesis, I approached 48 different monkey groups that consisted of variable species composition. I had a leopard cloth wrapped around my body because all monkey species (with the possible exception of olive colobus) react with clear alarm vocalizations to this stimulus while their response following the detection of a human is to fall silent and flee, making it difficult to assess which individual actually detected me first. I noted which species were present, to which species the individual that alarmed first belonged, and my distance to the nearest individual of each species. In particular, I was interested whether Diana monkeys would alarm before red colobus monkeys in situations where red colobus were closer to me.

As predicted, Diana monkeys were significantly better than red colobus in spotting me first. On 16 out of 19 occasions, a Diana monkey called first. On 10 of these occasions, a red colobus had been as close or even closer to me. On those three occasions where a red colobus alarmed first, individual Diana monkeys were still quite far away from me. Diana monkeys detected me from significantly larger distances than red colobus. This difference persisted when I controlled for the stratum where the alarming individual was. Diana monkeys alarmed first more often than any other monkey species with a similar home range (olive colobus, black and white colobus, lesser spot-nosed monkey, Campbell's monkey). Perhaps due to small sample sizes, these differences were not significant, however. Still, the results provide a clue as to why Diana monkeys are the main partner species of all other monkey species with similar home range sizes in the Taï forest. Note that sooty mangabeys are even better watchmen for ground predators (McGraw & Bshary 2002) however, they are not reliable partner groups as their home ranges are much larger than those of the other monkey species. Therefore, mangabeys visit each group of other species irregularly at low frequencies (5–10 per cent of daylight hours;

McGraw & Bshary 2002). In conclusion, in the absence of mangabeys, red colobus benefit from being with Diana monkeys because the latter often provide an early warning for ground predators. Note that Diana monkeys do not give alarm calls for the red colobus but for their own group members. However, there is increasing evidence that different monkey species recognize each other's alarm calls (Zuberbühler 2000). The warning of red colobus by Diana monkeys is thus a typical case of a by-product mutualism (Brown 1983) in which help is given without any costs involved. If chimpanzees are heard in the vicinity, red colobus increase association rates with Diana monkeys because of the risk that if the chimpanzees decide to hunt, they are likely to stalk a red colobus group that is nearby. Being with the Diana monkeys increases the probability of receiving a timely warning, allowing the red colobus to move into the high canopy and hide.

Measuring fitness consequences of associations with Diana monkeys with respect to predation from chimpanzees

The results from the playback experiments and from the approach experiment make a convincing case that red colobus associate with Diana monkeys to reduce predation pressure from chimpanzees. However, the data do not prove that red colobus are indeed at lower predation risk when associated than when on their own. Showing such fitness advantages for red colobus is not just important to complete the evidence but also because there is an alternative hypothesis. Boesch (1994) had argued that chimpanzees use calls of Diana monkeys to detect interspecific monkey groups, which they approach to hunt red colobus monkeys. He therefore proposed that associations with Diana monkeys are *disadvantageous* for red colobus with respect to predation by chimpanzees. According to Boesch's hypothesis, one would predict that red colobus should avoid Diana monkeys when chimpanzees are nearby, the opposite of what we observed.

We re-examined Boesch's original data (Bshary & Noë 1997a). While following chimpanzees, he had noted what monkey species he had heard (first if there was a mixed species group) whether or not the chimpanzees had gone to that group and which species they had hunted (Boesch 1994). It was true that *if* chimpanzees approached a group where he had heard Diana monkeys first, the chimpanzees most often hunted red colobus that were associated. However, chimpanzees rarely approached groups when he had heard Diana monkeys first (note that no information is given on how often groups of other species were present) i.e. in only 13 out of 236 occasions. In contrast, chimpanzees approached groups after Boesch had heard red colobus calls first on 41 out of 143 occasions. In conclusion, these data clearly show that chimpanzees avoid approaching groups when they hear Diana monkeys (Bshary & Noë 1997a). The results become even more impressive if one considers that Diana monkeys are rarely not in association with either red colobus or black and white colobus. Our project data revealed that our first Diana monkey study group spent almost 90 per cent of daylight hours intermingled with groups of either colobus species. Diana monkeys are thus a very good indicator of the presence of large colobus groups and, according to Boesch (1994), chimpanzees even prefer to hunt black and white colobus to red colobus. Black and white colobus are much more difficult to detect, however, due to their cryptic life style (Bshary & Noë 1997a). Thus, there is even greater reason for chimpanzees to follow Diana monkey calls to detect their favorite prey, however they rarely did so.

In their book on Taï chimpanzees, Boesch and Boesch (2000) provided additional data collected during a different time period than those reported in the Boesch (1994) paper. The new data include data on whether red colobus groups were in association (or on their own) and appear to contradict the previous ones. Red colobus in association were approached and hunted more frequently than were red colobus on their own (in association: approached 64 times, hunted 33 times out of 106 encounters; on their own: approached 18 times, hunted 14 times out of 143 encounters). While these new data include more information than the previous data and suggest that associations with Diana monkeys might indeed be costly for red colobus with respect to predation from chimpanzees, there are several potentially confounding variables. First, the new data set is conservative with respect to our hypothesis that associations are advantageous because on some occasions, chimpanzees may have refrained from approaching red colobus groups that were scored being on their own but actually were associated with Diana monkeys. One can only positively say that Diana monkeys are present; their absence is more difficult to confirm. This is particularly true if one follows chimpanzees since Diana monkeys become silent in their presence (Boesch 1994, Zuberbühler *et al.* 1997). Second, no association criterion is mentioned. Thus, there might have been several data points where Diana monkeys were in audible distance to a red colobus group, without being intermingled. According to data on the vigilance behavior of red colobus, only intermingled is the appropriate criterion for an association (Bshary 1995). Third, the data were collected a) during the chimpanzee-hunting season when red colobus spend about 65 per cent of daylight hours in association and, b) in May to July – that part of the year where chimpanzees rarely hunt and red colobus are much less associated (Noë & Bshary 1997). It is thus conceivable that the many data points where encounters between chimpanzees and monospecific red colobus groups that did not lead to approach and hunt may have been collected in the non-hunting season. Note that data in Boesch (1994) were collected not only during the hunting season, but also during the following dry season. However, the addition of data collected during the dry season mainly increases the variance as more encounters do not lead to approach and hunt but do not confound predictions as association rates of red colobus are very similar during the data collection period (Noë & Bshary 1997). Ideally, the data should be analyzed separately for the various seasons or at least corrected for variation in both chimpanzee hunting frequencies and red colobus association rates.

As it stands, a way to analyze the new data without having to worry about potential confounding variables is to investigate whether there is a difference in how frequently a chimpanzee approach results in an actual hunt when red colobus are associated compared with when they are on their own. The distinction between approach and hunt can be made because Boesch (1994) scored a hunt only if at least one chimpanzee was as high in the trees as the red colobus. When red colobus were in association, 64 approaches resulted in 33 hunts. In comparison, when red colobus were on their own, 18 approaches resulted in 14 hunts (Boesch & Boesch 2000). The probability that an approach resulted in a hunt was thus significantly higher when red colobus were on their own than when associated (G-Test, $G = 4.1$, $N = 82$, $df = 1$, $p = 0.044$). This result supports our original hypothesis and our observational/experimental data suggesting that being with Diana monkeys yields fitness advantages for red colobus with respect to predation from chimpanzees due to improved early detection of chimpanzees.

Comparison of red colobus-chimpanzee interactions at Taï, Gombe, Kibale, & Mahale

The arms race between red colobus and chimpanzees at Taï appears quite different from the arms race between red colobus and chimpanzees at Gombe (Table 6.1, see Bshary & Noë 1997a). Both predator hunting strategies and prey escape strategies vary considerably between the two sites. We argued that two factors account for these differences (Bshary & Noë 1997a). First, the relative body weights of predator and prey are much more in favor of chimpanzees at Taï (6:1) than at Gombe (about 4:1) (Struhsaker 1975, Morbeck 1989, Oates *et al.* 1990). These differences in relative weight between sites may explain why Taï chimpanzees dare to

Table 6.1. *Qualitative description of features of red colobus-chimpanzee arms races at four different study sites*

	Taï	Kibale	Gombe	Mahale
Chimp body size	large	small	small	small
Colobus body size	small	large	large	large
Canopy structure	high closed	high closed	low broken	low broken
Chimps: search	yes	yes	no	no
silent approach	yes	yes	no	no
collaborate	yes	no(?)	no	no
share meat	yes	yes	no	no
kill colobus males	yes	no	no	no
avoid associations	yes	?	no	no
Colobus: hide	yes	yes	no	no
male defense	no	yes	yes	yes
associations	yes	yes	no	no

hunt red colobus males while Gombe red colobus males dare to defend other group members against chimpanzees. A second major difference between Taï and Gombe is the structure of the canopy. At Taï, the canopy is high and relatively closed while it is low and open at Gombe (Wrangham 1975, Whitmore 1990). The forest structure at Taï allows red colobus to behave cryptically and to use escape routes during hunts that are inaccessible for the heavier chimpanzees. In return, the coordination between chimpanzee males during hunts overcomes the problem of how to follow the mobile red colobus through the canopy. In addition, Taï chimpanzees can silently stalk their prey, trying to surprise it. As a final counter adaptation, red colobus associate with Diana monkeys to improve early detection of stalking chimpanzees. At Gombe, the low broken canopy allows single chimpanzees to hunt successfully if they manage to get past the red colobus males. Silent escapes or surprise attacks are not possible, thereby considerably simplifying the arms race between red colobus and chimpanzees at that site.

The arms races between red colobus and chimpanzees at Kibale forest and the Mahale mountains provide a good test for the contrast we made based on the Taï and Gombe data. The forest structure of Kibale is very similar to the one in Taï with a high closed canopy (Mitani & Watts 1999). In contrast, the Kibale red colobus are relatively heavy compared to the Kibale chimpanzees, a feature that closely resembles the situation at Gombe. Mahale resembles Gombe very closely in that the canopy structure is broken and red colobus are relatively heavy compared to the chimpanzees. Thus, the following predictions can be made about the predator-prey arms race at Kibale.

1. Chimpanzees search for red colobus groups and approach them silently for a surprise hunt.
2. Chimpanzees coordinate their hunts and play different roles during a hunt. As a consequence, they share meat with co-hunters.
3. Chimpanzees hunt mainly immature and juvenile red colobus.
4. Red colobus males defend the group against chimpanzees.
5. Red colobus frequently associate with other species to improve early warning, allowing the males to form a defense line and other group members to move up to the high closed canopy to have many possible escape routes.
6. As a consequence of improved early warning in mixed species associations, chimpanzees preferentially hunt monospecific red colobus groups. The predator-prey arms race at Mahale should closely resemble the one at Gombe.

Comparisons of red colobus-chimpanzee interactions at the four study sites by Mitani and Watts (1999) support our original scenario quite well (see Table 6.1). Hunting behavior of chimpanzees and red colobus defense behavior are very similar at Gombe and Mahale. At Kibale, most existing data fit our predictions: red colobus frequently associate with other monkey species, mainly redtail monkeys *Cercopithecus ascanius*, and association rates correlate positively with chimpanzee densities (Chapman & Chapman 2000). It is still not clear how these associations improve early warning or whether chimpanzees preferentially hunt monospecific red colobus groups. Two factors about chimpanzee behavior do not fit our predictions. First, chimpanzees do not seem to obviously coordinate their hunts, but they nevertheless often share meat (Mitani & Watts 1999, 2001). This interpretation is based on observations by Mitani and Watts (1999) who state that assessing the degree of cooperation/ coordination was often difficult. These authors do mention that chimpanzees "sometimes collaborated" by encircling red colobus groups, blocking potential escape routes, or "driving" prey down hill slopes from taller to shorter trees (Mitani & Watts 1999, p. 446). Thus, Kibale chimpanzees could be seen as more cooperative than the authors conclude. An additional factor that may influence the degree of collaboration during a hunt is demography. The chimpanzee community studied in Kibale is extremely large and included 26 males in 1998 (Mitani & Watts 1999). Hunting party sizes included on average 13.3 males and are thus much larger than at the other study sites. Mitani and Watts (1999) argue that because of the large hunting party size, chimpanzees are extremely successful without elaborate coordination. Meat sharing may function for male-male bonding that is used in social interactions (Mitani & Watts 2001). In conclusion, our original scenario (Bshary & Noë 1997a) should be broadened to include a demographic factor, namely chimpanzee group size.

Conclusions

1. The anti-predation behavior of Taï red colobus corresponds in several features to the predation behavior of Taï chimpanzees. Thus, the two species appear to be involved in an arms race with several adaptations and counter-adaptations. The role of learning in this arms race is still unexplored.
2. A major component of the red colobus anti-predation strategy is to associate with Diana monkeys. Diana monkeys do not provide dilution advantages but rather an early warning against silently approaching chimpanzees.
3. As a consequence of the watchmen abilities of Diana monkeys, chimpanzees appear to avoid associated red colobus groups and/or are less likely to start a hunt after approach.
4. Recent data from Kibale and Mahale generally fit the idea that forest structure and relative body sizes between chimpanzees and red colobus may account for most of the observed differences in the arms races between study sites. In addition, demographic effects have to be considered.

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7 *Interactions between African crowned eagles and their prey community*

S. Shultz and S. Thomsett

Introduction

One explanation for the evolution of sociality among vertebrates as an adaptive response to predation pressure. Individuals in groups are able to invest less in vigilance behaviors, are more likely to detect a predator, less likely to be the victim of an attack, and can more effectively mount a defense against a predator. Although there is evidence that individual vigilance levels decline with increasing group sizes in birds and primates (Lima 1987, Cowlishaw 1994), documenting benefits of sociality in terms of predation rates has been difficult in either field or laboratory studies. Group size has been shown to reduce predator capture success in only a few controlled laboratory experiments (e.g. Krause & Godin 1994) or opportunistic field observations (e.g. Lindstrom 1989). Thus despite numerous models predicting how sociality and group size impacts predation risk, there remains little evidence from natural systems to support the theoretical predictions. Through comparing predator diet composition with prey behavioral characteristics we can assess how anti-predator behaviors influence predation rates by different predators.

The different primate species in Taï National Park exhibit a variety of social systems, making the community in Taï an ideal situation to test theories about the relationship between group size, composition, and predation risk. Crowned eagles (*Stephanoaetus coronatus*), leopards (*Panthera pardus*), chimpanzees (*Pan troglodytes*), and humans (*Homo sapiens*) are the four main predators of primates in Taï. The hunting strategy of each of these predators varies and each predator should show biases towards different prey depending on the habitat use and anti-predator strategies employed by the prey species. The rationale driving the study of the crowned eagles was to understand the role of predation

Monkeys of the Taï Forest, ed. W. Scott McGraw, Klaus Zuberbühler and Ronald Noë.
Published by Cambridge University Press.

by raptors in shaping the behavioral adaptations and polyspecific associations that are observed in the monkey species in Taï. The key advantage of Taï as a site to study crowned eagles is that not only have the ecology and behavior of primate prey been studied, but also that of their other main predators. Thus the primate community in Taï National Park represents the first primary forest site where there is a comprehensive picture of predation pressure from all main predators.

This chapter has several goals: (1) to describe crowned eagle natural history in Taï and relate diet preferences to prey behavior and ecology, (2) compare diet selection of the main predators, (3) outline the behavioral interactions between crowned eagles and the monkeys in Taï, and (4) explore the behavioral responses of monkeys to predation risk.

Crowned eagle natural history

African crowned eagles are found from Sub-Saharan equatorial forests south to South African subtropical and temperate habitats (Brown *et al.* 1982). Their genus, *Stephanoaetus*, is monotypic and closely related to the pan-tropical hawk eagles of the *Spizaetus* genus. Crowned eagles have been extensively studied in savanna and woodlands in East and South Africa (Brown 1971, Daneel 1979, Vernon 1984, Boshoff *et al.* 1994). However, in their primary lowland forest habitat, the few previous studies in primary forest have involved only bone collection from under nest sites (Skorupa 1989, Struhsaker & Leakey 1990, Mitani *et al.* 2001) or opportunistic observations of hunting incidents (Leland & Struhsaker 1993, Maisels *et al.* 1993). This study was the first time adjacent eagle nests have been concurrently monitored, providing a population level picture of the impact of eagle predation on the monkey community.

African crowned eagles are resident year-round and actively defend territories around their nest sites. In South Africa, some populations of African crowned eagles regularly breed annually (Steyn 1982), but throughout most of their range they breed in biennial cycles. Immature crowned hawk-eagles exhibit very prolonged dependency periods; young can remain dependent for up to 300 days after fledging (Brown *et al.* 1982). With such a long dependency period, an entire reproductive cycle from nest repair to independence lasts 20–22 months (Brown *et al.* 1982), making annual breeding impossible. In populations where eagles do breed annually, the dependency period appears to be shorter. Crowned eagles are non-migratory and new breeding cycles commence after previous young achieve independence or after brood failure; single nest sites have been known to be active continuously for several generations over a period of more than 50 years (Brown *et al.* 1982). During incubation and while there are dependent young at the nest, adults visit the nest sites regularly to bring prey items to attendant adults or dependent young.

Crowned eagles in Taï

The crowned eagle study in Taï began in October 1998 and ran through August 2000. During this time nests were located by several different means: primate researchers and technicians were asked to report nest specific vocalizations encountered while following primate groups, forest blocks without known nest sites were systematically searched, and aerial transects were conducted over parts of the park without adequate trail systems. In total, 12 nests were found within an approximate 80 km^2 block surrounding the primary research station. An additional 12 nests were located using aerial transects in other areas of the park. Detailed information on behavior, breeding biology, and diet composition was only collected from the nests near the research station.

Crowned eagle population density is extremely variable in different habitats; in Kenyan woodlands Brown *et al.* (1982) estimated a density of one pair every 100 km^2. At the other extreme is the estimated density in the relatively mature forest of Taï. Eagle density here is estimated to be one pair approximately every 6.5 km^2, and the average nearest-neighbor nest distance around the research station is 1.81 ± 0.43 s.d. km (Shultz 2002). Nests can be several meters across and are generally found in an exposed fork or branch of an emergent tree. In Taï, the average height of trees with nests was 52 ± 14 m and had an average DBH of 234 ± 66 cm; the nests were 36 ± 9 m high and were located on either the lowest side branch or in the central fork (Malan & Shultz 2002). The nests were also found exclusively in emergent trees, with the main fork above the surrounding canopy. This allows both easy access and protection from non-flying nest predators.

In Taï breeding is highly seasonal, nest repair begins in July/August and eggs are laid during the beginning of the dry season in late November or December (Shultz 2002). Chicks fledge in March before the rainy season recommences (see Figure 7.1). In all studied populations, crowned eagles have a clutch size that varies between one and two, but if the younger sibling hatches it is always killed by the older (Brown *et al.* 1977). Clutch size in Taï is also likely to vary between one and two, but all documented breeding attempts had a final brood size of one. Provisioning is frequent for young nestlings (1.53/day in the first four months), but nest visits reduce in frequency as the chicks age and are very infrequent when the chicks are nearly a year old (c. 0.13/day) (Shultz 2002).

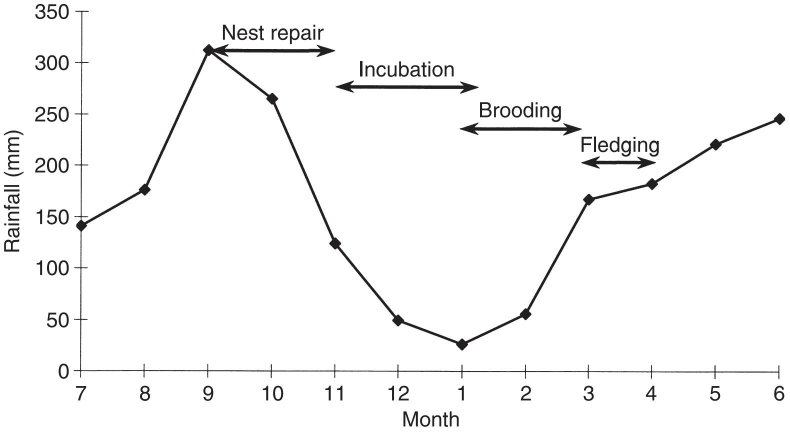

Figure 7.1. The timing of the crowned eagle breeding cycle in relation to rainfall in Taï National Park.

Ranging and activity

Crowned eagles are territorial and regularly display above the canopy near their nest sites. Despite these obvious territorial displays, little is known about patterns of home range use in any habitat. They are expected to use fairly small home ranges, because nest sites are evenly spaced and neighboring pairs are aggressive towards one another (Brown *et al.* 1982). Provisioning adults regularly return with food to the nest located near the center of their home range and thus are central place foragers (CPF) (Orians & Pearson 1978). This bias in space use means they should be found more often near the center of their home range than on the periphery and this will have implications on the encounter rate with different prey groups across their home range. In Taï, most primate home ranges are much smaller than the eagles' home range, and those groups that are found near the center of an eagle's territory should have higher encounter rates than primate groups on the periphery. We used radio telemetry to determine patterns of space use and the area exploited by each breeding eagle pair.

Methods

Two adult females and two juvenile eagles were captured and fitted with either tail-mounted or backpack radio transmitters with activity sensors. Eagles were captured using nooses attached to a piece of goat flesh. The piece of meat was then raised on a pulley system to a branch in a tree adjacent to the nest tree. Once captured, the eagles were lowered to the ground, hooded, and jessed for the duration of handling.

Ranging data were collected using two methods, depending on the signal strength of each radio signal. The transmitter for one female was fairly weak with a transmitting radius of no more than 250 m and it was not possible to maintain constant contact with the individual as she moved around her home range. In order to avoid biasing the locations we set up point locations across a predetermined grid that covered 16 km^2 and recorded presence or absence of individuals at each point. For the two juveniles, and the second female, we located individuals by searching across systematic transects. Once an individual's signal was heard, its exact location was determined using triangulation, and individuals were followed and locations recorded every ten minutes. If the individual remained inactive and the signal had not changed direction, only one point was registered until the individual moved and then two points were taken at 50 m intervals every five minutes. For evaluating space use, we took locations at hourly intervals to insure independence of the different point locations.

We also monitored eagle nest visits and eagle calls around each nest site to get a picture of the activity pattern of the eagles. Six nests were observed at least one day per month between December 1998 and December 1999. An observer sat under each eagle nest from approximately 7:00 to 17:00 hours on 26 days, totalling 312 hours of observation. Arrivals, departures, eagle vocalizations, and continuous behavioral observations were recorded during the observation period.

Results

The adult females were found more often near their nest sites than on the periphery of their range (see Figure 7.2). Females were found no further than 1625 m away from their nest on 61 hourly point locations (Shultz & Noë 2002). The juveniles were located at 183 hour samples across 31 days. Adult visits to the nests were more frequent in the mornings and in the late afternoon, whereas calls were most frequently recorded around mid-day (Shultz & Noë 2002). The juvenile eagles stayed within 200 meters on average (range 0–1200 m) of their nest site for the first ten months after fledging. After this period they were found increasingly far from the nests until their signals were rarely heard. During this period, regular searches for their signals were made across the research area. Although the data are insufficient to document where the juveniles were traveling, it is likely that they dispersed into areas of the park other than the research area. The lifespan of the transmitters was estimated to be approximately three to four years and at least one of the transmitters should have continued to transmit during the period when the locations became less frequent.

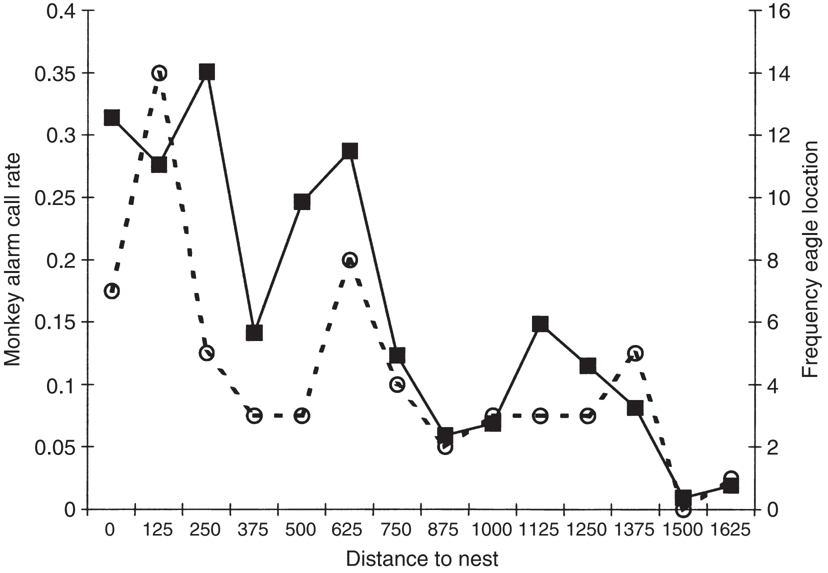

Figure 7.2. The relationship between eagle locations (circles), monkey alarm call rates (squares), and distance to the closest crowned eagle nest. Eagle locations and alarm call rates are significantly correlated ($r^2 = 0.47$, $p < 0.001$). Taken from Shultz & Noë (2002).

Eagle hunting behavior

Predation is an evolutionary contest, predators make behavioral decisions to maximize capture success, while prey employ counter-strategies to minimize their predation risk. The success of each strategy is dependent on the response given by the opponent. Predator hunting behavior can be broadly classified into two coarse strategies: sit-and-wait or searching. Sit-and-wait predators rely on surprise to catch their prey, hiding themselves until prey are within striking distance, whereas searching predators move through their environment until they encounter potential prey items. Many predators do not adhere exclusively to one hunting strategy, rather they employ a mixture of sit-and-await and searching behaviors. Of the main predators of primates in Taï, it has been suggested that crowned eagles and leopards ambush their prey and thus both rely on surprise by either hiding in dense vegetation or approaching a monkey group undetected and waiting for the optimal opportunity to capture an unwary individual. Once their presence has been detected, or an attempted attack has been unsuccessful, they move away from a group to find other less wary or alert individuals (Zuberbühler *et al.* 1999).

At other sites, crowned eagles have been observed to behave as sit-and-wait predators, dropping down onto an unsuspecting monkey group, as well as attacking on the wing from an unobserved vantage. In Taï, we have seen several instances where eagles position themselves in front of an approaching group and wait to attack until individuals have moved into trees directly below their perch (Shultz 2001). During two encounters, we have followed eagles as they track a monkey group, flying in large arcs around the group and then perching in the path of the approaching group. One occasion the eagle we were following changed its location three times as the monkey group changed direction. When it first flew over the monkey group, a male Diana gave a low intensity alarm call. The eagle then flew off in an oblique angle from the group for about 100 meters, then turned and perched in the path of the monkey group. Each time the group's trajectory changed, the eagle again flew away from the center of the group, then turned back and waited in the new anticipated path of the group. The monkeys appeared to be unaware of the eagle's movement, as they did not alarm call after the first encounter. The entire encounter lasted for more than an hour and a half.

Anecdotal evidence from Kibale forest (e.g. Leland & Struhsaker 1993) and Taï suggest crowned eagles may use cooperative hunting techniques to increase capture success, a trait seen in very few raptors. Research assistants in Taï have seen pairs of eagles attack monkey groups. However, as it is very difficult to observe two attacking eagles, it is unclear whether the two individuals are an adult pair, or a parent and offspring. It is generally believed that an attacking pair of eagles are both mature, but it is also possible that one individual is an older juvenile following a hunting parent.

Such behavior implies a fair amount of awareness in the eagles, as they were not only able to judge the direction of travel by the monkey group, but were able to respond and predict direction changes made by the monkey group. As eagles rely on surprise to attack successfully, it is necessary for them to be able to approach a monkey group undisturbed. An interesting implication of these observations is the apparent lack of effectiveness of vigilance by the monkeys. In the cases where we were able to follow individual eagles, the monkeys were unable to detect the eagle unless it was either attacking or flying directly over the group. Most models of sociality stress the adaptive importance of increased effectiveness of vigilance or decreased investment by individuals in vigilance behavior. Treves (2000) reviews the lack of a consistent group size affect in the primate literature. Two reasons may explain this inconsistency; one is that primate groups are generally larger than models predict for there to be an

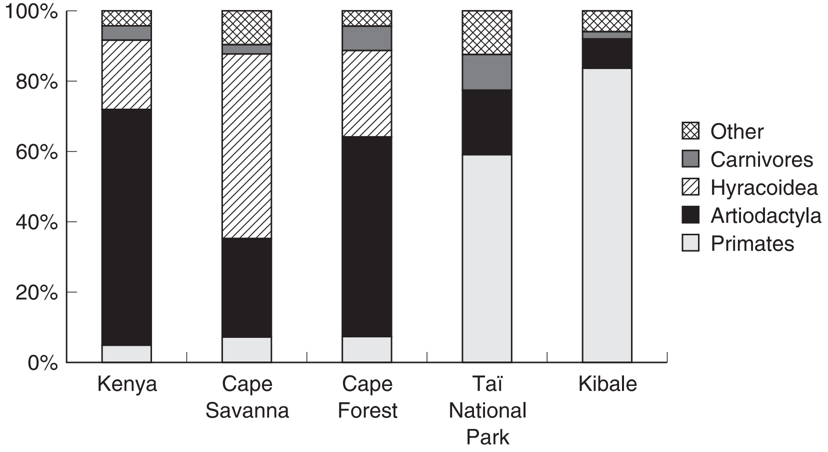

Figure 7.3. Variation in crowned eagle diets in different habitats across sub-Saharan Africa. Data are from Brown *et al.* (1982), Kenya; Struhsaker & Leakey (1990), Uganda; Boshoff *et al.* (1994), South Africa. Other category includes reptiles, birds, rodents, pangolins, and unidentified individuals. Figure from Shultz (2002).

effect of group size on individual vigilance levels and the second may be that vigilance is not the most important benefit of sociality. If individuals are not able to detect predators reliably in dense habitats, the benefits of sociality may lie more in communal defense and dilution rather than in increased vigilance.

Predator diet composition

Most predators eat more than one type of prey, but do not necessarily take each type in direct proportion to their abundance in the environment. Apostatic selection is commonly observed, where predators take a proportionally higher amount of common prey than rare prey (Murdoch 1969). However, in addition to selecting prey on abundance alone, predators prefer prey based on ecological characteristics such as body size, habitat use, activity pattern, and group size. Predators that preferentially prey on only a few of the available prey spectra are known as specialist predators, whereas predators that take prey roughly according to abundance are generalist predators.

Comparative data about crowned eagle diets in different habitats show them to be relatively opportunistic rather than specialized predators (see Figure 7.3). Hyrax and antelope dominate eagle diets in savannah habitats, as densities of medium sized primates are generally low; where