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Chimpanzees–red colobus monkeys: a predator–prey system

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Abstract. The arms race between a predator and its prey may lead to different outcomes in different environments. To follow such 'coevolution' between chimpanzees, *Pan troglodytes*, and red colobus monkeys, *Colobus badius*, populations of both species living in the Gombe Stream National Park, Tanzania, and in the Taï National Park, Côte d'Ivoire, were compared. Humans have a much stronger impact on hunting in Gombe than in the Taï forest and when this is accounted for, Taï chimpanzees hunt more frequently than Gombe chimpanzees. After excluding this human effect, Gombe colobus monkeys are more aggressive towards chimpanzees than Taï colobus monkeys, which might explain why Gombe chimpanzees are more afraid of the colobus than Taï chimpanzees. The initial factor that might have led to these differences is the lower height of trees in the woodland of Tanzania than in the tropical rainforest of Côte d'Ivoire. A dynamic arms race is in progress between the two species in both sites. In one case Gombe chimpanzees initiated a new strategy that was followed by a counter-response from the red colobus monkeys. A scheme is proposed that could account for the evolution between the two species from the aggressive colobus and fearful chimpanzees in Gombe to the more wary colobus and confident chimpanzees in the Taï forest.

The long-term evolution of species involved in a predator–prey interaction has frequently been regarded as an arms race or a case of coevolution (Dawkins & Krebs 1979; Rothstein 1990; Endler 1992). The specific evolutionary response of both species may be affected by the environment in which the interactions are taking place. Comparisons of the hunting behaviour of different populations of the same species have revealed that hunting success can vary from population to population (lions, *Panthera leo*: Schaller 1972; Van Orsdol 1984; hyaenas, *Crocuta crocuta*: Kruuk 1972; Mills 1990; chimpanzees, *Pan troglodytes*: Goodall 1986; Boesch & Boesch 1989; Uehara et al. 1992). Similarly, hunting success varies between different prey species (lions: Schaller 1972; hyaenas: Kruuk 1972). These results underline the complexity of the prey–predator system, but true cases of coevolution with specific defences of the prey continually counteracted by specific defence-breakers in the predator are notably rare. To understand the dynamics of such a system more observations are needed.

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The case of the chimpanzee is potentially promising since hunting success varies between populations hunting the same prey species in similar environmental conditions (in trees). Gombe chimpanzees in Tanzania hunt red colobus monkeys, *Colobus badius*, mainly as solitary hunters and their hunting success, about 50%, seems to be independent of the number of hunters (Busse 1978; Goodall 1986). In contrast, Taï chimpanzees in Côte d'Ivoire hunt the same red colobus monkeys mainly in groups with a hunting success that depends upon the number of hunters (Boesch & Boesch 1989). Behavioural observations strengthen the impression of differences between these two populations: Gombe chimpanzees are afraid of attacks by adult colobus monkeys and capture principally infants (78% of the prey), which they regularly snatch from the mother's belly without harming the mother (Goodall 1986). Taï chimpanzees seem unafraid of adult colobus and regularly capture adults (46% of the prey). This includes males that mob. They always kill both the mother and the infant when they catch the mother (Boesch & Boesch 1989). J. Goodall (personal communication) suggests that Gombe

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chimpanzees confuse the monkeys by chasing many targets in different directions, whereas we suggest that Taï chimpanzees actively overcome the monkeys' defence by concentrating on one selected quarry (Boesch & Boesch 1989).

With the data available so far, the differences between Gombe and Taï are difficult to explain. First, methodological contradictions confuse such a comparison, for example observation conditions, definitions of hunting and cooperation, and estimation methods differ between the two study sites (Goodall 1968, 1986; Teleki 1973; Wrangham 1975; Busse 1977, 1978; Boesch & Boesch 1989; Wrangham & van Bergmann-Riss 1990). Second, detailed observations of the interactions between the two species are missing from both populations. In addition, to make such a study reliable, one must be sure that the observers do not affect the behaviour of one (or both) of the two interacting species. As chimpanzees are habituated to human observers, but the red colobus monkeys are not, the observers may have a double predator effect in frightening away the prey. Goodall (1986) mentioned that red colobus monkeys did not react to the presence of a group of chimpanzees in a nearby tree, when, during the early days of her study, she observed them from the other side of the valley through her binoculars. Later, however, Gombe observers considered colobus to be fearful of the chimpanzees and to avoid them actively (Busse 1977, 1978; Teleki 1981; Wrangham & van Bergmann-Riss 1990; but see Wrangham 1975 who questioned this aspect). This apparent contradiction requires more scrutiny, especially in the comparison of two studies, Taï and Gombe, where the effect may differ in importance.

To investigate these questions, I spent 19 weeks in Gombe Stream National Park, Tanzania, in April to June 1990 and 1992 and used exactly the same methods in recording both Gombe and Taï chimpanzee interactions with red colobus monkeys. The comparative data were collected in August to October 1990 and January to March 1991 in Taï National Park, Côte d'Ivoire.

METHODS

I present here only methods relevant to the present study. More information can be found in Goodall (1986) for the Gombe study site and in Boesch & Boesch (1983, 1989, 1990) for the Taï study site.

The Two Habitats

Gombe

The chimpanzee community under study lives in the central part of the Gombe Stream National Park around the Kakombe Valley. This national park is on the shore of Lake Tanganyika in western Tanzania and consists of a mixture of five habitats, including 33% open woodland, 48% thicket woodland, 12% vine tangle, 4% closed forest and 3% miscellaneous habitats (Collins & McGrew 1988). The closed forests grow along the rivers where tree height is about 30 m, whereas the woodlands, including the vine tangle, grow on the steep slopes of the valley and tree height is at most 10–15 m (see Goodall 1986 for more details of the habitats).

Taï

This chimpanzee community lives near the western border of the Taï National Park, Côte d'Ivoire. The forest in this area is a homogeneous moist tropical rainforest with only the swamp forest along the rivulet less densely forested (see Boesch & Boesch 1983 for more details of the habitats). Canopy trees average 30 m in height and are dominated by the emergent trees 40–60 m high.

The Chimpanzees

In both study sites, all individual chimpanzees are identified and are followed on foot each day from nest to nest.

Gombe

The Kasakela study community consists of long-haired chimpanzees, *P. t. schweinfurthii*, and has been habituated to human observers since 1965 (Goodall 1986). The chimpanzees are regularly supplied with a small quantity of bananas every month (see Goodall 1986 for more detail of the provisioning methods). During my stays, I followed the chimpanzees on my own as in the Taï forest, switching between focal individuals according to my judgement of their motivation to hunt. In addition, I sometimes accompanied the two

Tanzanian observers who follow a target individual from nest to nest every day for long-term records (which is the standard procedure at Gombe). I could identify the individuals reliably after 5 days in the field. In spring 1990, the Kasakela community included seven adult males, eight adult females and 17 subadults.

Taï

The Taï community consists of the so-called 'masked' chimpanzees, *P. t. verus*, and has been habituated to human observers since 1983. During my study on the predatory behaviour of the chimpanzees I never systematically followed target individuals but rather tried to increase my chance of being with the individuals that may start a hunt by switching between them according to my judgement of their motivation to hunt (Boesch & Boesch 1989). In addition, during a hunt, I recorded the behaviour of all hunters rather than concentrating on one individual. In autumn 1990 (when the first set of comparative data was collected), the community included seven adult males, 15 adult females and 36 subadults.

The Red Colobus Monkeys

In both study sites, the red colobus have been studied only briefly and are not habituated to human observers. To evaluate their detectability by predators in the field, I used the following measure: for each sighting and call of a particular species of monkey within the same 60° auditory angle I entered one data point. I recorded only the first sighting/call per species within this 60° angle, considering any additional calls within this 60° angle as being given by members of one group. Calls given outside this angle were considered to come from another group and a new data point was entered. I used this simple measure because I assumed that chimpanzees have auditory abilities at least as good as my own and can identify the prey species from a single call. Therefore, any additional call from the same direction would yield no additional information for the potential hunter. In addition, I measured monkey detectability when I was following the chimpanzees as well as when I was alone in the field to evaluate the impact of the chimpanzees' presence on the monkeys' vocalizations.

Gombe

The red colobus monkeys of Gombe, *C. b. tephrosceles*, are much more brownish than the Taï subspecies, with the red limited to a cap on the head. Their weight and body size are similar and I noticed only one call that differed: an aggressive, high-pitched shriek they use when facing the chimpanzees (named tschick call by Struhsaker 1975). Group size, density and structure (Clutton-Brock 1972) seem to be the same as in Taï.

Taï

The Taï red colobus monkeys, *C. b. badius*, are red with a black back. In contrast to the eastern subspecies, females give a copulation call for most copulations. Groups average 36 individuals with a home range of about 1 km^2 and they live in multi-male groups (Galat & Galat-Luong 1985).

Data Collection

While following the chimpanzees on my own, during each close encounter between a chimpanzee and a red colobus monkey, I tried to remain as inconspicuous as possible by moving under thick leaf cover, by lagging further behind the chimpanzee or approaching the colobus from another direction than the chimpanzees when in more open habitat. I thereby accepted the risk of losing sight of any individual chimpanzee or of losing the group completely. Whenever I noticed the colobus reacting to my presence, either by calling or moving away in the trees, I would immediately slow down and choose thicker vegetation to be less conspicuous. In Taï, the much thicker vegetation cover provided by the many tree layers makes careful human observers generally less obvious. The problem in Taï forest is mainly a result of the noise of human walking, and I trained myself to walk beneath a group of red colobus without their noticing my presence. In Gombe, I spent several days with the Tanzanian observers following their target chimpanzee. Their objective was not to lose sight of the chimpanzee and to follow all its moves. I checked especially for an influence of their presence on the red colobus. From August to October 1990 and January to March 1991 in Taï, I collected similar data for two periods of

Table I. Detectability, in number of calls per h, of the different monkey species in the two habitats (see Methods for further explanation of the data collection procedure)

Monkey species	Taï chimpanzees		Gombe chimpanzees	
	Present	Absent	Present	Absent
Colobus badius	0·39	1·08	0·14	0·18
Colobus polykomos	0·13	0·29	—	—
Colobus verus	0·01	0·05	—	—
Papio anubis	—	—	0·73	1·43
Cercopithecus mitis	—	—	0·10	0·15
Cercopithecus ascanius	—	—	0·10	0·06
Cercopithecus diana	0·59	1·21	—	—
Cercopithecus petaurista	0·05	0·29	—	—
Cercopithecus mona	0·06	0·26	—	—
Cercopithecus nictitans	0·01	0·03	—	—
Cercocebus atys	0·16	0·26	—	—

Chimpanzees are considered to be present when I was following some of them by sight and absent when I did not see or hear any of them for more than 1 h.
— Monkey species absent in the considered study site.

9 weeks in exactly the same way as I did at Gombe in an attempt to make the data as comparable as possible.

RESULTS

Colobus' Reaction to Chimpanzees

Reaction upon hearing chimpanzees

Red colobus monkeys are noisier in the Taï forest than at Gombe (difference in the daily group detection rates between the two populations; $z=6{\cdot}46$, $P<0{\cdot}001$; Table I). This is mainly the result of frequent copulation calls and the quarrels these elicit among the males of the group. In addition, red colobus monkeys in the Taï forest vary the frequencies of their vocalization depending upon the presence of chimpanzees, becoming more silent whenever chimpanzees have been heard ($z=4{\cdot}43$, $P<0{\cdot}001$). In contrast, Gombe red colobus do not change their frequency of calling in relation to the chimpanzees' presence ($z=1{\cdot}05$, $P=0{\cdot}29$). They tend to produce more alarm calls when they see the chimpanzees, in order to organize themselves while facing them (see below).

In both sites, other monkey species are more easily detected than the red colobus (Table I): for example, in Gombe, the baboons are at least five times noisier than colobus monkeys but they become more silent when chimpanzees are around. In Taï, diana monkeys are easier to detect, and like all other monkeys at Taï, they become quieter in the presence of the chimpanzees. Thus, both chimpanzee populations concentrate their hunts on monkey species that are not the easiest to detect.

Reaction upon seeing chimpanzees

Within a few days at Gombe, it became obvious that red colobus monkeys are afraid of human observers. I appeared under a group of red colobus in seven instances, while walking alone and silently on the paths of the park; in all cases after a first alarm call, all monkeys fled in different directions giving additional alarm calls, stopping only after they had put three to four trees between us. Males would then face me but would move further away whenever I watched them while nodding my head. In contrast, when following the chimpanzees discreetly and alone and by trying to remain behind them hidden under some branches or shrubs, I could confirm Goodall's impression that the red colobus are not afraid of the chimpanzees and that normally infantless adults tend to move in trees towards the approaching chimpanzees.

Therefore, during my stay at Gombe I distinguished two levels of double predator effect caused by human observers. A low level effect

Table II. Frequency of double predator effect on red colobus due to human observers following the chimpanzees in the two study populations (see text for further explanations; $\chi^2=33{\cdot}19$, $df=1$, $P<0{\cdot}001$)

	Taï	Gombe
None	135	45
Low level	4	9
High level	0	11
Total	139	65

Presence or absence of a double predator effect was possible to judge only when the observer could see the colobus, which should see and be seen by the chimpanzees.

Table III. Percentage of different reactions of red colobus monkeys to the visual presence of chimpanzees in two different populations when a double predator effect was present or absent

	Double predator effect			
	Taï		Gombe	
	No	Yes	No	Yes
Panic	0	0	2	30
Flee/none*	93	100	42	20
Threat	0	0	13	10
Mobbing	7	0	2	40
Total	71	6	45	20

Panic indicates a high level of double predator effect by humans. A threat is when the colobus advance in the trees towards the chimpanzees calling aggressively. Mobbing is an attack against the chimpanzees with physical contact.

*Flight and no reaction are combined since they are regularly observed in the same group shown by the same individual during the encounter.

occurs when one or a few monkeys, after seeing the observers, move away from the intruder to be out of their sight. By doing so they should move at most to the adjacent tree to the one where they saw the observers. A high level effect occurs when many monkeys run further away into many different trees with alarm calls after seeing the observers. In attributing these two levels, care is given that such a reaction immediately follows a movement of the human observer and is independent of any movements of the chimpanzees.

The double predator effect plays a significantly larger role at Gombe (31% of all encounters) than Taï (3% of all encounters; Table II). In addition, no high level of human effect has been seen at Taï. Habitat differences between the two sites might explain such an effect. At Gombe, trees in the woodlands (93% of Gombe Stream National Park) are smaller and occur at lower densities than in the Taï forest, and this improves the view from the trees to the ground. Colobus monkeys see human observers much more readily at Gombe. In addition, the distance between them and the observers is much smaller and can sometimes elicit a real panic in the monkeys. Red colobus flee immediately when they see humans close by.

Does this double predator effect caused by humans affect the way the red colobus face the chimpanzees (see Table III)? At Taï, red colobus seem to react to chimpanzees independently of the effect humans may have on them (Fisher exact test: $P>0{\cdot}05$). On the other hand, Gombe red colobus panic more frequently when humans are around (Fisher exact test: $P=0{\cdot}002$). These data still underestimate the effect of humans at Gombe, since I entered only one data point per hunt. In the hunts in which chimpanzees attack frightened colobus, more than one type of reaction of the colobus can be seen. When attacked, the monkey would respond aggressively, and these reactions explain the high number of aggressive reactions despite the double predator effect: in 13 of 20 cases with the double predator effect, chimpanzees started to hunt and colobus responded aggressively in eight cases.

Normally, when red colobus spot a human observer, they move away from him immediately. However, at Taï, to do so the colobus monkeys most frequently climb higher in the emergent trees (the upper layer of trees in a tropical rainforest is between 40 and 60 m high) taking them out of sight of the human observers. They do not disperse and their defence is not disrupted. In contrast, at Gombe, the colobus can only rarely move higher owing to the small size of the trees and have to flee into adjacent trees so as to increase their distance from human observers. As they move in all directions away from the observers, they disrupt group cohesion and disorganize their defence, which makes them more vulnerable to hunters.

The red colobus' reactions to the chimpanzees differ in the two sites. When human observers do not affect the encounters, Gombe red colobus are

much more aggressive towards the chimpanzees than Taï red colobus (Table III; Panic plus Flee/No reaction versus Threat plus Mobbing: $\chi^2=33{\cdot}8$, $df=1$, $P<0{\cdot}001$). Generally in Gombe woodlands, the red colobus would immediately advance in the trees towards the approaching chimpanzees and start to make aggressive tschick calls. If the chimpanzees started to climb towards the colobus, as if to test their reactions, the adult monkeys would immediately come down the tree, while the females with infants and juveniles remained behind. The colobus not uncommonly attack the chimpanzees without the latter moving further. Gombe colobus are rather cooperative whenever they face the chimpanzees and only rarely would a single one attack them with others as a back-up guard. If the trees were small, i.e. less than 12 m high, the colobus would chase and pursue one or several chimpanzees on the ground in spite of the presence of other chimpanzees. In five of the 16 close encounters (less than 10 m apart) that I saw without being spotted, the colobus adults attacked and pursued screaming adult chimpanzees on the ground for about 20 m without other group members supporting the victim(s). The risks of wounds resulting from those attacks are not negligible: three times Frodo had cuts in the arm or the ears following seven mobbings which I observed. On one occasion he received two deep cuts in the fore-arm that were still wide open 10 days later.

Thus, the Gombe red colobus seem to pursue a harassing strategy inasmuch as they threaten the chimpanzees each time they see them in trees, whether the latter are about to hunt or not. Colobus may anticipate a possible threat and prevent it by threatening first. In addition, if chimpanzees interested in the monkeys are less than 10 m away, colobus mob them immediately with lots of threatening calls and some actual attacks. In four situations, the mere sight of the chimpanzees on the ground under the red colobus prompted their aggressive attacks because the monkeys were in such small trees. If the chimpanzees are not looking for them, lone individuals can attack them very suddenly without any previous warnings. Once Wilkie, the alpha male chimpanzee, was moving on his own under a group of colobus very close to the ground in vine tangle, when suddenly an adult male colobus jumped on his back. Wilkie ran away silently after brushing the colobus off.

Chimpanzees' Reactions to Colobus

Searching for colobus monkeys

I did not notice any particular behaviour of the Gombe chimpanzees aimed at finding prey before they heard or saw it. In other words, hunting by Gombe chimpanzees seems to be mainly opportunistic (see also Busse 1977; Goodall 1986; Boesch & Boesch 1989 about this aspect). In contrast, not only do Taï chimpanzees search for prey in half of the hunts (Boesch & Boesch 1989), they also often use indirect clues of their favourite prey given by other monkey species.

Taï chimpanzees moved more frequently under calling red colobus monkeys than under other monkeys (Table IV). Black-and-white colobus can be heard from further away than diana monkeys, but they rarely call more than once and remain totally silent after having detected the chimpanzees. Searching for them is very hazardous and chimpanzees rarely do so. However, the striking difference in the hunting frequency of the chimpanzees after arriving under the monkeys they heard (diana versus red colobus: $\chi^2=13{\cdot}44$, $df=1$, $P<0{\cdot}001$) seems to indicate that the detours chimpanzees make to arrive under these monkeys are for different purposes. They moved towards the calling red colobus in order to hunt them (57% of the time they come under such colobus they hunt them compared with only 3% of hunting on other monkey species associated with them), whereas they moved towards calling diana monkeys in order to look for other monkeys to hunt (only 8% of the time they arrived under diana monkeys did they hunt them compared with 44% of the time they hunted colobus monkeys associated with them; $\chi^2=30{\cdot}1$, $df=1$, $P<0{\cdot}001$). Chimpanzees at Taï seem to be aware of the fact that red colobus monkeys are regularly found in multi-species groups (87% of their time, Galat & Galat-Luong 1985) and they use the calls of the more noisy diana monkeys (55% of their time diana and red colobus monkeys are together, Galat & Galat-Luong 1985) as a way to find their favourite but less noisy prey.

Why do Taï chimpanzees not hunt diana monkeys, which are the most readily detected prey, more frequently? First, diana monkeys are about half the size of the colobus monkeys (Boesch & Boesch 1989). Further, when chimpanzees stop under them, diana monkeys swiftly and quietly move six or seven trees away. In contrast, colobus

Table IV. Frequency with which Taï chimpanzees detected the different monkey species and their behaviour following it

Species calling	Frequency of detection	Chimpanzees' reactions			Hunted when detected by calls of other monkey species
		Detour	Hunting monkeys detected	Hunting another species	
Colobus badius	143	27	39	2	8
Colobus polykomos	51	6	1	—	3
Cercopithecus diana	236	12	2	11	—
Other monkeys	117	—	1	—	2

I collected the data only when I was following chimpanzees by sight. Chimpanzees were observed either to move under the monkeys ('Detour') or to start to hunt either the detected species or another species associated with them. Chimpanzees moved more frequently under calling red colobus monkeys than under other monkeys (comparison for red colobus and diana monkeys between heard versus detour plus hunting: $\chi^2=29{\cdot}57$, $df=1$, $P<0{\cdot}001$; comparison for red and black-and-white colobus between heard versus detour plus hunting: $\chi^2=9{\cdot}19$, $df=1$, $P<0{\cdot}01$).

monkeys start to move only once the chimpanzees show an intention to hunt. In addition, diana monkeys are more agile and move much more rapidly between trees than colobus monkeys. The only four hunts on diana monkeys I observed occurred when chimpanzees surprised a group of them low in small trees. These three combined factors seem to render diana's hunting uneconomical in the Taï forest.

Reactions after hearing colobus

Although I have shown that human observers do influence red colobus behaviour at Gombe, the question remains whether the chimpanzees change their hunting behaviour in response to a double predator effect. During my observations, Gombe chimpanzees hunted 4·87 times more frequently when there was a double predator effect (Table V). Some behavioural observations indicate that while testing the colobus by moving underneath them, the chimpanzees are especially wary of any sudden reaction of the colobus. When colobus suddenly flee in the trees, chimpanzees would immediately rush and climb up to pursue them. Chimpanzees do this regardless of who is responsible for frightening the prey and thus the fear colobus have of humans directly helps the chimpanzees. Sometimes, I even had the impression that the chimpanzees moved rapidly under the colobus with no other purpose than to make the human observers follow them more quickly and noisily and thus to increase the chance of colobus spotting them.

Owing to this difference, in the following I compare Taï and Gombe chimpanzees' reactions

Table V. Gombe chimpanzees' reactions after hearing red colobus calling, when a double predator effect was present or absent ($\chi^2=17{\cdot}86$, $df=1$, $P<0{\cdot}001$)

Chimpanzees' reactions	Double predator effect	
	Yes	No
No interest	2	15
Detour	4	16
Test	1	8
Hunt	13	6
Total	20	45

Four reactions are considered; no interest, when the chimpanzees go on with their activities after having heard red colobus calling; detour, when they move towards the group they have heard; test, when in addition they charge or approach the colobus; and hunt, when they try to catch one of them.

only when there is no double predator effect. Taï and Gombe chimpanzees are equally likely to move towards the red colobus once they have heard them (no interest versus detour, test and hunt; $\chi^2=2{\cdot}77$, $df=1$, $P=0{\cdot}09$; Table VI). However, at Taï, this result is affected by the fact that chimpanzees have a distinct hunting season in August–November. In comparison, during the non-hunting season (December–July), they are even less attracted to the red colobus monkeys than Gombe chimpanzees (no interest versus detour, test and hunt; $\chi^2=15{\cdot}63$, $df=1$, $P<0{\cdot}001$).

Once under the colobus, their reactions differ: Taï chimpanzees start to hunt more frequently (detour and test versus hunt; $\chi^2=17{\cdot}69$, $df=1$, $P<0{\cdot}001$), whereas Gombe chimpanzees either

Table VI. Comparison of the two chimpanzee populations' reactions to the red colobus in encounters without a double predator effect once the colobus have been detected

Chimpanzees' reaction	Taï		Gombe %
	Hunting season %	Non-hunting season %	
No interest	51	88	63
Detour	16	4	20
Test	1	1	10
Hunt	32	7	7
Detection (Total)	135	98	83

just look at them or test their reaction by displaying under their trees, looking for different trees to climb up, or climbing but never reaching the height of the colobus (which is our criterion for a hunt, see Boesch & Boesch 1989). This difference is not affected by season in Taï chimpanzees (hunting/non-hunting season: detour and test versus hunt; $\chi^2=0{\cdot}02$, $df=1$, $P>0{\cdot}05$), which remain more keen to hunt than Gombe chimpanzees once under them throughout the year.

Gombe chimpanzees are more afraid of the aggressive reactions by red colobus than are their counterparts in the Taï forest and they often do not dare face them. When testing the Gombe red colobus, the chimpanzees evaluate their reactions without coming close enough to be attacked. If the colobus stand their ground or attack, the chimpanzees will usually climb down and look for some other parts of the colobus group, with the male colobus following the chimpanzees progression in the trees. If they find some infants easily attainable, they rush towards them. However, whenever the colobus face them, all Gombe chimpanzees, with one exception, stopped their approach and retreated to a safe distance. The only exception during my stay was Frodo, the keenest and bravest male hunter at the time. He sometimes continued and, by rushing and zigzagging through the aggressive adult colobus, pushing them aside if needed, he would try to catch one of the youngest. Once I saw the chimpanzees test a group of colobus for 45 min in a small woodland at the limit of the grassland, and despite the fact that 12 of them were cornered in two trees within the savanna with only one tree bridge to the forest, none of the 15 chimpanzees dared to climb up. On the contrary, two adult male colobus chased one chimpanzee around on the ground.

Table VII. Reaction of the Gombe chimpanzees when in visual contact with the red colobus in a continuous and interrupted canopy

Canopy structure	When hunting	When only detouring or testing
Continuous	12	7
Interrupted	21	25
Total	33	32

When Taï male hunters face a mobbing group of colobus monkeys, they always respond by trying both to repel them and to capture one or to pull one of them by the tail or a limb towards the ground. If the colobus pressure is too great, the hunters will retreat for some metres, but in most cases the hunt will go on against the same colobus group. Only colobus mobbing subadult chimpanzees usually interrupt a hunt.

Previously, Wrangham (1975) proposed from 12 well-observed hunts that the chimpanzees at Gombe prefer to hunt colobus when they find them in trees with interrupted canopy cover, since there they could more easily corner them. However, hunting is not affected by the continuity of the canopy cover ($\chi^2=1{\cdot}65$, $df=1$, $P>0{\cdot}05$; Table VII). Generally, the canopy at Gombe is more frequently interrupted than continuous and so hunting is more frequent in interrupted canopy area. However, the data do not show that chimpanzees prefer to hunt in trees with interrupted canopy cover.

Reactions when hunting colobus

My observations of hunting over 19 weeks represents a limited sample of what Gombe

Table VIII. Hunting strategies of the Gombe and Taï chimpanzees with red colobus monkeys

Site and study period	Number of hunts	Solitary A	Similarity B	Synchrony C	Concordance D	Collaboration E
Gombe						
1973–1975	45	26	8	5	3	3
1990–1992	17	4	4	3	4	2
N	62	30	12	8	7	5
%		48	19	13	11	8
Taï						
1984–1986	78	6	5	9	9	49
%		8	6	11	11	63

The last four categories are group hunts. Similarity: all hunters concentrate similar actions on the same prey but without any spatial or time relation between them; synchrony: hunters concentrate similar actions on the same prey and try to relate in time to the others' actions; coordination: hunters concentrate similar actions on the same prey and try to relate in time and space to the others' actions; collaboration: hunters perform complementary actions, all directed towards the same prey (Boesch & Boesch 1989).

chimpanzees do. Table VIII presents my observations analysed using our classification of hunting tactics (Boesch & Boesch 1989), together with hunting data from the long-term Gombe predation files from 1973 to 1975.

Taï chimpanzees hunt more in groups (comparing column A with B+C+D+E in Table VIII: $\chi^2=29{\cdot}94$, $df=1$, $P<0{\cdot}001$) and collaborate more when in groups (comparing columns B+C+D with E in Table VIII: $\chi^2=24{\cdot}39$, $df=1$, $P<0{\cdot}001$) than Gombe chimpanzees. Whenever Gombe chimpanzees hunt in groups, they tend to hunt independently, each chasing a different target, usually in different directions. They could be described as performing 'simultaneous solitary hunts' (81% of the hunts), whereas such hunts in Taï chimpanzees are much rarer (26% of the hunts; comparing columns A+B+C with D+E in Table VIII: $\chi^2=41{\cdot}8$, $df=1$, $P<0{\cdot}001$). Goodall (personal communication) proposed that the chimpanzees profit from the disorder created in the colobus' defence by the other hunters. More precisely, an individual, at present usually Frodo, would face the colobus while the others might place themselves low in adjacent trees where colobus are or might come. Only once the initial hunter has succeeded in making some colobus run away would the others attack whichever young colobus happened to move near their tree.

The important point in comparing the two populations is not that one is more sophisticated than the other, since Gombe chimpanzees collaborate in a comparable way to Taï chimpanzees. I once saw Frodo slowly driving the colobus down the slope in a region of high forest, while Beethoven and Prof chased them by climbing up under their line of retreat, whereas Evered, looking up at this progression in the trees, ran fast on the ground to get ahead of their advance and climbed into a tree in their path. As at Taï, the oldest male was taking up the more demanding role. The key point is that the Gombe chimpanzees, with their simple technique, achieve a success directly comparable, if not superior (in number of multiple captures), to the Taï chimpanzees; thus there is no selective pressure for them to elaborate their hunting techniques. Taï chimpanzees are in a rather different situation: human interference does not increase their success; and higher trees and more wary colobus make the hunting more difficult and time consuming. All these factors force the chimpanzees to elaborate their hunting techniques to keep hunting profitable.

In recent years, a change in the hunting behaviour of Gombe chimpanzees seems to have occurred; they hunt more in groups than they did before (comparing column A with B+C+D+E for the data from 1973–1975 with those from 1990–1992; $\chi^2=5{\cdot}97$, $df=1$, $P<0{\cdot}02$). This seems to be the group response to the especially large contribution of one male, Frodo. Other group members exploit his remarkable ability to face the colobus and put them to flight. However, the collaboration level remains rather low (comparing columns B+C+D with E for the data from 1973–1975 with those from 1990–1992; $\chi^2=0{\cdot}001$, $df=1$, $P=0{\cdot}97$).

DISCUSSION

Double Predator Effect at Gombe

These data suggest that at Gombe the observation methods were biased by an important double predator effect, since colobus monkeys are afraid of human observers and chimpanzees make use of this fact. The small distance between colobus and observers following their target chimpanzee affects the chimpanzees because the forest canopy is low. As this conclusion is at odds with most analysis of predation at Gombe, the question is whether it is a recent effect or if it had been overlooked before. Goodall (Table 11.2 in 1986) gives details of all captures observed since the beginning of the study in 1960. If we transform these data to a monthly capture rate (see Fig. 1), a striking result emerges. For the first 11 years (1960–1971) of the study, the chimpanzees had a fairly constant capture rate of 0·51 mammals per month (variance=0·037, SD=0·19), including 0·14 red colobus monkeys per month (variance=0·001, SD=0·038). This first period was also the one with the major changes in the methodology in Gombe research (Goodall 1986, pp. 51–55 and personal communication). From 1960 to 1963, naturalistic observations were the rule during the tedious habituation process, from 1964 to 1967 the artificial provisioning site and the progressive introduction of research assistants in the field were started. From 1968 to 1969, a major revision in the provisioning methods was undertaken so as to reduce the quantity and the way in which the bananas were given to the chimpanzees. At the same time, the first Tanzanian field assistants were introduced. Between 1970 and 1971, the banana provisioning was kept very low but an increased number of animal follows were performed nest to nest with most of the time observations made away from the provisioning site. Despite many methodological changes in the observation procedures, Gombe chimpanzees hunted for 11 years with a very stable hunting rate.

In 1972 and for the remaining 8 years, the capture rate for all mammals jumped to five times the previous level ($\bar{X}$=2·73, variance=0·93, SD=0·96; comparison between the two periods; Mann–Whitney *U*-test: $U=0$, $N_1=4$, $N_2=8$, $P<0·01$). For the red colobus, the increase was 13-fold ($\bar{X}$=1·81, variance=0·51, SD=0·25; comparison between the two periods; Mann–Whitney *U*-test: $U=0$, $N_1=4$, $N_2=8$, $P<0·01$). This

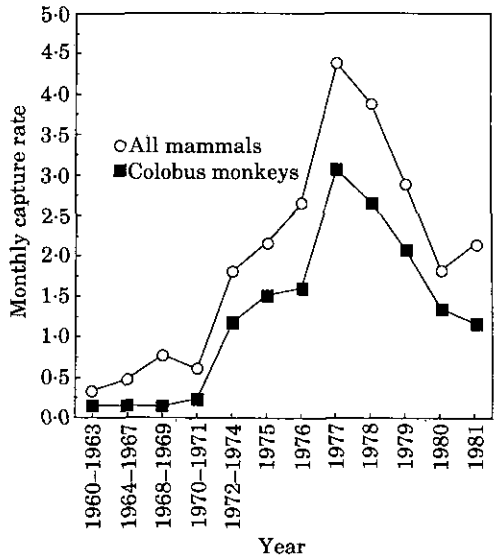

Figure 1. Monthly capture rate of all mammals and of red colobus monkeys by Gombe chimpanzees over 21 years (adapted from Goodall 1986).

occurred despite an absence of major methodological changes, i.e. banana feeding remained at the same level as in 1970–1971 and chimpanzees were followed on a daily basis from nest to nest. The only significant change in 1972 was the beginning of collaboration with the University of Stanford, which sharply increased the number of students following the Gombe chimpanzees. Further changes followed the kidnapping in 1975 of some students, as a consequence of which all chimpanzee follows from 1976 onwards were done only by the Tanzanian field assistants.

Thus, during this 21-year period at Gombe, two important changes in the number of observers following the chimpanzees led to related changes in the hunting success of the chimpanzees. I therefore suggest that the double predator effect resulting from human observation has a long history at Gombe and that as early as 1972 it significantly increased the hunting performance of the chimpanzees.

Estimation of Predation Rate

During my stays at Gombe, a double predator effect resulting from the Tanzanians following a target was at work in 71·4% of the encounters between the two species, and the chimpanzees

Table IX. Behavioural changes in the hunting tendencies of the Gombe chimpanzees when two Tanzanian observers were present or absent

Chimpanzees' reactions	Tanzanian observers	
	Absent %	Present %
No interest	57	42
Detour	21	19
Test	11	3
Hunt	11	36
Total	72	31

adapted themselves to it. Their tendency to move under a group of colobus when alone or with a Tanzanian team remained the same ($\chi^2=1{\cdot}95$, $df=1$, $P>0{\cdot}05$), but once near the colobus they were more prepared to hunt when with Tanzanians than when followed only by me ($\chi^2=5{\cdot}98$, $df=1$, $P<0{\cdot}02$; Table IX). This requires a revision in the estimated predation rate by the Gombe chimpanzees, for they were based on the assumption that chimpanzee hunting behaviour is unaffected by the presence of human observers (Wrangham 1975; Wrangham & van Bergmann-Riss 1990). Table IX shows that Gombe chimpanzees followed by a pair of human observers hunt 3·2 times more frequently than when on their own.

To estimate a predation rate that corrects for the double predator effect, I suggest using the encounter rate between chimpanzees and red colobus monkeys and the hunting rate I measured in both sites. Assuming that the hunting tendencies shown by the chimpanzees when followed only by me is about the same as the one when they are really alone, and using the 1972–1975 period data for the time target chimpanzees were followed, Gombe chimpanzees when on their own (63% of the time) killed 23 colobus per year [time of daylight per year (2759 h) × chimpanzees' encounter rate with red colobus (0·15; see Table I) × chimpanzees' hunting rate on those red colobus (0·11; see Table IX) × chimpanzees' hunting success against red colobus (0·5; see Goodall 1986)]. When the chimpanzees were with Tanzanian observers (37% of the time), they killed 43 colobus per year [time of daylight (1621 h) × encounter rate (0·15; see Table I) × hunting rate (0·36; see Table IX) × hunting success (0·5; see Goodall 1986)]. Thus, Gombe chimpanzees kill 66 colobus monkeys annually. Gombe chimpanzees are known to have very irregular and sudden 'crazes' during which they hunt daily for a week or more (J. Goodall, personal communication). I did not observe such a craze and may thus be underestimating the hunting frequency. But if we include two such crazes each lasting 2 weeks, this would at most add 14 colobus monkeys to their annual kills.

The same estimation with the same method could be done with the Taï chimpanzees. For the 3 months of the hunting season, Taï chimpanzees kill 72 colobus [time of daylight (1095 h) × encounter rate (0·4 see Table I) × hunting rate for the hunting season (0·32 see Table VI) × hunting success (0·5)], but for the rest of the year they kill 53 colobus [time of daylight (3285 h) × encounter rate (0·4 see Table I) × hunting rate for the non-hunting season (0·07 see Table VI) × hunting success (0·5)]. This gives an annual kill rate of 125 chimpanzees for Taï chimpanzees.

In conclusion, the double predator effect has a long history in Gombe chimpanzee hunting behaviour and inflated the estimation of predation rates as early as 1972. Estimates taking this effect into account as well as the different hunting tendencies over the year at Taï, indicate that Taï chimpanzees seem to hunt red colobus monkeys more frequently than Gombe chimpanzees.

Chimpanzee–Red Colobus Interactions

Why do Gombe colobus monkeys harass their potential predator and not Taï colobus monkeys? At Gombe, the forest is very low and irregular, and includes patches of pure vine tangles without any trees at all. These latter patches are at certain periods of the year very rich in young leaves and fruits, so that colobus as well as chimpanzees forage in this very low section of the park. If chimpanzees were not afraid of colobus, all age and sex classes could sneak silently under such low colobus groups and attempt a capture. This would significantly increase the cost of predation for the colobus. To prevent that, the colobus constantly harass all age and sex classes of their predators, which hesitate before attacking. Twice, while following chimpanzees in such forest, the chimpanzees were attacked when not even aware of the colobus' presence. In addition, attacks on subadult chimpanzees can be more productive from the colobus' point of view because wounds can be serious (Prof lost part of a toe to them as

an infant and was thought for a while to be dying from his wounds) and these individuals should respect colobus even more (Prof started to hunt very late, only when fully adult; J. Goodall, personal communication). Thus, harassment by colobus should increase the fear of them especially in subadults and adult female chimpanzees and that could lead to adult males hunting later and being afraid of the adult male colobus. It seems to work even for the especially courageous Frodo, the only chimpanzee I observed to brave mobbing by adult colobus. He never tried to capture an adult and merely tried to avoid them to reach younger ones. Such a fear of adult colobus might account for the puzzling observations that whenever the chimpanzees kill one, the meat seems not to appeal to them as much as that of a younger colobus and regularly much remains untouched. Of the three adults out of 26 prey I saw being killed, only one was wholly eaten; of the two others, all but the viscera and one arm remained; this has regularly been observed.

Cooperation when Hunting Colobus

The fear of chimpanzees when facing adult male colobus has been reported from all study sites where both species occur (Gombe: Goodall 1986; Mahale: Uehara et al. 1992; Kibale forest: Ghiglieri 1984; R. W. Wrangham, unpublished data). Even at Taï, most subadult chimpanzees are respectful of mobbing colobus, but this fear seems to disappear in adult chimpanzees. Such fear of the prey changes the attitude of the predator: Taï chimpanzees look for a large group of adult monkeys and then organize themselves to overcome their defence. Gombe chimpanzees test the colobus before hunting, and if they hunt, they look for subadult monkeys, take advantage of any disorganization among the monkeys or bypass their defences (see Boesch & Boesch 1989). Whenever possible, they exploit the colobus' fear of human observers and rush to catch one when they show signs of panic. Thus, the difference in the level of cooperation in hunting between the two sites seems to originate in the distance at which chimpanzees and colobus encounter each other, which is influenced by the ecology of the habitats.

Hunting colobus at Gombe requires five times less energy for a single hunter (measured as the hunting time) than at Taï (Boesch, in press). The ecological conditions prevailing within the small woodlands of Gombe allow the chimpanzees to hunt opportunistically with a net benefit despite their fear of the adult colobus. Thus, no selective pressure requires them to collaborate more. However, when chimpanzees hunt red colobus in an environment with taller trees, as at Taï, the distance between the prey and the hunter is bigger and accordingly the time for the hunter to catch a prey increases. In addition, in a tropical rain forest, emergent trees rarely touch each other and chimpanzees are prevented by their weight from jumping between them as do the red colobus. This further increases the hunting time. If these additional costs make the hunting time exceed 39 min, which is the time needed by a single Taï chimpanzee to achieve a capture, hunting with the Gombe technique would not be profitable any more. Thus chimpanzees should capture larger prey when they hunt colobus in taller forests. There they have two options: either hunt less often because it is not worthwhile, or overcome their fear and capture more adult colobus.

Once chimpanzees have overcome their fear of adult red colobus, the colobus are at much greater risk. At Gombe, adult colobus are relatively safe from chimpanzees, contributing only 18% of 130 kills (Goodall 1986). At Taï, 45% of 132 prey were adult colobus ($\chi^2=22{\cdot}21$, $df=1$, $P<0{\cdot}001$). Red colobus at Taï seem aware of this risk as they never attack chimpanzees on their own, in contrast to colobus at Gombe. The higher proportion of adult individuals captured makes predation more costly for the red colobus. This has led to two qualitative behavioural changes in the colobus. First, they try to keep a large distance beween themselves and the chimpanzees and never face a chimpanzee on their own initiative. Second, Taï colobus are conspicuously more silent whenever they hear the chimpanzees. This in turn increases the cost of hunting for the chimpanzees and has forced them to invest in searching for prey that are less easy to find. The hunting behaviour of forest chimpanzees has had to become more intentional and planned as opportunistic hunting chances became rarer. Chimpanzees facing colobus that try to keep their distance must coordinate their hunting strategies better so that individuals can attack from different directions. This reduces the distance between the colobus and the chimpanzees and allows a capture. At Taï, collaborative

movements between the hunters are used in the majority of the hunts. The arms race between the chimpanzee and the red colobus seems to have led to qualitative behavioural changes in both the colobus and the chimpanzees.

Are Arms Races between Predator and Prey Stable?

The above discussion gives the impression that within one habitat the interactions between the two species are stable. Is that really the case? Having followed only the chimpanzees, I can provide observations that this is not true from the hunters' side. At both Taï and Gombe, individuals may start a new hunting strategy that may destabilize the chimpanzee/colobus system and restart the arms race. At Taï, Ulysse, who was 22 years old at the time, started to hunt alone because of the reluctance of other group members to hunt. To ensure a success, Ulysse tried hard to elicit mobbing from the red colobus by climbing very slowly and in a very conspicuous way towards them, obviously shaking the small sapling when he started to climb. This gave the colobus an exceptionally long time to organize themselves. In addition, Ulysse would always move especially slowly when crossing between two emergent trees towards the colobus. Such points are always a weak moment for the chimpanzees, and colobus concentrate their mobbing at such times. Ulysse was seen to cross back and forth until the colobus would attack him. When that happened, Ulysse would invariably try to capture one of the males. Thus, for the first time a single Taï hunter was very successful. If his strategy was copied by other chimpanzees, the cost of predation for the colobus could increase sharply. Similarly at Gombe, Frodo, an adult male, increased the cost of predation for the colobus by his behaviour. In 1990, he was 15 years old and had been known already for some years as the keenest hunter. Two years later his attitude had changed radically, for he was no longer repelled by mobbing adult colobus. In 1990, he always abandoned the hunting attempt when mobbed ($N=6$); in 1992 he always kept on hunting when mobbed ($N=4$) and he was always successful. Thus, mobbing colobus present a weakness when facing such hunters, for their proximity means it is only a question of time before Frodo and Ulysse capture a monkey, the former by avoiding the mobbers, the latter by catching one of them. Interestingly, Frodo captured mainly infants whereas Ulysse captured mainly adults. At Taï, Ulysse's behaviour became rarer when other group members were willing to hunt together as previously. At Gombe, Frodo's behaviour seems to have led to an increase in the number of chimpanzees taking part in the hunt whenever he succeeded in making them run (see above), and this led to an increase in the proportion of multiple kills: 31% of the hunts resulted in multiple kills during 1975–1981 (Goodall 1986), whereas this proportion increased to 55% in 1990–1992 ($\chi^2=5{\cdot}86$, $df=1$, $P<0{\cdot}02$). This could have a profound effect on the colobus population, and I would expect them to react to it. As the forest structure makes it difficult to increase distance, they may have only one solution: be even more aggressive. They may already have started, for visible wounds on Frodo seem to be more common, especially when compared with Goodall's report (1986) stating that they never saw wounds on chimpanzees after an attack on colobus. Thus, the arms race in Gombe between colobus and chimpanzee might be developing further. After he was badly wounded in the hunt of 9 May 1992, Frodo was not seen to hunt for 3 weeks. This shows how colobus anti-predator behaviour could work. Another observation that may indicate an instability in the hunting behaviour at Gombe is the fact that recently chimpanzees have tended to capture more infant/juvenile colobus than previously [27 out of 29 captures during my observation period versus 101 out of 130 prey in 1975–1981 (Goodall 1986); $\chi^2=3{\cdot}58$, $df=1$, $P=0{\cdot}06$].

In conclusion, the arms race between chimpanzees and red colobus monkeys under the influence of one environmental factor, tree height, has produced two different strategies. When trees are short, chimpanzees adopt an opportunistic hunting strategy limited by the aggressive response of red colobus monkeys. When trees are tall, chimpanzees adopt a more planned and collaborative hunting strategy because red colobus monkeys maintain larger distances from them.

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REFERENCES

Boesch, C. In press. Cooperative hunting in wild chimpanzees. *Anim. Behav.*

Boesch, C. & Boesch, H. 1983. Optimization of nut-cracking with natural hammers by wild chimpanzees. *Behaviour*, **83**, 265–286.

Boesch, C. & Boesch, H. 1989. Hunting behaviour of wild chimpanzees in the Taï National Park. *Am. J. Phys. Anthropol.*, **78**, 547–573.

Boesch, C. & Boesch, H. 1990. Tool use and tool making in wild chimpanzees. *Folia primatol.*, **54**, 86–99.

Busse, C. D. 1977. Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution*, **31**, 907–911.

Busse, C. D. 1978. Do chimpanzees hunt cooperatively? *Am. Nat.*, **112**, 767–770.

Clutton-Brock, T. H. 1972. Feeding and ranging behaviour of the red colobus monkey. Ph.D. thesis, Cambridge University.

Collins, D. A. & McGrew, W. C. 1988. Habitats of three groups of chimpanzees (*Pan troglodytes*) in western Tanzania compared. *J. Hum. Evol.*, **17**, 553–574.

Dawkins, R. & Krebs, J. R. 1979. Arms races between and within species. *Proc. R. Soc., Lond. B*, **205**, 489–511.

Endler, J. A. 1992. Interactions between predators and prey. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 169–196. London: Blackwell Scientific Publications.

Galat, G. & Galat-Luong, A. 1985. La communauté de primates diurnes de la forêt de Taï, Côte d'Ivoire. *Rev. Ecol. (Terre Vie)*, **40**, 3–32.

Ghiglieri, M. P. 1984. *The Chimpanzees of the Kibale Forest*. New York: Columbia University Press.

Goodall, J. 1968. Behaviour of free-living chimpanzees of the Gombe Stream area. *Anim. Behav. Monogr.*, **1**, 163–311.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: The Belknap Press of Harvard University Press.

Kruuk, H. 1972. *The Spotted Hyena*. Chicago: University of Chicago Press.

Mills, M. G. L. 1990. *Kalahari Hyenas: The Comparative Behavioural Ecology of two Species*. London: Unwin Hyman.

Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. *A. Rev. Ecol. Syst.*, **21**, 481–508.

Schaller, G. B. 1972. *The Serengeti Lion*. Chicago: University of Chicago Press.

Struhsaker, T. T. 1975. *The Red Colobus Monkey*. Chicago: University of Chicago Press.

Teleki, G. 1973. *The Predatory Behaviour of Wild Chimpanzees*. Brunswick: Bucknell University Press.

Teleki, G. 1981. The omnivorous diet and eclectic feeding habits of chimpanzees in Gombe National Park, Tanzania. In: *Omnivorous Primates: Gathering and Hunting in Human Evolution* (Ed. by R. S. O. Harding & G. Teleki), pp. 303–343. New York: Columbia University Press.

Uehara, S., Nishida, T., Hamai, M., Hasegawwa, T., Hayaki, H., Huffman, M., Kawanaka, K., Kobayashi, S., Mitani, J., Takahata, Y., Takasaki, H. & Tsukahara, T. 1992. Characteristics of predation by the chimpanzees in the Mahale Mountains National Park, Tanzania. In: *The Symposium Proceedings of the 13th Congress of the International Primatological Society* (Ed. by T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. de Waal), pp. 143–158. Basel: Karger AG.

Van Orsdol, K. G. 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *Afr. J. Ecol.*, **22**, 79–99.

Wrangham, R. W. 1975. The behavioural ecology of chimpanzees in the Gombe Stream National Park. Ph.D. thesis, Cambridge University.

Wrangham, R. W. & van Bergmann-Riss, E. 1990. Rates of predation on mammals by Gombe chimpanzees, 1972–1975. *Primates*, **31**, 157–170.