

Influence of chimpanzee predation on the red colobus population at Ngogo, Kibale National Park, Uganda

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Abstract Frequent hunting of red colobus monkeys (*Procolobus rufomitratus*) takes place at all long-term chimpanzee (*Pan troglodytes*) study sites where both species are present. Red colobus are the most commonly selected prey of chimpanzees even when other monkey species are more abundant. In particular, the chimpanzee community at Ngogo, Kibale National Park, Uganda, preys heavily on red colobus monkeys: the chimpanzee hunting success rate is extremely high, and chimpanzees kill many individuals per successful hunt. Census data had suggested that the red colobus population is declining and that predation by chimpanzees may be contributing to this decline. In this paper, I address the impact of hunting on the red colobus population at Ngogo. To test the hypothesis that chimpanzee hunting is sustainable, I am using demographic data collected on red colobus monkeys over a period of 3 years, as well as fecundity and mortality data from previous studies of this species. I apply matrix models and vortex analyses using a sensitivity analysis approach to project future population development. Results show that current rates of hunting are not sustainable, but that chimpanzees are neither more “noble”, nor more “savage” than humans are, but that they also hunt to ensure maximum benefit without regard for the consequences for the prey population.

Keywords Red colobus monkeys · Chimpanzees · Hunting · Demography · Kibale · Uganda

Introduction

Hunting of primates is a major threat to their survival. Because primates have lower than expected intrinsic rates of population increase for their body sizes (Robinson and Redford 1986), they are more susceptible to over-hunting than other mammals (e.g., Bodmer 1995; Bowen-Jones and Pendry 1999; Kavanagh et al. 1987; Mittermeier 1987; Oates 1996). Previous studies, however, focus on the anthropogenic impact of hunting on primate populations. Here, I investigate a natural predator–prey system in which both species are nonhuman primates, by assessing the impact of hunting by chimpanzees (*Pan troglodytes*) on the population of red colobus monkeys (*Procolobus rufomitratus*) at Ngogo, Kibale National Park, Uganda.

Numerous studies (e.g., Alvard 1993; Alvard et al. 1997; Bodmer et al. 1997; Redford 1991; Robinson and Redford 1991; Slade et al. 1998) established that humans make hunting decisions not to ensure the sustainable harvest of a prey, but to exploit resources in the most efficient manner possible. These studies led to the rejection of the “ecological noble savage” theory, which suggested that indigenous people live at ease with nature and hunt sustainably (e.g., Alvard 1993; Redford 1991). Here, I am testing the hypothesis that chimpanzees live in concordance with nature and use their resources in a sustainable way, and—in contrast to humans—do not try to maximize short-term benefits by forgoing long-term sustainability, therefore being the true ‘noble savage’.

Frequent hunting of red colobus monkeys takes place at all long-term chimpanzee study sites where both species occur. Red colobus are the most commonly selected prey of chimpanzees even when other monkey species are more abundant (e.g., Gombe, Tanzania: Stanford et al. 1994; Wrangham and Bergman-Riss 1990; Mahale, Tanzania:

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Hosaka et al. 2001; Uehara and Ihobe 1998; Uehara 1997; Ngogo, Uganda: Mitani and Watts 1999; Watts and Mitani 2002; Tai, Ivory Coast: Boesch and Boesch 1989; Boesch 1994a, b). Stanford (1995) argued that chimpanzee predation has a major impact on red colobus density, group size, and group structure at Gombe. Red colobus groups were 46% smaller in the core area of one chimpanzee community range than on the periphery. At Kyambura Gorge, Uganda, where no red colobus occur and black-and-white colobus (*Colobus guereza*) are the selected prey species of chimpanzees, Krüger et al. (1998) found significant demographic differences in black-and-white colobus groups within and outside of the “chimpanzee activity centers”. The population density of black-and-white colobus was significantly lower within the chimpanzee activity center than outside. Fewer groups were present within activity centers, mean group size was smaller, and groups had fewer subadults, juveniles, and infants.

Chimpanzees at Ngogo prey heavily on red colobus monkeys. The chimpanzee community there is the largest known in the wild, with about 150 members. They are successful in more than 80% of hunts, and kill nearly four red colobus monkeys per successful hunt (Mitani and Watts 1999; Watts and Mitani 2002). Ngogo chimpanzees often hunt after extended hunting patrols during which they seem to search for red colobus groups: patrol members, mostly males, travel silently in single file and their movement is apparently directed. They scan the canopy and are attentive to arboreal movements and other possible signs of prey. Recent census data suggest that the red colobus population at Ngogo is declining (Mitani et al. 2000; Teelen 2007). Mitani and Watts (1999) reported that the chimpanzees at Ngogo killed about 102 red colobus in about 30 hunts per year. They estimated that this represented at least 3% of the red colobus population within the chimpanzees' range. More recent data adjust these figures upwards slightly to about 45 hunts with 167 kills per year, closer to 6–12% of the population (Watts and Mitani 2002). These estimates nevertheless represent rough extrapolations. In this paper, I present an analysis addressing the sustainability of chimpanzee hunting on red colobus monkeys.

Study site

The Ngogo research site covers about 30 km² in the central part of Kibale National Park in western Uganda. It is located approximately 10 km southeast of Kanyawara, the main research station in the park. The topography at Ngogo is hilly and most of the area is covered with moist, evergreen forest transitional between lowland and montane forest. Small patches of grassland or young forest in various stages of regeneration cover some hilltops (Lwanga

2003). Eight different diurnal primate species live in the Kibale forest: black-and-white colobus (*Colobus guereza*), red colobus, red-tailed monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), L'hoest's monkeys (*C. lhoesti*), grey-cheeked mangabeys (*Lophocebus albigena*), baboons (*Papio anubis*), and chimpanzees. Ghiglieri (1984), Struhsaker (1997) and Lwanga et al. (2000) provide detailed descriptions of the study site.

Methods

I conducted fieldwork on red colobus monkeys at Ngogo from January to December 2001, from June to December 2002, and in November 2003. During this time, I followed four different groups of red colobus monkeys for 3 and 5 consecutive days. During these periods, I counted individuals and collected demographic data on these groups whenever possible, although in practice this was only feasible when groups were traveling. I classified individuals into age- and sex-classes following Struhsaker (1975) and Stanford (1998): (1) infants were 1/4 to 1/2 the size of adult females, had dark and silky pelage when young, but adult coloration at the time of weaning, only rarely ventured away from females, and were carried most of the time by a female especially during group movements; (2) juveniles were 1/2 to 4/5 the size of adult females, had adult coloration, traveled and foraged independently, and rarely or never were carried by females; (3) subadults were slightly smaller than adults, had secondary sexual characteristics that were visible but not fully developed; (4) adult females had obvious nipples, and prominent and large clitorises, and sometimes conspicuous sexual swellings; and (5) adult males had large and bulky bodies, large canines, and broad heads.

I was not able to recognize all members of the four study groups individually, but I differentiated groups through “identifying individuals,” i.e., individuals with special marks like bent or shorter tails, stiff or missing fingers, and scars. Group counts presented here were confirmed 2–3 times in each of the corresponding study periods (accepting a 6% error margin), while group composition data represent maximum counts from this group count data set. However, given the difficulties in obtaining group counts (especially limited visibility) these data are good approximations rather than precise counts.

Analyses

To assess the impact of hunting on the red colobus population at Ngogo I used different off-take rates from 1995 to 1998 (Mitani and Watts 1999), 1995 to 1999 and 1998 to

1999 (Watts and Mitani 2002), and 2000, 2001 and 2002 (J. Mitani and D. Watts, unpublished data) on the population of red colobus monkeys in 2001, 2002, and 2003 (Table 1). I extrapolated data from four different study groups to calculate the percentage off-take from all red colobus groups within the territory of the Ngogo chimpanzee community under all possible scenarios. This was done to represent as many different scenarios as possible. These four study groups were subject to only very few hunts during the study period and therefore their demographic data are minimally affected by predation. Using another approach, I estimated the size of the red colobus population within the chimpanzee territory by using group density (0.62 per km²; Teelen 2005), average group size (39.5 individuals), and the size of the chimpanzee territory (25 km²; S. Amsler, personal communication).

To assess the sustainability of hunting by chimpanzees I used the computer program VORTEX (Lacy et al. 2003). I combined demographic data from four different groups, and treated them as one population. By definition, infants did not travel on their own during group progression, and juveniles could be relatively easily identified due to their size. Therefore, unclassified individuals were distributed evenly between the classes of subadults, adult females and adult males for analyses. I utilized fecundity and mortality estimates by T. Struhsaker from Kibale (Tables 2 and 3) as used in the Tana River Primate Reserve Conservation Assessment Workshop with VORTEX (Seal et al. 1991). The aim of this paper was not to undertake a population viability analysis, but to assess the impact of hunting on red colobus monkeys at Ngogo. Therefore, I did not incorporate inbreeding depression, environmental variability, the possibility of catastrophes, or dispersal in the model. Carrying capacity was set arbitrarily at 500 individuals for logistic reasons: to allow graphic presentation of the results as a visual aid in the analysis, and to eliminate the impact of carrying capacity as a potential cause for a decline in the red colobus population. It was therefore important to keep carrying capacity relatively low. This limit has no effect on the results of this study as will become clear later.

Although Struhsaker (1975) reported that the dominant male is responsible for the most copulations in a group, I assumed for simplicity that all adult males had the same chance of reproducing. Following Seal et al. (1991), I assumed a high age-specific mortality rate for subadult males in the last age class before maturity. Causes of mortality are poorly documented, but there are significantly fewer adult males than adult females in red colobus populations (Struhsaker 2000), and survivorship to adulthood is much lower in males than in females (Struhsaker and Pope 1991). Males close to maturity are probably taking high risks during displays and intergroup encounters to establish their status in the groups, and in combination with limited experiences therefore exhibit high mortality rates.

Struhsaker (1975) observed interbirth intervals of about 19 months. Based on the observation that approximately 50% of females in a group carry infants at any given time, he suggested that interbirth intervals are about 2 years, which yields a fecundity value of 50% (Seal et al. 1991). Struhsaker and Pope (1991) observed interbirth intervals of 27.5 months. However, after the death of an infant, the mother probably resumes cycling earlier than she otherwise might have, resulting in a shorter interbirth interval. Therefore, I also ran simulations assuming an interbirth interval of 1.25 year, or 80% fecundity. Reproduction was density dependent only when the population approached carrying capacity at which point 25% of females bred otherwise, I assumed 50 ± 20% of females bred per year (Table 2).

VORTEX was run with 1,000 iterations projecting the population development over a period of 100 years (following standards in population viability analyses). VORTEX uses an age distribution for its simulations. Data I collected were in stage classes. I distributed numbers for the stage classes over the age distribution as evenly as possible, using only whole numbers (e.g., 21 female subadult individuals spread out over a period of 2 years were entered as 11 individuals in one year and 10 individuals in the following year). In concordance with the conservative theme of this projection, I always rounded the numbers of

Table 1 Number of individual red colobus monkeys (*Procolobus rufomitratus*) killed by chimpanzees (*Pan troglodytes*) in 1995–1998 (Watts and Mitani 1999), 1995–1999 and 1998–1999 (Mitani and Watts 2002), and 2000, 2001 and 2002 (J. Mitani and D. Watts, unpublished data)

	Adult males	Adult females	Subadults	Juveniles	Infants	Unclassified individuals	Total	Time period (months)
1995–1998	2	18	11	45	20		96	23
1995–1999	20	48	38	74	78		258	34
1998–1999	17	29	24	29	52		151	11
2000	2	8	4	18	24		56	3
2001	0	6	2	11	17	2	38	2
2002	3	19	21	60	79	6	188	7

Table 2 VORTEX parameters for fecundity following T. Struhsaker (Seal et al. 1991) and as explained in the text

Parameter	Measurement
Age of first offspring for females	5 (late) and 4 (early)
Age of first offspring for males	7
Maximum age of reproduction	20
Maximum no. of progeny per year	1
Sex ratio at birth	50%
Breeding at low density	50% (long) and 80% (short) representing interbirth intervals of 2 and 1.25
Environmental variation in breeding	20%
Breeding at carrying capacity	25%
Steepness parameter	8 (breeding decreases as the population approaches carrying capacity)

Default conditions are highlighted in bold

Table 3 VORTEX parameters for mortality following T. Struhsaker (Seal et al. 1991) and as explained in the text

Mortality rates (Qx) and their standard deviation (SD)					
Females			Males		
Age	Qx	SD	Age	Qx	SD
0–1	30	15	0–1	30	15
1–2	5	3	1–2	5	3
2–3	10	5	2–3	10	5
3–4	5	3	3–4	5	3
4–5	5	3	4–5	5	3
>5	2.5 (low)	1.25 (low)	5–6	5	3
	5 (high)	2.5 (high)	6–7	60	30
			>7	2.5 (low)	1.25 (low)
				5 (high)	2.5 (high)
41% survival			16.5% survival		
59% mortality to age 5			83.6% mortality to age 7		

Default conditions are highlighted in bold

the initial population up (to even, 1/2 or at most 1/4 numbers), while I rounded hunting/off-take data down. I utilized demographic data for all 3 years as the initial population size in all simulations, and undertook three different kinds of analyses: (1) projection of population development given the life history parameters used; (2) projection of population development under theoretical off-take conditions using the harvest function in VORTEX; and (3) projection of population development under actual off-take conditions based on data collected by J. Mitani and D. Watts from 2000, 2001, and 2002.

For analysis (1), I used basic life history parameters as outlined in Tables 2 and 3, with no harvest. In analysis (2),

I simulated theoretical off-take conditions with harvest rates of 2, 4, 6, 8, and 10 individuals in each stage class, and each with a threshold of 20, 30, 40, and 50 individuals below which hunting ceases. For analysis (3), I used actual off-take data from hunts in 2000, 2001, and 2002 (J. Mitani and D. Watts, unpublished data). Approximately 15 red colobus groups use the territory of the Ngogo chimpanzee community. Chimpanzees successfully hunted red colobus monkeys at least 16 times in 3 months in 2000, 8 times in 2 months in 2001, and 45 times in 7 months in 2002 (J. Mitani and D. Watts, unpublished data). Extrapolating these data, each red colobus group was hunted on average approximately 3–5 times per year. However, I assumed that in the sample population each of the four groups was hunted only twice per year. This was done for three reasons: (1) most observed hunts between 2000 and 2002 took place in the periphery of the chimpanzee territory, while the four study groups used a more central area and therefore might have been hunted less often by chimpanzees than an average group; (2) I observed two successful hunts of red colobus monkeys by chimpanzees during 271 days of dawn-to-dusk follows; and (3) I wanted to maintain a conservative estimate of the impact of hunting. Consequently, the total off-take was 28 in 2000, 38 in 2001 and 32 in 2002. To maintain a conservative approach in these analyses, I rounded off-take data down if necessary (e.g., 4.178 individuals killed per hunt in 2002 were rounded down to 4 full individuals for the simulations; see above).

Results

The sizes of the different four study groups ranged from 17 to 70 individuals, and varied considerably over the years of the study (Table 4). The size of group A remained relatively stable with 46, 45, and 42 individuals. However, group B increased from 38 individuals to 70 individuals between 2001 and 2003. This might have been due to a merger of two groups; upon my return in 2002, group B had increased by about 25 individuals from the last count in 2001, 7 months earlier. Some of the individuals in group B were not habituated to human presence, while the majority including all “identifying individuals” clearly tolerated my presence. The size of group C decreased by about 10 individuals over the same time. Changes in group D were complex. Members of this group often moved as two subgroups in 2001, and in 2002 individuals of what was group D in 2001 could be found in two different groups, both using approximately the same home range and both larger than the original group D. This suggests that group D fissioned, with the subgroups joining other groups. The total number of individuals in all four study groups combined increased between 2001 and 2002 from 137 to 162

Table 4 Group composition of four study groups (A, B, C, and D) in 2001, 2002, and 2003 and the total number of individuals in the population

	A			B			C			D			Total population		
	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003
Infants	4	0	6	2	10	10	1	2	2	0	4	3	7	16	21
Juveniles	6	4	2	6	5	9	2	2	0	0	0	9	14	11	20
Subadults females	0	0	2	0	1	2	0	0	0	0	0	1	0	1	5
Subadult males	2	1	3	0	2	4	1	2	1	0	0	3	3	5	11
Unclassified subadults	0	2	0	1	5	0	0	0	0	2	0	0	3	7	0
Adult females	11	18	12	13	17	26	4	6	6	2	9	10	30	50	54
Adult males	7	11	8	7	9	11	6	4	4	3	4	7	23	28	30
Unclassified individuals	16	9	9	9	15	8	17	3	4	13	17	15	55	44	36
Total	46	45	42	38	64	70	31	19	17	20	34	48	135	162	177

probably because of (1) these mergers, and (2) there were very few hunts in the middle of the chimpanzee territory during the time of this study.

Group composition varied between groups between years, but trends remained the same. For example, the ratio of classifiable adult males and females was approximately 1:2 and the ratio of infants to females was 1:3 in most cases (Table 4). Immature individuals represent between 0 and 25% of the group, infants alone between 0 and 16% and juveniles between 0 and 19%.

My observations suggest that approximately 15 red colobus groups use the home range of the chimpanzee community at Ngogo. Given a mean group size of 33.75, 40.5, and 44.25 individuals, I therefore estimated that the red colobus population in that area was 506, 608, and 664 individuals in 2001, 2002, and 2003, respectively. Using group density data based on home range size (Teelen 2005) to estimate population density revealed a similar size of 612 individuals within the chimpanzee territory. Assuming different measures of off-take, I calculated that chimpanzees at Ngogo killed between 15 and 53% of the red colobus population within their territory (Table 5).

VORTEX analyses demonstrated that, without any hunting, the red colobus population at Ngogo is healthy. Data from 2001, 2002, and 2003 showed that populations hit carrying capacity and stabilized below it, resulting in very small probabilities for extinction under all scenarios over a period of 100 years (Fig. 1). The carrying capacity itself had no impact on the analysis, but was mainly employed to avoid unlimited growth of the population and to show that should any carrying capacity been reached at Ngogo, this would not have a deleterious effect on the population, but in fact only limits the population size from exponential growth. Simulations using different theoretical off-take conditions revealed that the population as a whole is able to sustain the harvest of about 4–6 individuals in all stage classes except adults (Fig. 2). The population is least susceptible to the harvest of subadult males than any other

Table 5 Off-take of red colobus monkeys from different years in percent of the total population of red colobus monkeys in the home range of the Ngogo chimpanzee community in 2001, 2002, and 2003, as well as off-take from the population of red colobus as determined with density data

	No. of kills/year	2001	2002	2003	Density
1995–98 ^a	102	20.2	16.8	15.4	16.7
1995–99 ^b	167	33.0	27.5	25.2	27.3
1998–99 ^b	258	51.0	42.5	38.9	42.1
2000 ^c	224	44.3	36.9	33.8	36.6
2001 ^c	228	45.0	37.5	34.4	37.2
2002 ^c	322	–	53.0	48.6	52.6

^a Mitani and Watts (1999)

^b Watts and Mitani (2002)

^c J. Mitani and D. Watts, unpublished data

class, and most susceptible to the harvest of adult males. They are able to withstand the harvest of six infants and four juveniles, but only two subadult females and two adult females every year with practically no risk of extinction over a period of 100 years. Setting the population size threshold at which hunting ceases at 50 or 40 individuals, population size stabilizes below these thresholds in most simulations, and the probability of extinction is below 50%. The exception is under the harvest of adult males: the population has a high probability of extinction even under threshold conditions if more than four adult males are harvested each year. The probability of survival is much lower if the threshold is set at 30 or 20 individuals for all age classes except for subadult males. The difference between models in which age of first reproduction is set at 4 or 5 years for females (early and late in Fig. 2) is noticeable but not large.

Analyses utilizing actual hunting rates without any threshold at which hunting might cease show that the red colobus population has an extremely low probability of

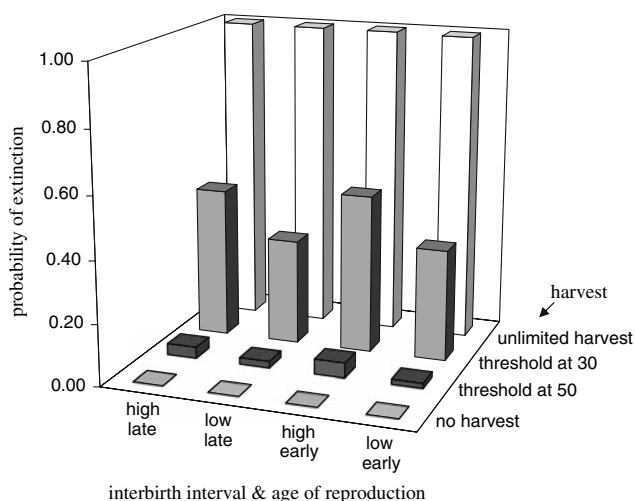


Fig. 1 Probability of extinction of the red colobus (*Procolobus rufomitratus*) population at Ngogo as the average outcome of VORTEX simulation for 2001, 2002, and 2003 under no harvest conditions, and under actual harvest conditions with and without a threshold at which harvest ceases (interbirth interval high and low, and age of reproduction late and early)

surviving (Fig. 1), with a mean time to extinction of 12 years. If a threshold was employed, populations stabilized below that threshold. However, at a threshold of 30 individuals simulations produced risk of population extinctions of about 50% (Fig. 1).

Discussion

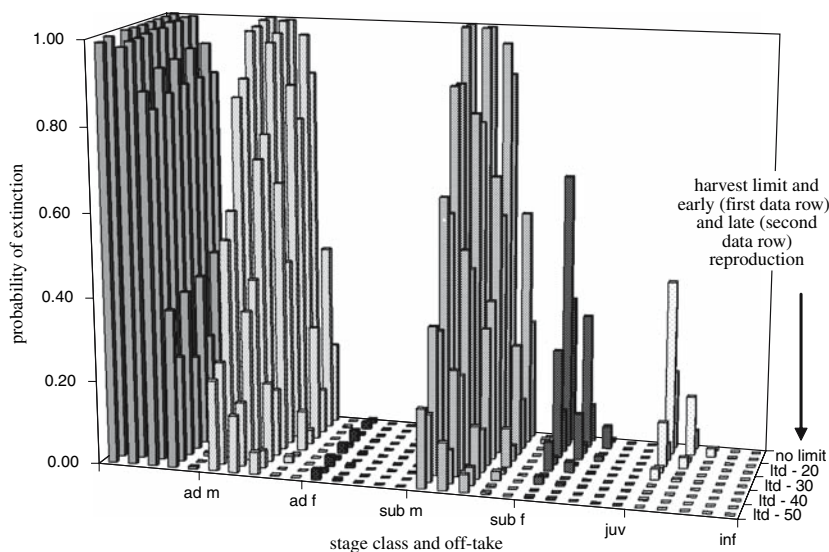
Results from this study suggest that chimpanzees at Ngogo kill between 15 and 53% of all individuals in the red colobus population there. These estimates include data from earlier years; more recent data suggest that the impact of hunting ranges from 40 to 50%. These estimates are much

higher than those from previous studies, with 3% (Mitani and Watts 1999) and 6–12% (Watts and Mitani 2002), which were based on higher estimates of red colobus population density and lower hunting rates. However, more accurate estimates show the red colobus population to be lower than these estimates, while chimpanzee predation actually increased in the interim.

Wrangham and Bergmann-Riss (1990, using data by Boesch and Boesch 1989), suggested that 4% of the red colobus population at Tai were killed by chimpanzees each year. Boesch and Boesch-Achermann (2000) adjusted that number to 3.2–7.6%. Boesch et al. (2002) reported for Mahale that 1.1–1.3% of the red colobus population were killed during 1981–1990, and 3.0–3.8% during 1991–1995. For Gombe, Busse (1977) estimated that 4–6% of the red colobus population were killed per year by chimpanzees, while Stanford (1996) provided estimates of 16–32% and Wrangham and Bergmann-Riss (1990) gave an even higher estimate of 42%. Stanford (1998) argued that the quantity of red colobus meat eaten did not change over the past 20 years. He suggested that the red colobus population at Gombe is able to withstand this kind of off-take because reproductive parameters there have evolved to counter the effects of the severe predation pressure.

At Ngogo this is not the case. Results from this study suggest that current rates of hunting of red colobus monkeys by chimpanzees are not sustainable. If hunting continues at the level of 2000–2002, the red colobus population will go extinct within the next two decades. However, the results of these demographic analyses are merely a projection, not a forecast. They represent a snapshot of population dynamics and reveal something about the present condition of the population, not about the future, and therefore cannot be used to predict what will happen. Stochastic events can have a high impact on

Fig. 2 Probability of extinction as the average outcome of VORTEX simulation for 2001, 2002, and 2003 with different theoretical off-take conditions (2, 4, 6, 8 and 10 individuals in every stage class), with early and late reproduction, and under conditions under which harvest ceases (i.e., at red colobus population sizes of 50, 40, 30 and 20 individuals), as well as unlimited harvest (*inf* infants, *juv* juveniles, *sub f* subadult females, *sub m* subadult males, *ad f* adult females, *ad m* adult males)



population demographics, as is highlighted by the observation that the total number of individuals in the four main study groups increased during the time of this study. However, more recent counts indicate that population of red colobus monkeys at Ngogo is indeed declining.

Analyses using a threshold at which hunting ceases show that the population of red colobus monkeys is able to survive at population densities as low as 40 individuals under the assumed harvest rates. However, this might be an overly positive outlook, as I used extremely conservative estimates not to overestimate the negative impact of hunting on the population. The chimpanzees–red colobus system differs from other predator–prey relationships, in that chimpanzees do not rely on red colobus monkeys as a necessary food source. Chimpanzees are primarily frugivores and one cannot expect an oscillating relationship between populations of the two species. Instead, as the number of red colobus in the population decreases, the number of chimpanzees should remain stable and it is therefore possible that the hunting by chimpanzees can lead to the extinction of red colobus monkeys at Ngogo within the near future. In this case, one endangered species (*Pan troglodytes*) would have a deleterious effect on another (*Procolobus rufomitratus*). This has important implications for conservation as it raises questions about priorities in conservation management plans and the right to interfere with natural systems.

However, it is possible that chimpanzees at Ngogo adjust their hunting behavior as red colobus monkeys abundance changes and as the relative returns from their hunting efforts also change. Depending on the importance and value of meat, both nutritionally and socially, for chimpanzees in the community at Ngogo, the ecological costs for searching might become too high. As most hunts at Ngogo take place after extended hunting patrols during which they seem to search for red colobus groups (Mitani and Watts 1999; Watts and Mitani 2002), the change in hunting frequency should be noticeable. More recent observations of chimpanzee hunting behavior seem to confirm this: in 2003 and 2004 chimpanzees at Ngogo have hunted less than during corresponding periods in earlier years (J. Mitani and D. Watts personal communication), and a decreased frequency of hunts and meat sharing episodes might help to determine the significance of hunts for social bonds and the formation of coalitions within the chimpanzee community (cf. Mitani and Watts 2001).

The costs of opportunistic hunting, however, are unlikely to change. If the decision whether to hunt is influenced by the chimpanzee hunting party size and by the numbers of adult and/or juvenile red colobus monkeys in a group, the number of opportunistic hunts should increase as red colobus groups get smaller and it becomes more likely that hunting parties outnumber the number of red colobus in the

group. It remains to be seen if the possible fission events observed represent an anti-predator strategy that red colobus monkeys at Ngogo have adopted.

Matrix analyses can help to project future population development and to determine whether the present rate of predation is sustainable (cf. Dobson and Lyles 1989). The initial population size has practically no impact on the outcome of a simulation, which also indicates that inaccuracies in group counts are of minor importance for the outcome of the simulations. In the Ngogo case, changing the red colobus interbirth interval, mortality, and age of first reproduction produced noticeable but negligible differences in the probability of extinction. In general, it is therefore safe to assume that the results presented here are robust.

The sensitivity analysis showed that subadult females and adult males and females are the stage classes most susceptible to hunting, while infants, juveniles, and subadult males are harmed less. This might explain why hunting at Ngogo is less sustainable than at Gombe. At Ngogo, between 53 and 75% (Mitani and Watts 1999; Watts and Mitani 2002; J. Mitani and D. Watts, unpublished data) of the kills were immature individuals, while at Gombe this proportion was between 86% (Stanford 1998) and 75% (Stanford et al. 1994). Thus, both absolutely and relatively more adults are killed at Ngogo. Reasons for this difference remain unclear. It may be that chimpanzees at Ngogo are more experienced and daring hunters, indifferent to red colobus attacks and defense strategies, and therefore more capable of killing adult individuals, or that red colobus at Ngogo, faced with high predation pressure, are more inclined to defend their young and therefore put themselves at greater risk than their counterparts at Gombe. Reports from Mahale (Uehara et al. 1992) and Gombe (Busse 1977; Stanford et al. 1994), as well as at Kibale (Chapman and Chapman 1996; Leland and Struhsaker 1993; Struhsaker and Leakey 1990; Treves 1999, personal observation) illustrate that red colobus males can be highly effective in defending their groups against attacks by chimpanzees. It is therefore not likely that adult red colobus at Ngogo are less capable of fighting chimpanzees than at Gombe. At Tai, approximately half of the kills are of adult individuals (Boesch and Boesch 1989), but red colobus density there is three times as high as at Ngogo (cf. Boesch and Boesch-Achermann 2000). It is therefore possible that the negative impact of hunting by chimpanzees on the population is not (yet) detectable.

Results from this study suggest that chimpanzees at Ngogo are not more or less “noble” or “savage” than we are, but that they also hunt to ensure maximum benefit without regard for the consequences for the prey population. This might indicate that the characteristic to maximize short-term benefit and possibly ignore long-term consequences is not just a human problem, but is deeply rooted

in evolutionary history. Whether this constitutes a problem for the survival of the red colobus population at Ngogo, or whether mechanisms to counter the high predation rates (e.g., increased birth rates) have evolved or whether a source-sink situation exists, remains unclear at this point and will be the subject of future research.

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References

- Alvard M (1993) Testing the “Ecologically Noble Savage” hypothesis: interspecific prey choice by Piro hunters of Amazonian Peru. *Hum Ecol* 21:355–387
- Alvard MS, Robinson JG, Redford KH, Kaplan H (1997) The sustainability of subsistence hunting in the Neotropics. *Conserv Biol* 11:977–982
- Bodmer RE (1995) Susceptibility of mammals to overhunting in Amazonia. In: Krausman PR (ed) Integrating people and wildlife for a sustainable future. Proceedings of the first international wildlife management congress. The Wildlife Society, Bethesda, pp 292–295
- Bodmer RE, Eisenberg JF, Redford KH (1997) Hunting and the likelihood of extinction of Amazonian mammals. *Conserv Biol* 11:460–466
- Boesch C (1994a) Chimpanzees-red colobus monkeys: a predator-prey system. *Anim Behav* 47:1135–1148
- Boesch C (1994b) Cooperative hunting in wild chimpanzees. *Anim Behav* 48:653–667
- Boesch C, Boesch H (1989) Hunting behavior of wild chimpanzees in the Taï National Park. *Am J Phys Anthro* 78:547–573
- Boesch C, Boesch-Achermann H (2000) The chimpanzees of the Taï Forest—behavioural ecology and evolution. Oxford University Press, Oxford
- Boesch C, Uehara S, Ihobe H (2002) Variations in chimpanzee-red colobus interactions. In: Boesch C, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 221–230
- Bowen-Jones E, Pendry S (1999) The threat to primates and other mammals from the bushmeat trade in Africa, and how this threat could be diminished. *Oryx* 33:233–245
- Busse CD (1977) Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution* 31:907–911
- Chapman CA, Chapman LJ (1996) Mixed-species primate groups in the Kibale forest: ecological constraints on association. *Int J Primatol* 17:31–50
- Dobson AP, Lyles AM (1989) The population dynamics and conservation of primate populations. *Conserv Biol* 3:362–379
- Ghiglieri MP (1984) The chimpanzees of the Kibale Forest. Columbia University Press, New York
- Hosaka K, Nishida T, Hamai M, Matsumoto-Oda A, Uehara S (2001) Predation of mammals by chimpanzees of the Mahale Mountains, Tanzania. In: Goodall J (ed) All apes great and small. Kluwer, New York, pp 107–130
- Kavanagh M, Eudey AA, Mack D (1987) The effects of live trapping and trade on primate population. In: Mittermeier RA (ed) Primate conservation in the tropical rain forest. Liss, New York, pp 147–177
- Krüger O, Affeldt E, Brackmann M, Milhahn K (1998) Group size and composition of Colobus guereza in Kyambura Gorge, Southwest Uganda, in relation to chimpanzee activity. *Int J Primatol* 19:287–297
- Lacy RC, Borbat M, Pollak JP (2003) VORTEX: a stochastic simulation of the extinction process, version 9. Chicago Zoological Society, Brookfield
- Leland L, Struhsaker TT (1993) Teamwork tactics. *Nat Hist* 102:42–48
- Lwanga JS (2003) Forest succession in Kibale National Park, Uganda: implications for forest restoration and management. *Afr J Ecol* 41:9–22
- Lwanga JS, Butynski TM, Struhsaker TT (2000) Tree population dynamics in Kibale National Park, Uganda 1975–1998. *Afr J Ecol* 38:238–247
- Mitani JC, Watts DP (1999) Demographic influences on the hunting behavior of chimpanzees. *Am J Phys Anthro* 109:439–454
- Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61:915–924
- Mitani JC, Struhsaker TT, Lwanga JS (2000) Primate community dynamics in old growth forest over 23.5 years at Ngogo, Kibale National Park, Uganda: Implications for conservation and census methods. *Int J Primatol* 21:269–286
- Mittermeier RA (1987) Effects of hunting on rain forest primates. In: Marsh CW, Mittermeier RA (eds) Primate conservation in tropical rain forest. Liss, New York, pp 109–146
- Oates JF (1996) Habitat alterations, hunting and the conservation of folivorous primates in African forests. *Aust J Ecol* 21:1–9
- Redford KH (1991) The ecologically noble savage. *Orion* 9:24–29
- Robinson JG, Redford KH (1986) Intrinsic rate of natural increase in Neotropical forest mammals: relationship to phylogeny and diet. *Oecologia* 68:516–520
- Robinson JG, Redford KH (1991) Sustainable harvest of neotropical forest mammals. In: Robinson JG, Redford KH (eds) Neotropical wildlife use and conservation. The University of Chicago Press, Chicago
- Seal US, Lacy RC, Medley K, Seal R, Foose TJ (1991) Tana River primate reserve conservation assessment workshop. Captive Breeding Specialist Group (CBSG/SSC/IUCN) & Kenya Wildlife Service
- Slade NA, Gomulkiewicz R, Alexander HM (1998) Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. *Conserv Biol* 12:148–155
- Stanford CB (1995) The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Anim Behav* 49:577–587
- Stanford CB (1996) The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of pliocene hominids. *Am Anthropol* 98:96–113
- Stanford CB (1998) Chimpanzee and red colobus: the ecology of predator and prey. Harvard University Press, Cambridge
- Stanford CB, Wallis J, Matama H, Goodall J (1994) Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *Am J Phys Anthro* 94:213–228
- Struhsaker TT (1975) The red colobus monkey. University of Chicago Press, Chicago

- Struhsaker TT (1997) Ecology of an African rain forest—logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville
- Struhsaker TT (2000) Variation in adult sex ratios of red colobus monkey social groups: implications for interspecific comparisons. In: Kappeler PM (ed) Primate males—causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 108–119
- Struhsaker TT, Leakey M (1990) Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. Behav Ecol Sociobiol 26:435–444
- Struhsaker TT, Pope TR (1991) Mating system and reproductive success—a comparison of 2 African forest monkeys (*Colobus badius* and *Cercopithecus ascanius*). Behaviour 117:182–205
- Teelen S (2005) The impact of hunting by chimpanzees (*Pan troglodytes*) on Demography and behavior of red colobus monkeys (*Procolobus rufomitratu*s) at Ngogo, Kibale National Park, Uganda. PhD thesis, Yale University, New Haven
- Teelen S (2007) Primate abundance along five different transect lines at Ngogo, Kibale National Park, Uganda. Am J Primatol 69:1030–1044
- Treves A (1999) Has predation shaped the social systems of arboreal primates? Int J Primatol 20:35–67
- Uehara S (1997) Predation on mammals by chimpanzee (*Pan troglodytes*). Primates 38:193–214
- Uehara S, Ihobe H (1998) Distribution and abundance of diurnal mammals, especially monkeys, at Kasoje, Mahale Mountains, Tanzania. Anthropol Sci 106:349–369
- Uehara S, Nishida T, Hamai M, Hasegawa T, Hayaki H, Huffman MA, Kawanaka K, Kobayashi S, Mitani JC, Takahata Y, Takasaki H, Tsukahara T (1992) Characteristics of predation by the chimpanzees in the Mahale Mountains National Park, Tanzania. In: Nishida T, McGrew WC, Marler P, Pickford M, deWaal FBM (eds) Topics in primatology 1: human origins. University of Tokyo Press, Tokyo, pp 143–158
- Watts DP, Mitani JC (2002) Hunting behavior of chimpanzees at Ngogo, Kibale National Park, Uganda. Int J Primatol 23:1–28
- Wrangham RW, Bergman-Riss EVZ (1990) Rates of predation on mammals by Gombe chimpanzees, 1972–1975. Primates 31:157–170