

Crop raiding patterns of solitary and social groups of red-tailed monkeys on cocoa pods in Uganda

Authors: Baranga, Deborah, Basuta, G. Isabirye, Teichroeb, Julie A., and Chapman, Colin A.

Source: Tropical Conservation Science, 5(1): 104-111

Published By: SAGE Publishing

URL: https://doi.org/10.1177/194008291200500109

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Short communication

Crop raiding patterns of solitary and social groups of red-tailed monkeys on cocoa pods in Uganda

Deborah Baranga¹, G. Isabirye Basuta¹, Julie A. Teichroeb², and Colin A. Chapman^{1,2,3}*

¹Department of Zoology, Makerere University, P.O. Box 7062, Kampala, Uganda

Abstract

Crop damage by wildlife is a very prevalent form of human-wildlife conflict adjacent to protected areas, and great economic losses from crop raiding impede efforts to protect wildlife. Management plans are needed to decrease damage by raiding wildlife, yet conservation biologists typically lack the basic information needed for informed conservation strategies. Red-tailed monkeys (*Cercopithecus ascanius*) raid a variety of crops adjacent to protected forests in East Africa; however, the role of group structure on crop raiding has not been explored. Here, crop raiding patterns of solitary males and social groups were investigated during 10 months in a plantation of mature cocoa in Uganda. Monkeys gained access to the plantation via trees planted as wind breaks and shade trees, and the sighting frequency of groups was negatively related to the distance from the forest edge. In contrast, solitary males were sighted more frequently far from the forest edge and caused proportionately greater damage than members raiding in a social group. These results highlight that for social animals, crop raiding behavior can vary among types of social groupings; appropriate strategies to cope with raiding must therefore respond to this variation.

Keywords: crop raiding, social groups, solitary red-tailed monkeys, cocoa

Resumen

Los daños a los cultivos por la fauna silvestre es un conflicto común entre humanos y la fauna silvestre que se presenta adyacente a las áreas protegidas y donde el alto costo económico de los daños previene esfuerzos de protección a la fauna. Por lo tanto, los planes de manejo deben considerar la disminución de las intrusiones a los cultivos por la fauna silvestre, sin embargo los biólogos conservacionistas típicamente carecen de la información adecuada para construir estrategias informadas de conservación. El cercopiteco cola roja (*Cercopithecus ascanius*) se alimenta de una variedad de cultivos en áreas adyacentes a bosques protegidos en el este de África, sin embargo el papel que juega la estructura grupal en los daños a los cultivos no ha sido explorada aun. Aquí investigamos los patrones de incursiones a los cultivos por machos solitarios y grupos sociales durante 10 meses en una plantación madura de cacao en Uganda. Los grupos de monos accedieron a las plantaciones a través de árboles plantados como cercas vivas y como árboles sombra, y la frecuencia de avistamientos estuvo negativamente relacionada con la distancia del borde del bosque. En contraste, machos solitarios fueron observados frecuentemente más lejos del borde del bosque y causaron proporcionalmente más daño que miembros de un grupo social. Esos resultados indican que para especies sociales, el comportamiento de incursiones a cultivos puede variar dependiendo de la estructura social, por lo tanto las estrategias apropiadas para prevenir daños a los cultivos deben tomar en cuenta esta variación.

Palabras clave: daños a cosechas, grupos sociales, monos solitarios colirojos, cacao

²Department of Anthropology, McGill University, Montreal, Quebec, Canada H3A 2T7

³McGill School of Environment and Department of Anthropology, McGill University, Montreal, Quebec, Canada H3A 2T7 and Wildlife Conservation Society, Bronx, New York, USA

^{*} Corresponding Author Email: Colin.Chapman@McGill.ca

Received: 15 January 2012; Accepted: 6 March 2012; Published: 19 March 2012.

Copyright: Deborah Baranga, G. Isabirye Basuta, Julie A. Teichroeb, and Colin A. Chapman. This is an open access paper. We use the Creative Commons Attribution 3.0 license http://creativecommons.org/licenses/by/3.0/ - The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that the article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

Cite this paper as: Baranga, D., Isabirye Basuta, G., Teichroeb, J. A., and Chapman, C. A. 2012. Crop raiding patterns of solitary and social groups of red-tailed monkeys on cocoa pods in Uganda. *Tropical Conservation Science* Vol. 5(1):104-111. Available online: www.tropicalconservationscience.org

Introduction

Humans and nonhuman primates have had a long association and, in many instances, have antagonistic relationships [1]. This antagonism is often due to nutritional reliance on similar foods [2]. However, with increasing conversion of forest to agriculture, crops have become vital supplements to the diet of many nonhuman primates and will be important for their conservation [3, 4]. In the case of Africa, antagonistic relationships between human and nonhuman primates have been exacerbated by the increasing amount of land under cultivation with crops that are very attractive to primates [5-8]. Subsistence farmers living adjacent to protected areas have borne the bulk of the crop depredation associated with primates [9-11]. Such negative interactions between people and animals from protected areas hinder both conservation area protection and wildlife management [12, 13]. As a result, understanding what promotes crop-raiding is critical to devise means of improving people-parks interactions and effective protected area management.

Studies conducted on subsistence farms around tropical forests often list primates as pests of several crops, and red-tailed monkeys (*Cercopithecus ascanius*; Fig. 1) are often one of the major crop-raiding species [10, 12, 14]. Studies on crop-raiding by red-tailed monkeys have focused on one-male, multifemale social groups [11, 12], and the effect of other social groupings has not been considered. Adult male red-tailed monkeys live as resident males in heterosexual groups or as non-resident, outside male groups [15, 16]. The males outside of groups live solitarily, or a few males may reside together in bachelor groups. Little attention has been paid to solitary males and bachelor groups as crop raiders. It is important to understand how different social groupings (e.g., group size, solitary animals) contribute to the exploitation of crops because human activities along forest edges or in forest fragments have been shown to promote formation of specific types of social groups [17-19]. Thus, it could be possible to partially manage crop damage by changing human activities in the forests in which crop-raiding primates typically live. For example, in some regions small fragments promote the formation of small groups and solitary males [18]; if either of these social groupings is more likely to raid crops than large groups that are more typical of larger fragments, a regional strategy to decrease crop raiding would be to leave a few large fragments, rather than many small ones.

Cocoa (*Theobroma cacao*) is a crop that is commonly raided by animals [20-22]. Cocoa agro-ecosystems provide conditions that simulate the crop's natural forest environment, so that cocoa trees are planted below larger trees, which provide shade [23]; this system means that forest-dwelling species often raid cocoa plantations [20]. In Uganda, red-tailed monkeys exploit the favorable habitats created for cocoa farming by eating cocoa pods and feeding on fruits of the shade trees promoted by agro-forestry practices.

Our study quantifies the influence of the social grouping patterns of red-tailed monkeys on the destruction of cocoa pods in an agro-forestry plantation adjacent to a conservation area in Uganda. We addressed three objectives: (1) determine the ranging patterns during raiding, (2) quantify the destruction intensity caused by social groups and solitary males, and (3) determine the per capita damage caused by monkeys in different social groupings.

Methods

Feeding observations of red-tailed monkeys were conducted in the cocoa plantations bordering Kasala Forest Reserve in the Mukono District of Uganda (close to Mbira Forest Reserve). The reserves in this area of Uganda were traditionally classified as a *Celtis-Chrysophyllum* mid-altitude, moist, semi-deciduous forest or as *Piptadeniastrum-Albizia-Celtis* mid-altitude, moist evergreen forest [24], but much of the forest has been degraded and is dominated by early successional species such as *Markhamia lutea*, *Albizia* spp., *Sapium ellipticum*, and *Celtis* spp.

Observations were collected over 10 months (April 1989 - January 1990) in a 2.4 ha plantation of mature cocoa planted in 1957 with the Upper Amazon cocoa variety (Forastero) at the Coffee Research Centre, Uganda (COREC). At the time of the plantation establishment some natural trees were left standing, while others were planted to serve as wind-breaks and for shade. Field activities were conducted every two weeks and lasted three days. The 2.4 ha plantation was divided into twelve plots arranged in pairs and positioned linearly away from the forest edge, and were used to describe the ranging of the red-tailed monkeys. There was a 5 m canopy gap between the plantation and the forest, which was often overgrown with tall bushes. These bushes gave the monkeys convenient access to the cocoa field and hiding places to flee to when they were disturbed during crop raiding. A small road ran along the outside of six of the 12 plots.

The red-tailed monkeys' crop raiding activities were observed starting around sunrise (between 0600 and 0700hrs) and ending at sunset (approximately 1845hrs). Ten minute scans were taken every 30 minutes and the following were noted: raiding subgroup size, the entry and exit points per plot where possible, and plots where they ranged during each raid.

To determine the number of cocoa pods eaten by solitary males versus social groups, first the cocoa plantation was cleared of all damaged pods prior to the beginning of each study session. Subsequently, at the end of the 3 days of sampling, damaged pods were counted and removed from the trees and plots and the total number of pods damaged per month was established. While we did not collect information on seasonal variation in pod production, pods suitable for red-tailed monkey consumption were available year round. Cocoa damage caused by solitary males and members of social groups could easily be distinguished in two ways. Individuals in social groups always harvested and detached the pods from tree trunks and made a relatively bigger hole in the pod to remove the seeds. Thereafter, the damaged pods would be dropped anywhere in the plantation by the monkeys as they escaped into the forest. In contrast, solitary males often left pods on the cocoa tree after feeding and dropped the seeds directly below (Fig. 2).

We tested the relationship between the mean monthly raiding subgroup size and the total number of pods damaged that month, the number of pods damaged on a daily basis, and the effect of proximity to the forest edge on pod damage, using Pearson correlations. A Mann Whitney U-test was used to examine the relationship between distance from the road and pod damage. A paired t-test was used to contrast plots

near versus far from the road, which were progressively farther from the forest. The statistics were computed using the SPSS programme and an alpha level of 0.05 was set for significance.

Results

A single social group of 19 to 20 members and two solitary males (one adult and one immature) raided the cocoa plantation. Mean monthly raiding subgroup size varied throughout the study (mean = 12.5; range = 7 to 16; Fig. 3) though at times the whole social group entered the cocoa field to raid. Mean monthly raiding subgroup size was related to the total number of pods damaged (r = 0.538, P < 0.05, N = 10 months). However, daily pod damage was negatively correlated to raiding subgroup size (r = -0.683, P < 0.05), implying greater involvement of solitary males in raiding. Given the secretive nature of crop-raiding, redtailed monkey group counts should be considered cautiously as they are likely underestimates; however, any bias this would create would only increase the difference between animals in social groups versus solitary animals.



Fig. 1: A red-tailed monkey from Uganda (C. Chapman photo credit).



Fig. 2: Evidence of feeding by red-tailed monkeys on the pods on a cocoa tree cocoa in the plantation at Kituza Research Station, Uganda

Red-tailed monkeys in the social group ranged most frequently in plots close to the forest edge, while solitaries ranged more extensively. Hence, cocoa pods in plots near the forest edge were more damaged by social groups than those far away (r = 0.61, P < 0.05, N = 12 plots). Furthermore, plots farthest from the road suffered higher damage than the corresponding plots near the road (paired t-test = 3.675, P=0.001). On the other hand, adult solitary males were sighted more frequently in plots distant from the forest edge (r = -0.828, P < 0.001; N=12 plots), and consequently, the pod damage caused by solitaries increased with distance from the forest edge (r = 0.745, P < 0.008).

Overall, the red-tailed monkey social group caused greater damage than the solitary males; however, on average an individual solitary male destroyed each month 76.3 ± 48.4 pods, while a member in the social group damaged 22.6 ± 22.2 pods. Therefore, the per capita crop damage caused by one solitary male was greater than that caused by an individual member of the social group.

Discussion

While farmers living in proximity to protected areas suffer great losses to crop raiding animals [9, 25], these areas are attractive for farming because forests provide ecosystem services, such as predictable rainfall, regulation of microclimate, soil fertility, and protection from erosion, as well as access to forest products [26-28]. In this study, red-tailed monkeys' movements to and from the cocoa plantation, were facilitated by close proximity to the forest and by trees planted as wind-breaks and for shade [29]. The plantation was within the red-tailed group's feeding range and they appeared to have good knowledge of the local environment. Knowledge of the local environment is an important factor promoting the regular use of a specific area of the home range [30, 31]. Through repeated use, the animals become familiar with the distribution and phenological cycles of food species [32], the location of safe refuges, and the shortest routes between resource patches [30]. Thus, the time and energy to locate key resources is minimised.

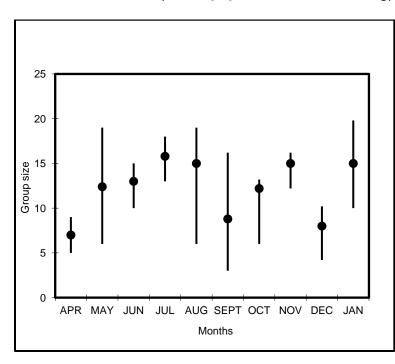


Fig 3: The size of subgroups of red-tailed monkeys raiding a cocoa plantation at Kituza Research Station, Uganda (April 1989 - January 1990). Circle = mean; vertical bar = range.

Red-tailed monkeys have been reported to live in relatively large groups and achieve high densities [33]. However, in a crop raiding situation, small feeding subgroups were typically observed in the cocoa plantation, which may allow members to be less conspicuous and reduce the risk of being detected. Though small monkeys may raid crops at large distances from forest edges [14], we found that red-tailed monkey social groups typically remained close to the forest edge. Increasing the distance from the forest that monkeys raid crops may increase the chances of being confronted by humans or of being spotted by guard dogs. Many primates species do not travel great distances from the forest edge [34] and thus, as was observed here, crop fields nearest to a forest suffer greater crop damage from social groups than gardens which are more distant [11, 12].

In contrast, solitary red-tailed males frequently ranged far from the forest edge. This could possibly be due to their deliberate spatial avoidance of social groups, or to the fact that they may be able to avoid humans and guard dogs better than social groups. By staying close to the forest edge, the more vulnerable individuals in social groups are likely closer to escape routes that would provide a secure refuge after raiding. For farmers, a strategy comprised of planting crops unpalatable to primates near forest edges (e.g., tea) could mitigate damage by social groups of primates because of their tendency to stay close to forest edges [12]. However, we quantified that plots far from the forest had higher damage from solitary males than plots closer to the forest. Thus, it is unlikely that planting unpalatable crops would be an effective strategy to deter raiding by solitary males.

Although red-tailed monkeys in the social group caused greater overall damage, the per capita destruction intensity by one solitary male was greater than an individual member of the social group. Moreover, since the quantity of damaged pods after a raid by the social group did not always equate to the number of individuals in the group, this indicated that not all the members in a raiding party actually caused damage to the pods. Solitary males caused damage to crops that was intensive and thorough, perhaps because they had more time to spend in the plantation due to the lack of co-operative activities they had to engage in, compared to individuals living in social groups. For primates in other types of human-modified landscapes, it has been previously found that age-sex classes may vary in their participation in interactions with humans. For instance, Fuentes and Gamerl [35] found that male macaques (*Macaca fascicularis*) in Bali were more likely to be involved in aggressive interactions with humans than females or juveniles.

Solitary red-tailed males are quite secretive when crop raiding. Farmers often rank crop raiding species as more destructive when they see a large group of animals [8, 36-38]. However, in the case of red-tailed monkeys the relationships between group size, destructive activity, and distance from the forest is complex. For local farmers, this has implications for the effort to be invested in detecting solitary red-tailed monkeys and controlling or preventing their damage. Protecting fields from crop raiders can be time consuming and dangerous [9, 39]. If solitary raiders, which are secretive, cause proportionally more damage, greater time and vigilance will be required for farmers to guard against this threat.

Implications for conservation

Wildlife crop raiding is a very prevalent form of human-wildlife conflict adjacent to protected areas, and since its economic loss can be high, it detracts from efforts to protect wildlife. Here we have demonstrated that red-tailed monkeys vary the nature of their raiding as a function of group structure in Uganda. Since different forms of human-induced habitat change (e.g., fragmentation, logging) are known to alter group structure. More comprehensive understanding is needed on the cascading effect of human actions both on non-human primates and on people themselves.

Acknowledgments

Appreciation is due to IPPL and Makerere University for funding which made this study possible, and CC and JT would like to thank NSERC, NIH, and the Canada Research Chair program for assistance during the writing stage. The logistical support provided by the Department of Zoology and COREC, Peter Akoll's invaluable assistance with statistical analysis, as well as C. Mazala's field assistance is acknowledged with much gratitude. We thank Rafael Reyna-Hurtado for translating the abstract and for very constructive comments on this research.

References

- [1] Fuentes, A. 2006. Human-nonhuman primate interconnections and their relevance to anthropology. *Ecological and Environmental Anthropology* 2: 1-11
- [2] Paterson, J.D. 2005. Residents and immigrants: perceptions of crop-raiding in Masindi District, Uganda. In *Commensalism and confict: the human primate interface*. Paterson, J.D. and Wallis, J., (eds), American Society of Primatology, Norman, Oklahoma.
- [3] Estrada, A. 2006. Human and non-human primate co-existence in the Neotropics: A preliminary view of some agricultural practices as a complement for primate conservation. *Ecological and Environmental Anthropology* 2: 17-29
- [4] Hockings, K.J., Anderson, L.R., and Matsuzawa, T. 2009. Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced landscape. *American Journal of Primatology* 71: 636-646
- [5] Struhsaker, T.T. 1978. Food habits of five monkey species in the Kibale Forest, Uganda. In *Recent advances in primatology*. Chivers, D.J. and Herbert, J., (eds), pp. 225-248, Academic Press, London.
- [6] Cords, M. 1986. Interspecific and intraspecific variations in the diet of two forest guenons, Cercopithecus ascanius and C. mitis. Journal of Animal Ecology 55: 811-827
- [7] Hill, C.A. 1998. Conflicting attitues towards elephants around the Budongo Foreste Reserve, Uganda. *Environmental Conservation* 25: 244-250
- [8] Hill, C.M. 2000. Conflict of interests between people and baboons: Crop raiding in Uganda. *International Journal of Primatology* 21: 299-315
- [9] Hill, C.M. 1997. Crop raiding by wild animals: the farmers perspective in an agricultural community in western Uganda. *International Journal of Pest Management* 43: 77-84
- [10] Naughton-Treves, L. 1997. Farming the forest edge: Vulnerable places and people around Kibale National Park, Uganda. . *Geographical Review* 87: 27-49
- [11] Tweheyo, M., Hill, C.M., and Obua, J. 2005. Patterns of crop raiding by primates around the Budongo Forest Reserve, Uganda. *Wildlife Biology* 11: 237-247
- [12] Naughton-Treves, L. 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology* 12: 156-168
- [13] Lee, P.C. 2010. Sharing space: Can ethnoprimatology contribute to the survival of nonhuman primates in human-dominated globalized landscapes. *American Journal of Primatology* 72: 925-934
- [14] Hartter, J. 2009. Attitudes of rural communities towards wetlands and forest fragments around Kibale National Park, Uganda. *Human Dimensions of Wildlife* 14: 433-447
- [15] Struhsaker, T.T. and Pope, T.R. 1991. Mating system and reproductive success A comparison of 2 African forest monkeys (*Colobus badius* and *Cercopithecus ascanius*). *Behaviour* 117: 182-205
- [16] Struhsaker, T.T. 1980. Comparison of the behaviour and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. *African Journal of Ecology* 18: 33-51
- [17] Baranga, D. 2004. Red-tail monkey groups in forest patches outside the protected area system in the Kampala Area. *African Journal of Ecology* 42: 78-83
- [18] Chapman, C.A., Saj, T.L., and Snaith, T.V. 2007. Temporal dynamics of nutrition, parasitism, and stress in colobus monkeys: implications for population regulation and conservation. *American Journal of Physical Anthropology* 134: 240-250
- [19] Chapman, C.A. and Rothman, J.M. 2009. Within-species differences in primate social structure: Evolution of plasticity and phylogenetic constraints. *Primates* 50: 12-22
- [20] Arlet, M.E. and Molleman, F. 2010. Farmers' perceptions of the impact of wildlife on small-scale cacao cultivation at the northern periphery of Dja Faunal Reserve, Cameroon. *African Primates* 7: 27-34

- [21] McLennan, M.R. 2008. Beleaguered chimpanzees in the agricultural district of Hoima, Western Uganda. *Primate Conservation* 23: 45-54
- [22] Monney, K.A., Dakwa, K.B., and Wiafe, E.D. 2010. Assessment of crop-raiding situation by elephants (Loxodonta africana cyclotis) in farms around Kakum conservation area, Ghana. International Journal of Biodiversity and Conservation 2: 243-249
- [23] Duguma, B., Gockowski, J., and Bakala, J. 2001. Smallholder cacao (*Theobroma cacao* Linn.) cultivation in agroforestry systems of West and Central Africa: challenges and opportunities. *Agroforestry Systems* 51: 177-188
- [24] Langdale-Brown, I., Osmaston, H.A., and Wilson, J.G. 1964. *The vegetation of Uganda and its bearing to land-use*. Ugandan Government Printer
- [25] Hartter, J., Goldman, A., and Southworth, J. 2011. Responses by households to resource scarcity and human-wildlife conflict: Issues of fortress conservation and the surrounding agricultural landscape. *Journal of Nature Conservation* 19: 79-86
- [26] Hartter, J. and Goldman, A. 2010. Local responses to a forest park in western Uganda: Alternative narratives on forest conservation. *Oryx* 45: 60-68
- [27] Hartter, J. 2010. Resource use and ecosystem services in a forest park landscape. *Society and Natural Resources* 23: 207-223
- [28] Naughton, L., Alix-Garcia, J., and Chapman, C.A. 2011. A decade of forest loss and economic growth around Kibale National Park, Uganda: Lessons for poverty reduction and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America* 108: 13919-13924
- [29] Baranga, D. 1995. The ecology and conservation status of the red-tailed monkey *Cercopithecus ascanius schmidti* in the Kampala area. In *Department of Zoology*, Makerere University
- [30] Di Fiore, A. and Suarez, S.A. 2007. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Animal Cognition* 10: 317-329
- [31] Janson, C.H. 2007 Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition* 10: 341-356
- [32] Janmaat, K.R.L., Chapman, C.A., Meijer, R., and Zuberbuhler, Z. 2012. The use of fruiting synchronicity by foraging mangabeys (*Lophocebus albigena*). *Animal Cognition*. In press.
- [33] Struhsaker, T.T. and Leland, L. 1979. Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Advances in the study of behaviour* 9: 159-228
- [34] Saj, T.L., Sicotte, P., and Paterson, J.D. 2001. The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology* 39: 195-199
- [35] Fuentes, A. and Gamerl, S. 2005. Disproportionate participation by age/sex classes in aggressive interactions between long-tailed macaques (*Macaca fascicularis*) and human tourists at Padangtegal Monkey Forest, Bali, Indonesia. *American Journal of Primatology* 66: 197-204
- [36] Litsinger, J.A., Canapi, B., and Alviola, A. 1982. Farmer perceptions and control of rice pests in Solana, Cagayan Valley, a pre-green revolution of the Philippines. *Philippine Entomologist* 5: 373-383
- [37] Siex, K.S. and Struhsaker, T.T. 1999. Colobus monkeys and coconuts: a study of perceived human-wildlife conflicts. *Journal of Animal Ecology* 36: 1009-1020
- [38] Linkie, M., Dinata, Y., Nofrianto, A., and Leader-Williams, N. 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. *Animal Conservation* 10: 127-135
- [39] Treves, A. and Naughton-Treves, L. 1999. Risk and opportunity for humans living with large carnivores. *Journal of Human Evolution* 36: 275-282