

## Human – Elephant (*Elephas maximus*) Conflict in Southern India: People's perception on conflict and elephant conservation in Coimbatore Forest Division.

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### Abstract

Nowadays the Human-Elephant Conflict (HEC) is a challenging issue faced by the managers for conserving elephant population in all its ranges. Understanding the mind sets of the local people is essential for implementing any mitigating mechanisms. The present study provides information regarding the people's perception in and around the Coimbatore Forest Division in the Nilgiri Biosphere reserve of Western Ghats. 281 persons were interviewed in and around Coimbatore Forest Division using questionnaire method, representing 77% of people (n=281) who live for many generations, 12% of people were belonged to second generation, and 11% of people were settled very recently. Among them, people who live for many generations experienced (82%) more crop damage by elephants. Among the forest ranges, peoples from Sirumugai (86%) and Karamadai (85%) forest ranges were severely affected by elephants, at least once during their life time. Respondent's opinion on 1<sup>st</sup> elephant visit in their place revealed that frequent elephant visit during the year of 2001-2005, followed by 2006-2010 (25%), 1996-2000 (17%) and 2011-14 (15%). It was interesting to note that just 3% of people had experienced before 1995. The reasons attributed for the increased human-elephant conflict include revealed that less availability of elephant food plants inside the forest followed by water scarcity (29.2%), increase of elephant population (15.5%) and elephants' preference on agricultural crops rather than the forest plants (13.9%). The suitable mitigating methods used by the local people against HEC, were electric fence (34.8%) followed by Elephant Proof Trench (EPT) (28.6%), and just 1% of them responded for money compensation, use of kumkies, elephant driving squad and also for culling. Opinion on worth for conserving elephants revealed that most of them (87%) supported in favour of elephant conservation and only 13% not supported. About 80% of the respondents believed that elephants have the Right to live.

**Keywords :** Asian elephant, Coimbatore Forest Division, elephant conservation, human-elephant conflict, People's perception.

### INTRODUCTION

Human-Elephant conflict (HEC) is a major threat to the future survival of elephants, particularly in rural agricultural regions where human populations continue to expand and encroach on habitat used by elephants (Hoare and du Toit, 1999; Sitati *et al.*, 2003). The consequences of elephant behaviour for communities are often tangible and can be devastating for individual farmers (Naughton-Treves and Treves, 2005; Osei-Owusu and Bakker, 2008). As a result elephants can elicit fear and anger on rural communities (Sitati, 2003; Parker *et al.*, 2007), often leading to farmers persecuting elephants (Parker *et al.*, 2007). HEC undermines support for elephant conservation and threatens the future of elephant populations outside protected areas. The spatial relationship between elephants, people and associated socio-economic factors influences the occurrence and severity of HEC. Globally, communities on the periphery of wildlife areas are often more susceptible to conflict with wildlife, which can be exacerbated by a low capacity to deal with the problem (Karanth, 2005).

Wildlife managers and biologists in India have identified that elephant induced conflicts erode local goodwill and create hostility towards conservation efforts because of the losses suffered by people (Karanth and Madhusudan, 2002; Madhusudan, 2003). The escalating incidences of crop raiding have led to increased people's antipathy towards the elephant and in certain instances resulted in retaliatory killing of elephants (Hedges *et al.*, 2005; Kulkarni *et al.*, 2007).

In areas where elephants persist they are often forced into close contact with people, and contemporary social conditions often lower people's tolerance of elephants (Naughton-Treves *et al.*, 2000). Wildlife damage can change a person's perception about wildlife especially when damage exceeds his or her tolerance. Attitudes of local people to wildlife and particularly to large animals are an increasingly important element of conservation work but attitudes may vary according to gender and prior experience of wildlife (Hill, 1998). Some wildlife species may have social and cultural significance in some countries therefore differentiating the attitudes towards the same animal irrespective of the damage it causes. However as mentioned earlier, when the damages exceed a certain limit perceptions may change and conservation issues hence arise. The

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propensity of respondents to exaggerate depredation by wildlife reflects important social dimensions to human-wildlife conflict (Lee and Graham, 2006).

The Coimbatore Forest Division one of the severe HEC forest divisions in the Nilgiri Biosphere reserve of Western Ghats, has a sizeable elephant population and viable habitat for the population of resident and also for the migratory elephants. The elephants regularly or sometimes occasionally raid in the agriculture fields though the Coimbatore Forest Division shares the boundary at the length of about more than 350 km with the human habitations and farm lands, the villages located adjoining the reserve forest boundary are highly prone to elephant depredation. The elephant movements in this division are mostly restricted to very narrow paths of the foothills of the large mountains naturally near the human habitations. However, depredation is higher when compared to other largely populated elephant habitats. Crop fields located even after 2km away from forest boundary also highly prone for elephant visits. Interestingly elephants visited more than 5 km outside the forest areas of Coimbatore Forest division on few occasions (unpublished data)

Human-elephant conflict incidents are notably on the increasing trend due to many factors. There is a big question arises as to how best elephant and human beings can live in a human induced environment in the future. The management of HEC is one of the important challenges to the wildlife researchers, conservationists and forest managers. Unless we understand the attitude and perception of the stake holders on HEC, it is very difficult to prepare the feasible management plan.

A community-centered approach provides opportunities to improve the attitudes of communities towards elephants and increases the potential of long-term conservation strategies such as habitat protection. To develop and direct effective community-led mitigation strategies it is vital to gain a thorough understanding of the HEC problem on both community and regional scale.

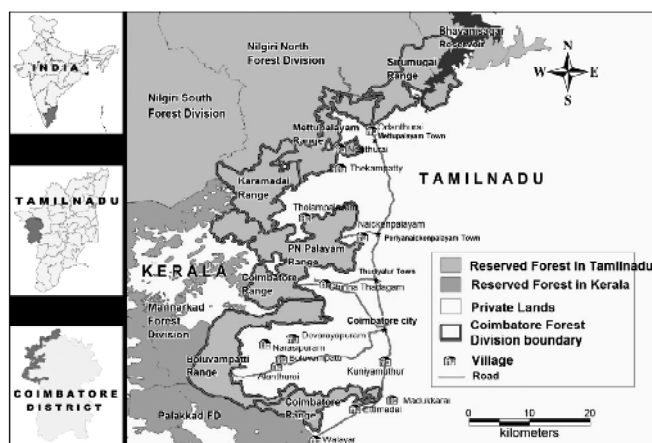
The overwhelming majority of studies have focused on protected areas. Little is known about the status of conflict in territorial division like Coimbatore Forest Division. However, the Coimbatore Forest Division gets less attention in terms of scientific study except Ramakrishnan (2008) and also no detailed information is available on these aspects. The present paper deals with the assessment of the status of elephant depredation in the past, people's perception on HEC, people's perception on methods suitable to reduce HEC and people's attitude towards elephant conservation.

## STUDY AREA

The Coimbatore Forest Division covers an area of 694 km<sup>2</sup> and is situated in the South-east of the Nilgiri

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Biosphere Reserve (NBR). Also Coimbatore Forest Division falls under the Elephant Reserve No. 8, in which Nilambur-Silent Valley of Kerala forming the major portion of the tract. It is also part of Nilgiris and Eastern Ghats Landscape (Map. 1) which is holding single largest Asian elephant population in the world. This forest division has six ranges namely Sirumugai, Mettupalayam, Karamadai, Perianaickenpalayam (PN Palayam), Coimbatore and Boluvampatty. The area lies between latitude 10°51' and 11°27' and longitude 76° 39' and 77° 4'.

This forest division has wide range of altitude from 450m to 1450m. The Pillur slopes are the steepest, a shear drop is observed as the ground falls from 450m to 1530m suddenly. The Melur slopes, Hulical Durg and Nellithurai forests are on the lower hill mountains. The Boluvampatty hills elevation ranges from 450m to 530m. Above 530m the ground rises sharply to the crest of the hill range to the north, west and south, the maximum elevation is 1986m on the Velliangiri Peak. Apart from these sloping hillocks, this reserve has Velliankadu Valley, Nayakkan Palayam Valley, Thadagam Valley, Boluvampatty Valley and the Walayar Valley. The Nayakkan Palayam rises sharply from 460m to 1614m on the Nadukondanboli forming a tri junction point for the entire three valleys. Innumerable little streams originate from Coimbatore Forests and drain the plateau. This network of streams resolves itself into Bhavani and Noyyal river. The vegetation types range from tropical thorn forest at the foothills to evergreen forest, in relation to terrain, altitude and rainfall. The study was carried out in the villages located all along the foot hills of forest ranges such as Coimbatore, Boluvampatty, PN Palayam, Karamadai, Mettupalayam and Sirumugai.

## MATERIALS AND METHODS

Questionnaire method was followed to assess the people's perception on HEC and elephant conservation. Villages were visited randomly near forest fringes of the Coimbatore forest division. Information was

gathered through “broad and open ended” questions giving the respondent an opportunity to express his views freely (Balakrishnan and Ndhlovu, 1992; Ramakrishnan *et al.*, 1997; Ramkumar *et al.*, 2014). The questionnaire survey was conducted over a period of five months from October 2013 to March 2014.

## RESULTS

### Status of crop depredation by elephants

Status of crop depredation by elephants in and the Coimbatore forest division revealed that about 64.06% of people (n=281) experienced crop damage by elephants at least once in their life time (Table 1). Whereas about 35.94% of people never experienced any crop damage by elephants during their life time in this region.

This study has found that 77% of people (n=281) were living in and around the forest areas for many generations (Fig.1). Whereas about 12% of people were belonged to second generation and 11% of people were settled very recently. Among them, people who live for many generations had more experienced (82%) on crop damage by elephants than second generation (11%) and recent settlers (7%) (Fig.2). Table 2 shows the relative percentage of respondent's opinion on ever experienced crop damage with respect to each group of people from different generations. Among these groups of people, there was no much difference between 'many' generation (68.2%) and second generation (60.6%). On the contrary, the recent settlers had less experience on crop damage by elephants.

The relative percentage of respondent's opinion on ever experienced crop damage with respect to each forest range of the Coimbatore Forest Division is shown in Figure 3. Opinion of people from six forest ranges was considerably varied. Peoples from Sirumugai range (86%) (n=49) and Karamadai range (85%) (n=20) experienced more crop damage by elephants at least once during their life time followed by Boluvampatty (65%) (n=20), PN Palayam (61%) (n=41), Coimbatore (57%) (n=121) and Mettupalayam (47%) (n=30).

Opinion on ever experienced crop damage by elephants with respect to overall Coimbatore division (n=281) revealed that people from Coimbatore range (38%) had more experience than by Sirumugai (23%), PN Palayam (14%), and Karamadai (10%) (Fig.4). Less than 10% people experienced ever crop damage by elephants from remaining two forest ranges such as Boluvampatty and Mettupalayam.

Respondent's opinion (n=260) on 1<sup>st</sup> elephant visit that they had encountered in their place revealed that large number of people (35%) experienced elephant visit during the year of 2001-2005, followed by 2006-2010 (25%), 1996-2000 (17%) and 2011-14 (15%) (Fig.5). Just

3% of people were experienced before the year of 1995. Even though 281 persons questioned, only 260 respondents expressed their opinion clearly and the rest had no clear opinion.

### Causes for the increasing Human - Elephant Conflicts

Causes cited for the conflict reflected varied opinions. A large number of respondents (33.6%) believed that less availability of elephant food plants inside the forest is responsible for increasing HEC (Table 3) followed by water scarcity inside the forests (29.2%), elephants' preference on agricultural crops as better choice rather than forest plants (15.5%). In a nutshell 23.4 % of respondents have opined that more than one reasons caused for HEC (Fig. 6).

People's opinion on age and sex of elephants frequently visited the crop fields revealed that female led elephant herds (55%) visited more frequently than by solitary males (38%) and certainly associated male groups (5%) (Fig.7). When question was asked from the respondents regarding the category of elephants which were highly responsible for more economic loss, the analysis revealed that 52% economic loss was caused by the elephant herds followed by solitary males (43%) (Fig.8).

### Effective mitigating measures used by the local people against Human - Elephant conflicts

Respondents were also asked to suggest suitable methods to reduce HEC. Electric fence was found highest (34.8%) support from respondents followed by Elephant Proof Trench (EPT) (28.6%) to reduce HEC (Table 4). Habitat improvement was supported by 19.8% of respondents. Surprisingly just 1% suggested that paying money for compensation, using kumki elephant to drive away the wild elephants and establishing elephant driving squad. It was quite interesting to note that none of them supported culling of elephants as one of the mitigating methods to reduce HEC. In general 41.5 % of respondents (n=281) have opined that combination of various methods only considered as the most effective method to reduce HEC (Fig. 9).

### People's attitude on elephant conservation

When asked the people regarding the worthiness of conservation of elephants, most of the respondents (87%) supported in favour of conservation and only 13% not supported (Fig.10). The suggested reasons for supporting elephant conservation were that most of them believed that the elephants have the right to live (80%), followed by the elephants are considered as Lord Ganesh's avatar (19%) (Fig.11).

Table.1. Status of crop damage by elephants ever experienced by people who live in and around forest areas.

Opinion	No. of respondents	Relative %
Yes	180	64.06
No	101	35.94

Table.2. Status of crop damage by elephants ever experienced by people from different generations

Opinion	Many generation		Second generation		Recently settled	
	No.of respondents	Relative %	No.of respondents	Relative %	No.of respondents	Relative %
Yes	148	68.2	20	60.6	12	38.7
No	69	31.8	13	39.4	19	61.3

Table.3. People's opinion on causes of Human – Elephant Conflict

Sl.No	Reasons for HEC	No. of respondents	
		Opinion in favour	Relative %
1	Increase of human population	34	6.2
2	Increase of elephant population	85	15.5
3	Less availability of elephant food species in forest	184	33.6
4	Water scarcity in forest	160	29.2
5	Elephants prefer crops by choice than forest food	76	13.9
6	Location of crops close to forest foothills	6	1.1
7	Location of huge buildings close to the forest foothills	0	0.0
8	Others	3	0.5

Table.4. People's opinion on methods considered suitable to reduce Human – Elephant Conflict

Sl.No	Methods suitable to mitigate HEC	No. of respondents	
		Opinion in favour	Relative %
1	Elephant Proof Trench (EPT)	126	28.6
2	Electric Fence	153	34.8
3	Stone Wall	46	10.5
4	Elephant capture	22	5.0
5	Culling	0	0.0
6	Elephant scaring squad	1	0.2
7	Chasing by Kumki	2	0.5
8	Money compensation	3	0.7
9	Habitat improvement	87	19.8

Fig.1. Percentage of people from different generation living in and around the forests.

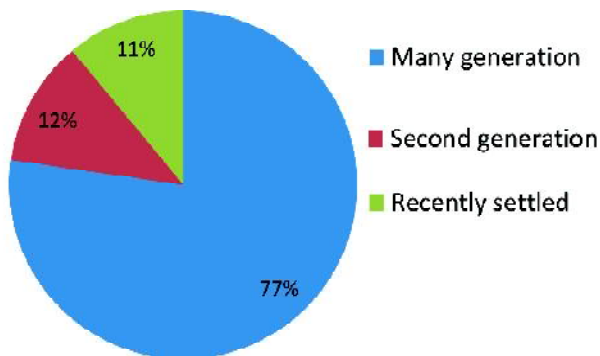


Fig.2. Percentage of people from different generation experienced crop damage at least once in their life time.

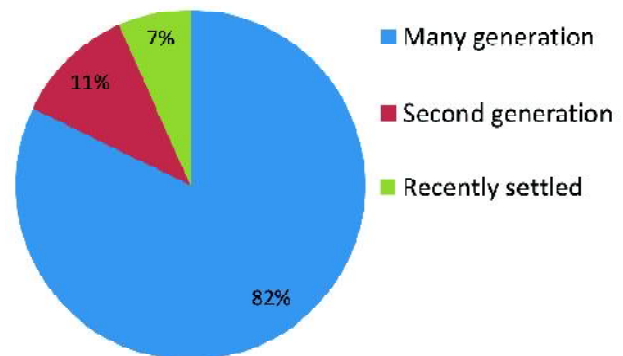


Fig.3. Relative percentage of respondent's opinion on ever experienced crop damage in each forest range.

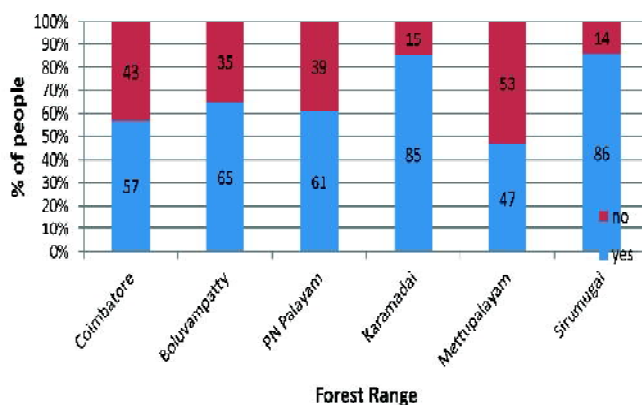


Fig.4. Over all percentage of people in different forest ranges experienced crop damage by elephants at least once in their life time

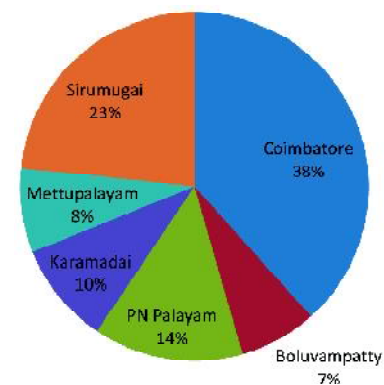
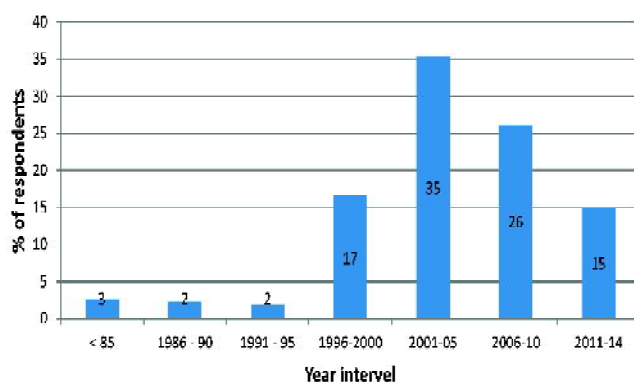
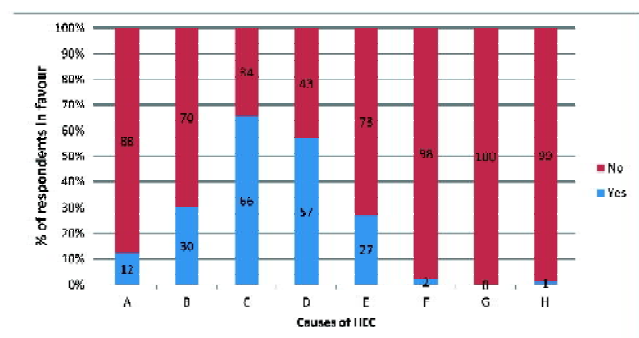
Fig.5. People's opinion on 1<sup>st</sup> elephant visit in their place

Fig.6. Relative percentage of respondent's opinion on each cause of Human - Elephant Conflict



A. Increase of human population, B. Increase of elephant population, C. Less availability of elephant food species in forest, D. Water Scarcity in forest, E. Elephants prefer crops by choice than forest food, F. Location of crops close to forest foothills, G. Location of huge buildings close to the forest foothills, H. Others

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Fig.7. Category of elephants coming frequently into crop fields

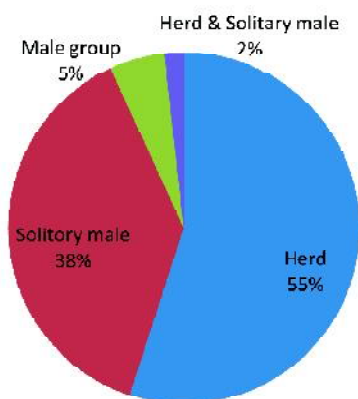


Fig.8. Category of elephants responsible for more economic loss of crops

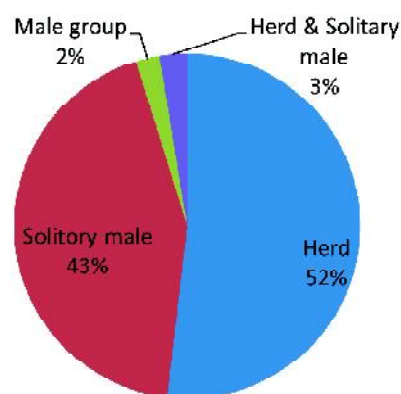
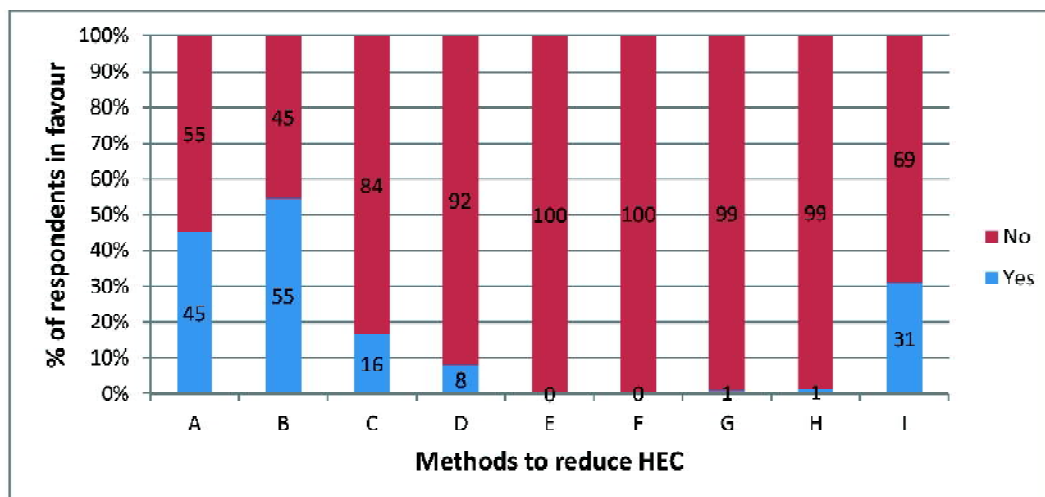


Fig.9. Relative percentage of respondent's opinion on different methods considered suitable to reduce HEC



A. EPT, B. Electric Fence, C. Stone Wall, D. Elephant capture, E. Culling, F. Elephant scaring squad, G. Chasing by Kumki, H. Money compensation, I. Habitat improvement

Fig.10. Worth of conserving elephants

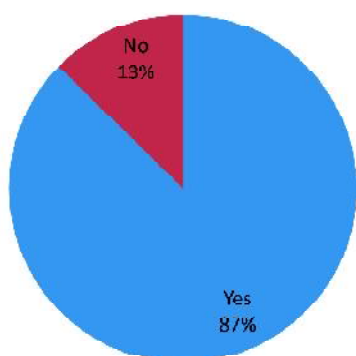
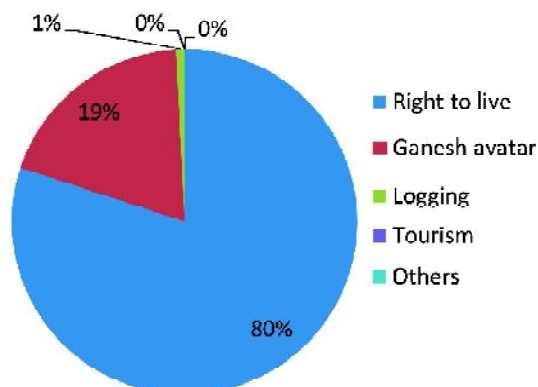


Fig.11. Reason for supporting elephant conservation



## DISCUSSION

Attitudes of local people to wildlife and particularly to large animals are an important element for conservation. But attitudes may vary according to gender and their experience with wildlife. The complex human sociological, psychological and economical dimensions play important role in shaping the perception of conflict among local communities (Naughton-Treves *et al.*, 2000; Hedges *et al.*, 2005). The present study revealed that 64.06% of people (n=281) had experienced crop damage by elephants at least once in their life time. On the contrary, the recent settlers had less experience on crop damage by elephants. According to a study conducted by Røskaft *et al.* (2007) on human attitudes towards large carnivores in Norway, safety was the major concern that changed the attitudes of human towards wildlife. The higher level of fear seems to be associated with a more negative attitude, they also saw that age and education also influenced the attitude of a person. The older people had a more negative attitude and people with higher level of education had a more positive attitude. Larger communities had a more positive attitude which could also because of the sense of security among a bigger group of people. Therefore they said that the attitude of people towards carnivores is complex and it cannot be said whether it is more towards the negative side or positive. As in all cases the media always play a vital role in drawing the attention to any issue.

Szinovatz (1997) in Norway, found that better information levels made many people more critical in their attitudes, and also more willing in outing them. According to another study on Brown Bears in Slovenia by Kaczensky *et al.* (2004), the past negative experiences and fear of the animal created a more negative attitude. It was usually the women who had a more negative attitude possibly because they feared the bears more (Kaczensky *et al.*, 2004). Hill (1998) in her study found that most people felt that elephants were dangerous and that they were known to cause harm to people as well as to property.

This present study also provide several interesting results with respect to people perception on HEC and elephant conservation. A large number of respondents believed that less availability of elephant food species in the forests were highly responsible for HEC. Nath (1998) also received the same opinion from the respondents in Kodagu district of Karnataka. Interestingly, only 1.1 % respondents felt that location of crops closer to forest foothills was responsible for HEC. Remaining 99% of respondents still not felt that this is one of the major causes for HEC. None of the respondents supported in favour of huge buildings close to the forest foothills, a cause for HEC.

Nevertheless, this study found that more than one reasons caused for HEC in many places.

Respondent's opinion on methods suitable to reduce HEC revealed that electric fence and EPT were received maximum support. Interestingly habitat improvement also received remarkable support from respondents. Capture of elephants was supported by below 8% of respondents. On the contrary 49% of respondents from Kodagu district of Karnataka supported in 1998 for elephant capture (Nath, 1998). None of the respondents considered culling of elephants and elephant scaring squad as the suitable method to reduce HEC. One thing completely surprised that money compensation received only 1% support from respondents. About 41.5 % of respondents believed that combination of various methods considered as the most effective method to reduce HEC in and around the Coimbatore Forest Division. Ramakrishnan (2008) also recorded similar result from the people those who were living along the critical elephant corridors in the Coimbatore Forest Division. The perceptions of farmers reflect rare extreme damage incidents caused by large elephants rather than persistent, small losses caused by smaller wildlife that may actually cumulatively be greater (Naughton *et al.*, 1999).

Even though there was a mixed of opinion from respondents, one thing was very clear that people showing more interest towards prevention of HEC rather than compensation for the loss of crop, asset and human life.

Respondent's opinion towards worth for elephant conservation (87%) revealed positive attitude of stake holders. The present study also found that most of them believed that the elephants have the right to live (80%) and the elephant is considered as Lord Ganesh's avatar. Sometimes this kind of sentimental beliefs would help for the conservation of many wild animal species. On the contrary Maunglang (2003) pointed out that "Once worshipped as God, it is now considered an enemy, Considered as asset in the past it is now becoming a liability". The negative attitude towards any problem of wildlife is further increased when the media emphasises on the issue for a long time. The way the problem is presented could also be an influential factor (Røskaft *et al.*, 2007).

Even though HEC is increasing over the years in Coimbatore Forest Division, still people showed positive attitude towards elephants conservation is a good sign for long term survival of asian elephants in this region.

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## REFERENCES

- Balakrishnan, M. and Ndhlovu, D.E. 1992. Wildlife utilization and local people. A case study in Upper Lupande game management area. Zambia. *Environmental Conservation*, 19: 135-144.
- edges, S., Tyson, M.J., Sitompul, A.F., Kinnaird, M.F., Gunaryadi, D. and Aslan. 2005. Distribution, status and conservation of Asian elephants (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. *Biological Conservation*, 124: 35-48.
- Hill, C.M. 1998. Conflicting attitudes towards elephants around the Budongo Forest Reserve, Uganda. *Environmental Conservation*, 25(3): 244-250.
- Hoare, R. E. and Du Toit, J. T. 1999. Coexistence between people and elephants in African savannas. *Conservation Biology* 13: 633-639.
- Karanth, K.U. and Madhusudan, M.D. 2002. Mitigating human-wildlife conflicts in southern Asia. In: Terborgh, J.W., Van Schaik, C., Davenport, L., Rao, M (Eds.), *Making Parks Work: Identifying key factors to implementing parks in the tropics*. Covelo, CA. Island Press. P. 250-264.
- Karanth, K.K. 2005. Addressing relocation and livelihood concerns: Bhadra wildlife sanctuary. *Economic & Political Weekly*: 40, 4809-4811.
- Kulkarni, J., Prachi, M., Boominathan, D. and Sujoy, C. 2007. A Study of Man-Elephant Conflict in Nagarhole National Park and Surrounding Areas of Kodagu District in Karnataka, India. Final Report. Envirosearch, Pune.
- Lee, P.C. and Graham, M.D. 2006. African Elephants *Loxodonta africana* and human-elephant interactions implications for conservation. *The Zoological Society of London* 40:11.
- Madhusudan, M.D. 2003. Living amidst large wildlife: livestock and crop depredation by large mammals in the interior villages of Bhadra Tiger Reserve, South India. *Environmental Management* 31(4): 466-475.
- Nath, C. D. and Sukumar, R. 1998. *Elephant-human conflict in Kodagu: southern India*. Asian Elephant Research and Conservation Centre, Bangalore.
- Naughton-Treves, L., Treves, A. and Rose, R. 2000. *The Social Dimensions of Human-Elephant Conflict in Africa: A Review of the Literature and Case Studies from Cameroon and Uganda*. IUCN, African Elephant Specialist Group, Nairobi, Kenya.
- Naughton-Treves, L. and Treves, A. 2005. Socio-ecological factors shaping local support for wildlife: crop-raiding by elephants and other wildlife in Africa. In: Woodroffe, R., Thirgood S. and Rabinowitz, A (Eds.), *People and Wildlife: Conflict or Coexistence*. Cambridge Univ. Press, UK, P. 252-277.
- Osei-Owusu, Y. and Bakker, L. 2008. *Human-Wildlife Conflict*, FAO. *Elephant Technical Manual*, P. 45.
- Parker, G.E., Osborn, F.V., Hoare, R.E. and Niskanen, L.S. 2007. *Human-Elephant conflict Mitigation: A training course for Community-based Approaches in Africa. Participant's manual elephant pepper development Trust*, Livingstone, Zambia.
- Ramakrishnan, B., Sivaganesan, N. and Srivastava, R.K. 1997. Human interference and its impact on the elephant corridors in Sathyamangalam and Coimbatore forest divisions, Tamil Nadu, Southern India. *Indian Journal of Forestry*, 20(1): 8-19.
- Ramakrishnan, B. 2008. Status of Wildlife Corridors and their use by selected endangered mammals in the Nilgiri Biosphere Reserve, India. Ph.D. dissertation, Bharathidhasan Univ., Thiruchirappalli, India.
- Ramkumar, K., Ramakrishnan, B., and Saravanamuthu, R. 2014. Crop damage by Asian Elephants *Elephas maximus* and effectiveness of mitigating measures in Coimbatore Forest Division, South India. *Int. Res. J. Biological Sci.* (In Press)
- Røskft, E., Händel, B., Bjerke, T., Kaltenborn, BP. 2007. Human attitudes towards large carnivores in Norway. *Wildl. Biol.* 13(2):172-185.
- Scott, W., Tammy, E.D., Nandita, H. and Alexandra, Z. 2013. Understanding spatial and temporal patterns of human-elephant conflict in Assam, India. *oryx*. P. 1-10.
- Sitati, N. 2003. *Human-elephant conflict in Trans Mara district adjacent to Masai Mara National Reserve*. Ph. D. dissertation, University of Kent, Canterbury, UK.
- Sitati, N.W., Walpole, M.J., Smith, R.J. and Leader-Williams, N. 2003. Predicting spatial aspects of human-elephant conflict. *Journal of Applied Ecology*, 40: 667-677.
- Szinovatz, V. 1997. *Attitudes of the Norwegian public toward bear and lynx*. Diploma thesis. Vienna, University of Agricultural Sciences. 124 pp.
- Kaczensky, P., Blazic, M. and Gossow, H. 2004. Public attitudes towards brown bears (*Ursus arctos*) in Slovenia. *Biological Conservation*, 118: 661-674.