The human wildlife conflict: towards a theoretical foundation

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Abstract: Multiple angles of human wildlife conflict have been increasingly haunting conservation biology over the last few decades despite many mitigation attempts. We argue here that the field suffers from the lack of a theoretical foundation. As a result, researchers have failed to collect data on some of the most critical variables, and are unable to determine the predominant causes of the conflict. In the absence of causal analysis, the management has failed to deploy appropriate mitigation measures. As a result, the conservation policies are divided by mutually incompatible philosophies, sentiments and opinions. We identify here the alternative causal factors of the conflicts along with their differential testable predictions. Further we incorporate them in a unified model based on foraging optimization by the animals. At different parameters the same model fits into different observed conflict patterns. Identifying the predominant cause is a pre-requisite for designing any effective short and long-term solutions for any given locale. The model results reveal that across contexts the most critical parameter is fear of humans. If the human avoidance behaviour of animals decreases below a threshold, conflict escalates even at a small population size. Mitigation measures such as habitat restoration, population control, fencing or deterrents are effective only if the fear factor is adequately high. The model can direct the focus of research towards the missing variables in empirical work. With adequate empirical support, the theory would provide an appropriate basis for long term conservation management maximizing stable population sizes and survival probabilities with minimum conflict.

Key words: Human wildlife conflict, conservation biology, wildlife management, foraging optimization, population regulation, human wildlife co-existence

Highlights:

1. We treat crop damage by wild animals, a predominant component of human wildlife conflict (HWC), as a foraging optimization problem in order to identify the conditions under which wild animals would indulge in crop raiding.
2. Each of the putative causal factors make differential predictions which would enable determining the context specific predominant cause.
3. The model also evaluates the potential effectiveness of different mitigation measures.
4. Theoretical analysis identifies the loss of fear of humans as the most critical causal factor for HWC across the board. Only above a certain threshold fear, any other mitigation approach can be fruitful.
5. The analysis necessitates new directions for empirical research, a new foundation for wildlife conservation and novel mitigation approaches for resolving human wildlife conflict.

Introduction:

Increase in human-wildlife conflict (HWC) is a serious concern on a global scale (IUCN 2023). Although it is a widely recognized problem, there is a dearth of studies addressing fundamental questions. Damage to crops is an important component of the conflict apart from livestock and property damage and occasional attacks on humans. The problem can be qualitatively different in countries like India with a total ban on hunting of a large number of species, from countries where regulated hunting is practiced. With a remarkable success in large carnivore conservation along-side poverty and high human population density (Jhala et al 2025), it may not be a surprise that India represents a high frequency of human deaths by wild animal attacks (Government of India 2024). While the frequency of human attacks has been a focus of media attention and the role of hunting is debated (Vajpeyee 2025), being an agriculture centered society, farmer-herbivore conflict is the most serious form of conflict (Dandekar *et al* 2025) in India. As initially perceived, conservation was intended to facilitate agricultural productivity (Gadgil and Meher-Homji 1986) but the outcome appears to be on the contrary. Although a number of possible causal factors for crop damage by wild animals are recognized (Prabhulkar and Watve 2025) along with their testable predictions, data to test any of the predictions are conspicuously absent. The neglect of the field is evident in the absence of any attempt to develop sound and validated methods of quantifying crop damage and maintaining systematic data. In the absence of data on the most crucial variables, the alternative causal hypotheses cannot be tested. Further in the absence of causal knowledge, appropriate solutions are unlikely to be effectively implemented. We argue here that the field lacks a rigorous theoretical foundation. We attempt a generalized theoretical model that incorporates the alternative factors speculated to contribute to the problem. The model, based on the principles of optimum foraging, makes differential testable predictions coming from different causes, so that the most important causal factor for a given context can be identified and appropriate cause-specific solutions be implemented. The model also permits developing guidelines about which mitigation measures will be most effective in a given context. Although our main focus is HWC in the Indian context, the theoretical model can be applied in the global context with appropriate sets of parameters.

Although a thorough causal analysis has not been performed it is often rhetorically stated that increasing human population, encroachment, deforestation, habitat fragmentation and pressure from developmental activities is responsible for the conflict. (Lamarque *et al* 2009, IUCN 2023, Mishra *et al* 2025, Chettry *et al* 2025, Bharti *et al* 2025, Routray *et al* 2025, Tiwari *et al* 2025, Akhila *et al* 2025). There is no doubt that human population pressure and habitat loss are serious problems, but whether they are necessary and sufficient causes of HWC remains an unaddressed question. Apart from habitat fragmentation as the most widely stated cause, population growth of potentially destructive species, greater food availability in human dominated landscapes and the rapidly vanishing human avoidance behaviour in animals are the alternative causes identified (Prabhulkar and Watve 2025).

Encroachment by agriculture and the loss of wilderness habitat: This is the most often stated cause of HWC. Although globally it is true over the last century that the human population has increased, land use patterns changed substantially and there is degradation or fragmentation of natural habitats; there are instances of local reversal as well. Villages have been relocated out from protected areas. Farmers have given up agriculture and migrated as labourers deserting villages which returned harboured wild populations again. Large scale habitat protection as well as restoration programs have been implemented. So, a correlational analysis of change in habitat quality and area with severity of conflict should be possible if appropriate data are available. Data on damage are not available with consistent methodological rigor across different areas for such an analysis. Certain anecdotes suggest on the contrary. For example, in the Tadoba Andhari Tiger Reserve (TATR) in India, active habitat management, weed control, village relocation and expansion of protected area are actively implemented (Habib *et al* 2019). But with better habitat restoration HWC has not decreased, instead these areas reported alarming increase in both herbivore and carnivore conflict. It is doubtful whether on a larger scale the expected correlation of habitat management with severity of conflict will be observed. Since wide scale data are not available, we take a different approach in this paper, that of modelling to examine the theoretical soundness of the causal hypothesis.

Population growth of the wild species: This is another commonly assumed cause and often the suggested mitigation measures are towards population control either by hunting/culling or by birth control. Many countries practice calculated licenced hunting. Occasionally active programs of sterilization/contraception of males and/or females are undertaken (Kumara and Venugopal 2023). But whether they are effective in reducing the agricultural loss is difficult to decide in the absence of standardized and validated methods for damage quantification.

Disappearance of human fear: This causal hypothesis states that animals avoid the vicinity of humans owing to an intrinsic fear. It is possible that this fear was established because human ancestors were efficient hunters, the only species that can inflict fatal injury from a considerable distance. With the blanket ban on hunting or strict restrictions on it and increased wildlife viewing tourism, animals are rapidly losing human fear. The notion that forests/wilderness is the natural habitat of animals is likely to be an effect of the human avoidance behaviour. Otherwise, there is no reason why animals do not inhabit the human modified landscapes. The availability of food and water is very often greater in and around human habitation. If animals lose human fear, they would occupy human landscapes freely (Prabhulkar and Watve 2025).

The alternative causes are not mutually exclusive and different causes may predominate in different contexts. The different causal factors demand different mitigation measures and a mismatched mitigation may not only be ineffective but counterproductive. For example, if vanishing human fear is the predominant cause, then even a small population can cause substantial damage. In such a case population control is not only bound to be ineffective, it may invite local extinction of the species.

We first start with an approach of examining each causal factor separately under a defined set of assumptions and treating other factors constant. A matrix of baseline assumptions and causal hypotheses makes testable predictions from each of the combinations. The matrix can be used to see which combination explains the main observed patterns in crop depredation by wild animals. At a second stage we take a comprehensive approach that incorporates all sets of assumptions and causal factors in a single model. This model allows studying the interactions and combinations of factors. The model also allows predictive analysis from different classes of mitigation measures so as to select the appropriate solutions in appropriate contexts.

The models:

Making testable predictions for single factors under different sets of assumptions:

The following assumptions have been discussed in literature and the expected effects of different causal factors would depend upon the set of assumptions. A common oversimplified assumption is that there is a wilderness landscape and a human settlement landscape. Although in reality they are often inseparable, we will start with the simplistic assumption.

1. Conflict along the interface: This assumes that most of the conflict takes place along the interface of agriculture and forest/wilderness (Rathi *et al* 2020, Mamo *et al* 2021). By this assumption the damage is incidental and wherever the animal population, their home ranges or migration routes border agricultural lands, will happen inevitably. The animals are not assumed to proactively invade crops in this assumption. The length of interface and the animal density along the interface are the main determinants of damage. An interesting implication of this assumption is that if corridors are established between two or more pockets of wilderness, the interface length is bound to increase thereby increasing the conflict. The alternative assumption is that conflict can arise anywhere, not restricted to interface and animals invade crops because it is nutritionally beneficial for them in the given context.

2. Push or pull: When damage is not restricted to the interface and animals come out for a considerable distance to eat crops, two distinct phenomena called push and pull have been identified earlier. Push implies that animals prefer to stay in the wilderness habitat. Only when it is inadequate in some or the other way (which may be seasonal), they are compelled to come out. Pull implies that there are features of the human landscape (which may be seasonal) that attracts them independent of the status of things in the wilderness habitat (Sukumar 2019). If we consider the pull

factor in the absence of human fear, animals are expected to be free to access the entire agricultural area.

3. Natural regulation of population: The assumption is that population growth is restricted by the carrying capacity of the wilderness habitat. There are natural mechanisms of population control. Population converges to and remains stable at the carrying capacity which is decided only by the characteristics of the wilderness habitat and is independent of human landscape. Alternative to this assumption is that there is no definite habitat dependent carrying capacity. If they get more nutrition and more opportunities they will grow more (Watve 2026).

Conservation management is often based on a set of implicit assumptions including carrying capacity, natural population regulation, preference of animals to the wilderness habitats and the belief that they won't come out unless the habitat is degraded. The upcoming patterns of HWC are challenging these assumptions (Watve 2026). Here we will examine the possible outcomes with and without such assumptions.

The causal hypotheses:

To predict the effect of different causal factors on agricultural loss, we consider the following variables. The total land is considered one unit which is divided into wilderness W and human land use, predominantly agricultural as A so that $W + A = 1$. If there is agricultural expansion $\Delta A = - \Delta W$. As a baseline assumption, if we consider the wild population of the species under consideration distributed only on the wild land, the population density of the wild species over W is P, so the total population is $P.W$. Only a fraction of the population P_d would be involved in crop raiding, the relationship between P and P_d would depend upon the set of assumptions. Only a fraction of total agricultural area would be accessed by wild animals A_{ac}, and the relationship between A and A_{ac} depends upon the set of assumptions. Let Y be the crop yield and we consider Y_0 = Initial yield and Y_t = yield after time t during which the causal factor has acted, so that $Y_0 - Y_t = L$ total loss. Loss per unit area = $Y_0/A_0 - Y_t/A_t$. We consider that the causal factor acts only during time t. We use time $t+1$ for making further predictions where it is assumed that the external causal factor does not change between t and $t+1$.

With this set of variables agricultural losses will be

$$L \propto P_d.A_{ac} \qquad \text{Eq. 1}$$

The following causal hypotheses are assumed to act one at a time.

A. Encroachment/habitat loss/fragmentation: We ask the question, if some agriculture is newly established by encroachment on the wildland, how is it expected to affect the interface and crop destruction patterns under the above set of assumptions?

The interface of wilderness and agriculture is expected to be a non-linear function of encroachment. Suppose the land was all wild to begin with and we assume human habitation establishing and spreading over time. The human occupied land will increase locally as well as new centres occupied. The interface will be a function, *I = f(A.W),* where *I* is the length of the interface. It is obvious that interface will be zero when *A* is zero or *W* is zero. Interface will be maximum at intermediate values of A and W, the exact length being dependent upon the shapes and patterns of human occupation. Accordingly, the function can be varied (figure 1) depending upon the pattern of encroachment.

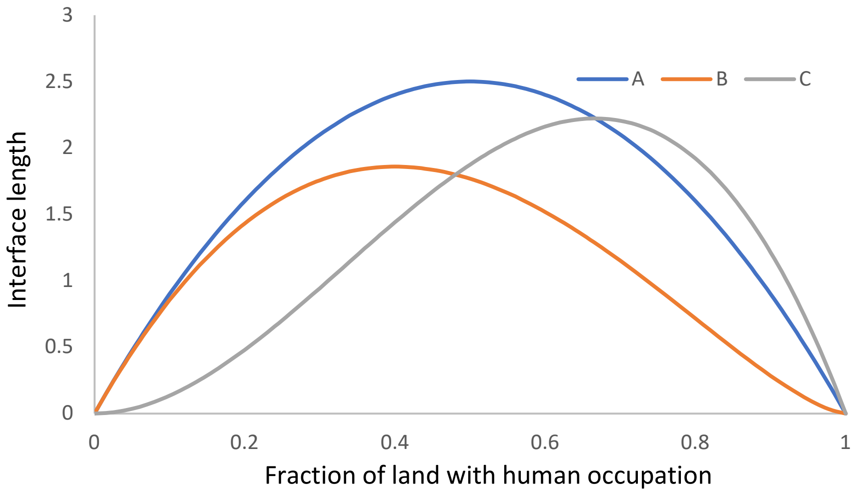


Figure 1: The interface length as a function of human occupation. The change is necessarily non-monotonic going to zero at both extremes although the function f will decide the actual curve, depending upon the shapes and patterns of human occupation.

Whether the interface will increase or decrease with agricultural encroachment depends upon the position along the curve. Where the landscape is predominantly wilderness, increased agricultural encroachment will increase the interface length. This might be true in many African countries with large wilderness areas. When wilderness exists in smaller pockets and human occupied landscapes are predominant (as in India today), the net interface is bound to decrease with greater agricultural encroachment. Further, if we assume that crop damage happens mainly along the interface, the damage will depend upon the change in the interface length and the density of herbivores along the interface. If an existing pocket of wilderness is pushed to be smaller by encroaching human occupation, the animal density along the interface will increase but the interface length is most likely to decrease.

With simplistic considerations, if we consider the wilderness pockets as circles, we simplify the mathematics.

When $\Delta W < 0$ and we assume that population continues to inhabit the wilderness area, the population density within the wildland will increase.

$Animal\ density\ at\ time\ 0\ =\ \frac{P}{W_0}$ and $animal\ density\ at\ time\ t\ =\ \frac{P}{W_t}$

Considering *b* to be the breadth of the interface area

$Interface\ area\ at\ time\ 0 = 2\sqrt{W_0}b$ and $interface\ area\ at\ time\ t = 2\sqrt{W_t}b$

P_d is the animal density that actually damages the crops

$$P_d\ =\ animal\ density\ along\ the\ interface\ \times\ area\ of\ interface$$

$$P_d\ at\ time\ 0 = \frac{P}{W_0} \times 2\sqrt{W_0}b$$

$$P_d\ at\ time\ t = \frac{P}{W_t} \times 2\sqrt{W_t}b$$

$$Proprtionate\ Change\ in\ P_d\ = \frac{P_d\ at\ time\ t}{P_d\ at\ time\ 0}\ =\ \frac{\sqrt{W_0}}{\sqrt{W_t}}$$

Change in area accessed $A_{ac} = \frac{I_t}{I_0}$

$$= \frac{\sqrt{W_t}}{\sqrt{W_0}}$$

Net proportionate change in the loss = change in the Pd x change in the Area accessed

$$= \frac{\sqrt{W_0}}{\sqrt{W_t}} * \frac{\sqrt{W_t}}{\sqrt{W_0}}$$

$$= 1$$

So, net change in the loss is expected to be nil under the interface assumption. Therefore, if the assumption that the conflict is restricted to the interface is true and human encroachment reduces the area under wilderness, encroachment will not increase the net damage. The shape of the wilderness area need not be circular for the principle to be true. As long as the change in interface and animal density along the interface change in reciprocal way, the net loss is not expected to change.

In the other extreme case, when *A* is in small pockets among a larger wilderness, the change in animal density as a result of a small increase in *A* can be considered negligible. If net damage increases due to increase in interface, the damage per unit agricultural area would decrease because by the laws of geometry proportionate increase in area is expected to be greater than proportionate increase in perimeter.

Encroachment when the damage is not restricted to the interface: Under the push paradigm, because of decrease in wilderness area, animal density will increase. if the increased density is greater than the carrying capacity *C* (expressed in terms of density), some animals will move out and feed on agricultural land by accessing some of it. So

$P_d \propto (P.\frac{\sqrt{W_0}}{\sqrt{W_t}} - C)/A_{ac}$

Net loss $\propto P_d * A_{ac} = P\frac{\sqrt{W_0}}{\sqrt{W_t}} - C$

Therefore, if W decreases such that the increased animal density exceeds the carrying capacity, the net loss will increase. If both P and $P\frac{\sqrt{W_0}}{\sqrt{W_t}} > C$ then the net loss will increase by $\frac{P.\frac{\sqrt{W_0}}{\sqrt{W_t}}-C}{P-C}$. Since the total population remains the same, the loss per unit population would increase. However, since A is also increasing, the increase in loss per unit agricultural land will be less than proportionate. If $W >>> A$ then it might even decrease. If $A >>> W$, it will increase and approach the proportion $\frac{P.\frac{\sqrt{W_0}}{\sqrt{W_t}}-C}{P-C}$. With increase in P_d the area accessed also might increase such that the proportionate increase in A_{ac} and L/A_{ac} would together account for the increase in net loss.

Further if the assumption of population regulation at carrying capacity is true, the increased population density may return to the new carrying capacity and if there is no further encroachment, the net loss will reduce by time $t + 1$, returning to the original eventually. The long-term effect of encroachment will be reduced damage under this set of assumptions. If the carrying capacity assumption is not true the change at t will persist at $t+1$.

With pull assumption (and absence of human fear) animals can access the entire agricultural area. When $A_t > A_0$, the same population would spread over a larger agricultural land.

Since Net Loss = $L \propto P_d.A_{ac}$

Proportionate change in $P_d = \frac{\mathrm{P} / A_t}{\mathrm{P} / A_0}$

Proportionate change in $A_{ac} = \frac{A_t}{A_0}$

Therefore, change in net loss L $= \frac{\mathrm{P} / A_t}{\mathrm{P} / A_0} \cdot \frac{A_t}{A_0}$

$= 1$

Since the total area under agriculture has increased, the loss per unit area would decrease. Encroachment does not appear to increase the damage in any way under the pull assumption. In effect, encroachment of agriculture on the wildland can result into increase in crop damage under a very restricted set of assumptions. The currently widely held view that shrinking habitat and increasing human encroachment is the main cause of HWC needs to be seriously reconsidered in a context specific way.

A. Population increase: The effect of increase in animal population on crop damage depends upon the underlining assumptions. Under the assumption that the population saturates at the carrying capacity along with the assumption of the push phenomenon, conflict will not arise. If either or both of these assumptions are not true, only then conflict is expected to arise with increase in animal population. If the interface assumption is true, there would be increase in net loss as well as increase in loss per unit area which is equal to $\frac{P_t}{P_0}$. But the increase would be restricted to the interface. If a moving gradient away from the interface is observed the interface-population combination can be rejected. If the push hypothesis is true, $P_0 <= C$ and $P_t > C$ one would see the beginning of loss outside the wilderness area, not experienced earlier. If both P_0 and $P_t > C$ the net loss, loss per unit area as well as loss per unit population would increase by $(P_t - C)/(P_0 - C)$.
If the pull hypothesis is true and assuming no fear element, the animals had access to the entire agricultural land all the time and therefore loss would increase in proportion to the population change i.e. $\frac{P_t}{P_0}$ and the loss per unit population will remain unchanged.

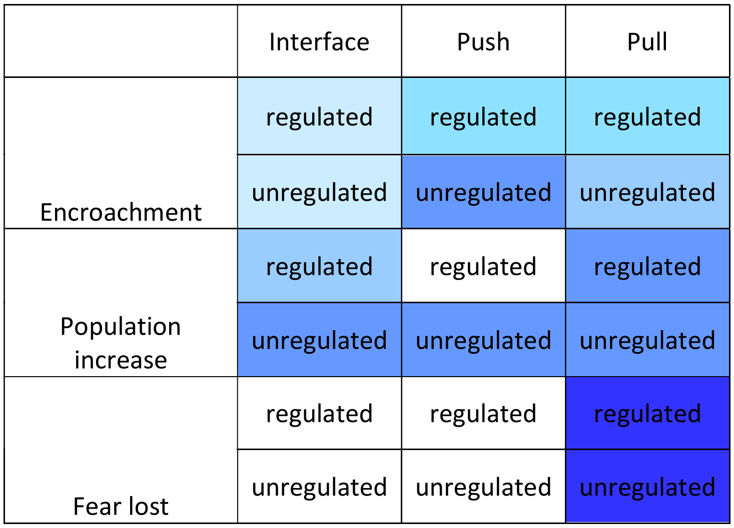
C. Loss of human avoidance behaviour: By this hypothesis, animals prefer to live in forests/wilderness because of human fear. The availability of food and water is often greater in and around human habitation. If animals lose human fear, they would occupy human landscapes freely. However, the loss of fear would be a gradual process requiring several generations and the damage would be seen increasing gradually. If the interface assumption is true, the damage is incidental and loss of fear will not make any difference. Assuming push hypothesis and regulated population, there is no reason for the animals to come out. However, if the nutritive content of crops is better than that of wild forage, then independent of population regulation, progressive loss of fear would increase the net damage, damage per unit area and damage per unit population by the same proportion and there is expected to be a moving gradient of damage away from the interface. Currently there is no empirical measurement of human fear or the lack of it. We assume that the habitats and agricultural context remaining constant, the time spent in the agricultural land (t_a) will be negatively related to the perceived fear. Further the damage to crops, at least in the beginning will be a linear function of the time spent on crops, although it will show a saturating relationship at large values of t_a. Therefore the net damage, damage per unit area and damage per unit population will increase by ta_t/ta_0. Also, the animals will tend to move more in the interior of the agricultural landscape as the fear reduces and there would be a moving gradient of damage. Further the loss of fear being a gradual process, we will see a continued trend of increasing damage when there is no further change in the external context. This is a unique prediction of the loss of fear hypothesis.

Table 1 summarizes the testable predictions from every combination of assumptions and causal factors. By matching with real life patterns, we can decide the predominant cause of crop damage by wild herbivores in any given context. Currently there is hardly any reliable and methodologically consistent crop damage data available to do the prediction matching. Based on preliminary data and anecdotes, at least in India, the net damage, damage per unit area, moving gradient and damage per unit population all seem to be rising (Dandekar et al 2025). If this is true, figure 2 shows which combinations predict all these patterns simultaneously.

Table 1: The testable predictions of the assumption-hypotheses combinations

Causes	**Where**	**Population**	**Change in Pd**	**Change in Aac**	**Net loss**	**Loss/A**	**Loss/Aac**	**Net Loss/P**	**trend t to t +1**	**Moving gradient**
Encroachment	Interface	Regulated	$\frac{\sqrt{W_0}}{\sqrt{W_t}}$	$\frac{\sqrt{W_t}}{\sqrt{W_0}}$	unchanged	decrease	increase	unchanged	decreased	NA
Encroachment	Interface	Unregulated	$\frac{\sqrt{W_0}}{\sqrt{W_t}}$	$\frac{\sqrt{W_t}}{\sqrt{W_0}}$	unchanged	decrease	increase	unchanged	constant	NA
Encroachment	Push	Regulated	Increase $only\ if$ $P\frac{\sqrt{W_0}}{\sqrt{W_t}} > C$	Increase	Increase $\frac{P.\frac{\sqrt{W_0}}{\sqrt{W_t}}-C}{P-C}$	Increase $<$ $\frac{P.\frac{\sqrt{W_0}}{\sqrt{W_t}}-C}{P-C}$ or decrease	Increase	Increased	decreased	Yes
Encroachment	Push	Unregulated	$increase$ $only\ if$ $P\frac{\sqrt{W_0}}{\sqrt{W_t}} > C$	Increase	Increase $\frac{P.\frac{\sqrt{W_0}}{\sqrt{W_t}}-C}{P-C}$	Increase $<$ $\frac{P.\frac{\sqrt{W_0}}{\sqrt{W_t}}-C}{P-C}$ or decrease	Increase	Increased	constant	Yes
Encroachment	Pull	Regulated	$\frac{\mathrm{P} / A_t}{\mathrm{P} / A_0}$	$\frac{A_t}{A_0}$	unchanged	Decrease	Decrease	unchanged	decrease	NA
Encroachment	Pull	Unregulated	$\frac{\mathrm{P} / A_t}{\mathrm{P} / A_0}$	$\frac{A_t}{A_0}$	unchanged	Decrease	Decrease	unchanged	constant	NA
Population increase	Interface	Regulated	$\frac{P_t}{P_0}$	unchanged	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	unchanged	decrease	NA
Population increase	Interface	Unregulated	$\frac{P_t}{P_0}$	unchanged	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	unchanged	constant	NA
Population increase	Push	Regulated	0	0	0	0	0	0	0	0

Population increase	Push	Unregulated	$P_d = P\text{-}C$	Increase	Increase $\frac{P_t - C}{P_0 - C}$	Increase $\frac{P_t - C}{P_0 - C}$	Increase	Increase	constant	Yes
Population increase	Pull	Regulated	$\frac{P_t}{P_0}$	unchanged	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	unchanged	constant	NA
Population increase	Pull	Unregulated	$\frac{P_t}{P_0}$	unchanged	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	$\frac{P_t}{P_0}$	unchanged	constant	NA
Loss of fear	Interface	Regulated	unchanged	unchanged	unchanged	unchanged	unchanged	unchanged	unchanged	NA
Loss of fear	Interface	Unregulated	unchanged	unchanged	unchanged	unchanged	unchanged	unchanged	unchanged	NA
Loss of fear	Push	Regulated	0	0	0	0	0	0	0	NA
Loss of fear	Push	Unregulated	0	0	0	0	0	0	0	NA
Loss of fear	Pull	Regulated	unchanged	ta_t/ta_0	ta_t/ta_0	ta_t/ta_0	ta_t/ta_0	ta_t/ta_0	Increase ta_{t+1}/ta_0	Yes
Loss of fear	Pull	Unregulated	unchanged	ta_t/ta_0	ta_t/ta_0	ta_t/ta_0	ta_t/ta_0	ta_t/ta_0	Increase ta_{t+1}/ta_0	Yes



	Interface	Push	Pull
Encroachment	regulated	regulated	regulated
	unregulated	unregulated	unregulated
Population increase	regulated	regulated	regulated
	unregulated	unregulated	unregulated
Fear lost	regulated	regulated	regulated
	unregulated	unregulated	unregulated

Figure 2: The number of predictions matched with the crop raiding patterns observed in Maharashtra. Zero matches indicated by no colour and all 6 matches by the deepest colour.

We see from table 1 and figure 2 that the damage along the interface assumption is completely rejected since the moving gradient is a predominant picture (Bayani *et al* 2016, Dandekar *et al* 2025) and also many other predictions do not match. Similarly, the encroachment hypothesis is unable to predict all the observed patterns by its own. So, encroachment or habitat loss is unlikely to be the sole or the most important cause. Increasing population can explain the trends under a certain set of assumptions. But for population increase to explain the observed trends it is necessary to reject the implicit beliefs such as carrying capacity and natural mechanisms of population regulation etc which are implicit in conservation policies so far (Watve 2026). All the observed parameters i.e. temporal increase in net damage, damage per unit area, damage per unit population, continued trend and the moving gradient are explained only by the loss of fear hypothesis.

The first level of model examining one causal factor at a time has its own limitations. In reality the factors are not mutually exclusive and do not act one at a time but interact dynamically. Therefore, at a second level of modelling, we attempt a unified model that incorporates all the factors together and can also allow their dynamic interactions.

<u>An inclusive model</u>:

Animals are known to optimize their foraging behaviour to maximize the fitness returns while minimizing the cost and risk associated with the foraging strategy adopted (Price and Maynard-Smith 1990, Baig *et al* 2019, Shinde *et al* 2022). We assume that wild herbivores optimize their gains by choosing appropriate amount of time and efforts in feeding on crops. They prefer to feed on crops when and so long as the net gains from crops is greater than those from foraging in the wild. Since every animal has a saturating capacity of food intake, and food intake affects reproductive success in a saturating way, the nutritional benefits are expected to follow a saturation curve, while the risk from predation or hunting is expected to increase linearly with the time spent on the risky patch. This a typical consideration of an optimization model (Parker and Maynard-Smith 1990, Stephens and Krebs 1986). The net optimum is the t where the distance between the curve and the line is maximum (figure 3A). A simple equation for this has been used for optimize foraging (Stephens and Krebs 1986, Baig *et al* 2019, Shinde *et al* 2022, Watve *et al* 2016) which is

$$R = \frac{N.t}{K+t} - F.t \qquad \text{Eq 2}$$

Where *R* is the net fitness return from the foraging activity; *N* = the maximum possible nutrition component of fitness obtained from foraging; *F* = the risk from predation/hunting and other hazards expressed in terms of fitness loss; *K* = the half saturation constant, such that at small *K* the nutritional fitness benefits are achieved faster and at large *K* it takes more time and efforts to obtain the benefits; *t* is the time spent in foraging in that habitat.

Since there are two available options for grazing, foraging in the wild versus feeding on crops, we write a joint equation, if and when the additional returns from feeding on crops R_a is positive, animals should prefer feeding on crops.

$$R_a = \frac{N_a.t}{K_a+t} - \frac{N_w.t}{K_w+t} - t(F_a - F_w) \qquad \text{Eq 3}$$

Where the subscripts *a* and *w* denote the parameters in agricultural and wilderness habitats respectively. For simplicity, in the starting model we will assume $K_a = K_w = K$. We will relax this assumption at a later stage. We also assume $F_a > F_w$ and denote $F' = F_a - F_w$. With this assumption, the equation simplifies as

$$R_a = \frac{(N_a - N_w).t}{K+t} - F't \qquad \text{Eq 4}$$

We can calculate the optimum time spent on the agricultural crops by taking derivative $\frac{dR_a}{dt}$, making the derivative zero and second derivative negative, we find the optimum time spent feeding on crops as

$$t_a = \sqrt{\frac{K.(N_a - N_w)}{F\prime}} - K \qquad \text{Eq 5}$$

It follows that only when $t_a > 0$ animals gain by raiding crops. If $\sqrt{\frac{K.(N_a - N_w)}{F\prime}} < K$ then $t_a < 0$, therefore animals have no benefit in feeding on crops.

The total agricultural loss is expected to be a function of the population and optimum foraging time on crops. We have already defined the saturation relationship between time of foraging and nutritional gains, so that the net loss,

$$L \propto P \frac{\overline{N_a}.t_a}{(\overline{K_a} + t_a)} \qquad \text{Eq 6}$$

The $\overline{N_a}$ and $\overline{K_a}$ in Eq 6 are not identical to *Na* and *Ka* in earlier equations although the shape of the relationship would be quite similar. Eq 3 and 4 capture the fitness contribution of nutrients whereas Eq 6 captures the actual crops devoured by the animals leading to loss of farmers.

Apart from the crops eaten there will be incidental damages to property and to lives, particularly from larger herbivores which might be directly proportional to the time spent in *A*. For our further inferences, more than the actual shape of the relationship, it is important to realize that the net damage will be a linear or non-linear function of the time spent in the human landscape.

It is possible to write a similar set of equations for distance from the interface to which the animals would invade inside the agricultural land. In the above equations t_a can be replaced by *d* the distance, the two also being interrelated. The equation may remain similar, with somewhat different interpretations of parameter K_a.

Figure 3 graphically represents the optimum time spent or optimum distance travelled inside agricultural land and how the critical parameters affect the optimum. As the fear factor reduces, animals would spend more time and invade greater distances in the agricultural landscape. If *F′* approaches zero and $N_a - N_w > 0$, they would stay and breed inside the agricultural landscape itself and may make little use of the wilderness habitat.

Fig 3

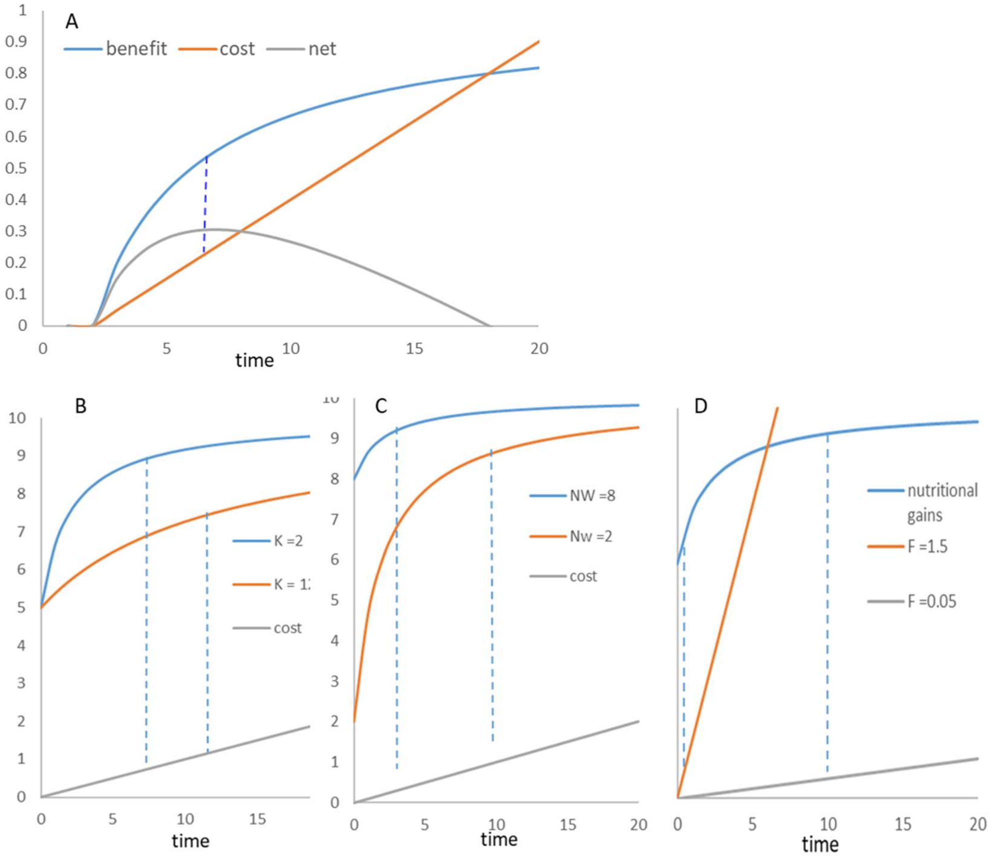


Figure 3: (A) The optimization concept. The nutritional benefits and cost in terms of the risk of attack, both expressed in terms of their contribution to fitness on the Y axis. The optimum is at the time where the net is maximized i.e. the distance between the benefit line and cost line is maximum. (B) The effect of K at $N_a = 10$*,* $N_w = 5$ *and* $F' = 0.1$ *(C) The Effect of* N_w *at* $K = 2$ *and* $F' = 0.1$ *(D) The effect of F at* $K = 2$*,* $N_w = 6$ *and* $N_a = 10$ *on the optimum time spent feeding on crops.*

It can be seen that with this equation, each one of the assumptions and causal factor combinations of our earlier approach are true in certain parameter space. When $F' > \frac{N_a - N_w}{K}$ damage will be seen only along the interface. Also only under such conditions, the population will reach a steady state at the carrying capacity of the wilderness habitat since no other resource is available (Watve 2026). If $F' < \frac{N_a - N_w}{K}$ there will be crop raiding resulting into greater fodder availability leading to the population growing beyond the carrying capacity of the wilderness habitat. Carrying capacity has been an elusive concept. Wildlife researchers have not been able to estimate the carrying capacity and show that if left on its own the population stabilizes there (Dhondt 1988, McLeod 1997, Cang 2009). The only examples where the populations have stabilized near the carrying capacity are on islands or habitats that are completely isolated. A high F' is likely to result into an island like situation where the assumption is more likely to work. Otherwise, when there is extra availability of food from the human dominated landscape, populations are unlikely to stabilize at the carrying capacity. If N_w declines so much that $N_a - N_w > KF'$ the push factor is at work, whereas if this inequality is because of increase is N_a it can be called pull factor. Both N_a and N_w depend upon the season and push or pull factors may apply differently to different seasons. Encroachment or habitat loss can be represented by reduction in N_w. Population and human avoidance behaviour are directly represented by P and F_a respectively. Thus, using a single model, the entire spectrum of considerations can be analyzed, simulated, if necessary, used to make testable predictions and design mitigation measures for a given context. All the predictions of the single factor approach (table 1) can be made from this unified model. But combinations and interactions of causal factors can be better addressed by the unified model.

First, it can be seen that crop damage can increase either when the population is large, the wilderness habitat quality is nutritionally degraded, K is small and the fear of humans F_a is reduced. However, the mathematical position of these variables reveals that the effects of these factors is interdependent, and their relative contributions widely different. Particularly important is the denominator position of the risk or perceived fear factors. If $(F_a - F_w)$ is above a threshold $\frac{N_a - N_w}{K}$, then crop damage can be prevented even when population is large. In contrast if the fear of humans goes down to be equal or less than the fear of natural predators, that is $F_a < F_w$ then crop damage is bound to happen even at small populations of wild herbivores and well-maintained natural habitats. This needs to be considered before population control for mitigation of HWC.

The model can be used to optimize the mitigation measures to minimize crop damage by animals while maintaining a viable and genetically diverse population of the wild species. There are four types of mitigation measures suggested

(a) Regulate the animal population
(b) Maintain and restore habitat quality so that N_w is maximized
(c) Increase K_a by using fences and deterrents
(d) Restore the human avoidance behaviour, or human fear in animals, i.e. increase F_a

From eq 5 it is clear that large F_a is both necessary and sufficient to prevent crop damage. If human fear is less than or only slightly greater than that from natural predators, other measures are unlikely to work. There is a natural limit to which N_w can be increased, increasing K over large areas by fencing and other devices can be expensive, as well as has limitations, the situation can become unsolvable if $F_a - F_w$ tends to be zero or negative. This can easily happen with a total ban on hunting or a wrong hunting policy. Therefore, in mitigation strategies restoring the minimum necessary fear response or human avoidance behaviour among animals needs to be the top priority. Other mitigation measures will be effective or even unnecessary if fear can be restored.

So far, we have been assuming that the parameters N_w, K, P are independent. In reality they are bound to affect each other. P depends upon the food availability and therefore will be proportionate to $N_w + L$. A higher population density in the wilderness area might lead to overgrazing and thereby depleting N_w. High population density would cause competition for the available forage, depletion of the resource and thereby increase K. This leads to negative and positive feedback loops in time. The relationship between P and N_w operates in a negative feedback in the absence of L. Increase in P will deplete N_w which would in turn regulate P. However when L is large a positive feedback loop can initiate. L provides greater nutrient resource that would lead to population increase and the increased population further increases L. We assume simple linear effects with proportionality constants C_1, C_2 and C_3 so that,

$$P_{(t+1)} = C_1(N_{wt} + L_t) \qquad \text{Eq 7}$$

$$N_{w(t+1)} = N_w\,(basal) - C_2.P_t \qquad \text{Eq 8}$$

Where $N_w(basal)$ is N_w when the population is zero and therefore there is no consumption of nutrients.

$$K_{a(t+1)} = K_a(basal) + C_3.P_t \qquad \text{Eq 9}$$

Where $K_a(basal)$ is K_a when the population is zero and therefore there is no foraging.

We incorporate these factors assuming simple linear relationships and incorporate them in a simulation model. In the simulations incorporating these interactions, at time $t+1$ the loss is calculated and then the variables at $t+2$ computed from those at $t+1$. At part of the parameter space a steady state or stably oscillating state is achieved soon where the loss is limited. However, below or above certain thresholds the positive feedback loops lead to vicious cycles and the loss escalates. When such autocatalytic cycles begin, the system is out of control. We assume that the system is bound to collapse and stop the simulations when such an uncontrollable autocatalytic escalation process begins. There are sharp tipping points in the parameter space where stability collapses.

For examining the possible effects mitigation measures, we assume that we are able to control the parameter targeted by the mitigation using appropriate facilitation and regulation strategies. In the absence of empirical knowledge of parameters, we can use the model results for qualitative conclusions only. Even qualitatively they can contribute substantially to our insights into HWC. Keeping the value of the targeted mitigation focus constant, we ask how this regulation would affect other variables and ultimately crop damage. Since our interest is in securing the survival of the wild populations as well as minimizing the damage to agriculture, minimizing L/P should be the most important parameter. Minimizing L/P at a reasonably sufficient population size is the most desirable outcome and that should be taken as the most successful mitigation strategy.

Population regulation: If P is regulated, it will affect N_w negatively and K positively. Incorporating these effects the net agricultural loss can be computed. But since P is regulated, L is not allowed to change P again. The relationship between the net loss and L/P with the regulated level of population (figure 4A) shows that the same population can cause different levels of damages at different F'. A high level of F' allows a larger population while keeping the damage to a minimum. Qualitatively this result remains unchanged as long as $Nw < Na$ and $K <$ the threshold. In the unlikely situation of $Nw >= Na$ there will be no crop damage. Again, the threshold K depends upon F' and at higher F' the threshold becomes smaller. Therefore, at large F', damage can be effectively prevented independent of other parameters.

Increasing N_w: Improving habitat quality can increase N_w (fig 4B) but this has limitations. Increasing the nutrient content in the wilderness habitat by artificial means is not compatible with the philosophy of conservation. One cannot and should not exceed the nutritional potential of natural habitats by too much of intervention. This would lead to a zoo like state rather than a natural reserve. So, except for extremely degraded environments, habitat restoration would be of little value in resolving HWC. There are other ecological reasons for which habitat restoration attempts are desirable, but they are unlikely to be effective in resolving HWC across different contexts.

Regulating K: Large K reduces damage and loss becomes zero beyond a threshold K. However the threshold K increases reciprocally at small F' and increasing K is costly. Therefore fencing and other deterrents can be effective only when F' is sufficiently large (fig 4C).

Restoring F': Human ancestors have been a hunting species and that must be the most important reason why most wild animals avoid human vicinity and prefer to live in the wilderness habitats secured at least partly from humans. This context has changed only recently with various models of conservation implemented. Some of the models have total ban on hunting of a range of species. Others may have regulated hunting but here too the type of hunting and its regulations matter. If most of the hunting happens within wilderness reserves, it is likely to contribute to F_w rather than to F_a. It is also possible that conservation policies led to increase in carnivore threat making F_w larger. If the risk of attack by carnivores or by hunters is greater in the wilderness than in the agricultural land, then $F_w > F_a$ which is bound to escalate the conflict. Apart from changed hunting practices, wildlife tourism is critically based on dissolving mutual fear. The tourists are preached to remove fear of animals from their minds, and animals get increasingly habituated to presence of tourists. This would be inviting more intense HWC. Since animals in most habitats have lived with human fear for generation, we take it as their “natural” behaviour. But behaviours are often plastic and context dependent. A change in the human avoidance behaviour might not be rapid. It may happen over generations through individual learning, cultural inheritance as well as selection on genetic predisposition to boldness. But after a few decades of altered hunting practices, there are indications that animals are increasingly losing human fear and therefore do not hesitate to venture into human dominated landscapes. If this is true, the question how to reinstate the fear response should be a focal research question.

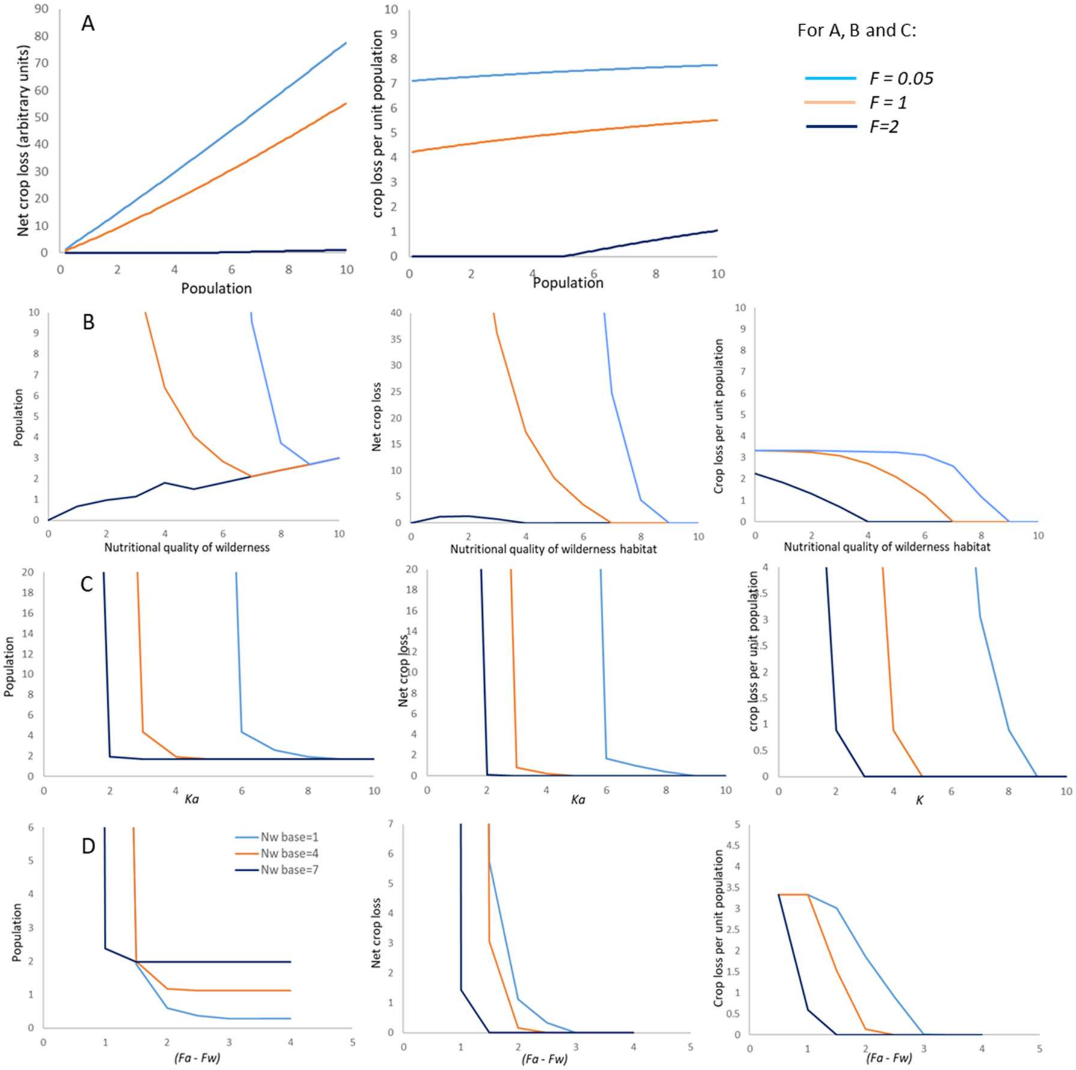


Figure 4: Effects of different mitigation measures on the population, net crop loss and crop loss per unit population. The sharp rising lines indicate the tipping point at which the vicious cycle begins leading to unlimited escalation of the problem. The most desirable outcomes are those when the population is large but loss per unit population minimum. It can be seen that at large F_a-F_w, the loss is minimized in spite of supporting a stable and sizable population. A: When population is regulated: At large F' the loss is zero till a considerable population size. At very high population size N_w tends to zero, forcing the herbivore to come out to feed on crops. B: When N_w is maintained: There is greater loss at low N_w as expected. Ironically at lower F' values the population is large at low habitat quality. But this is because they

increasingly feed on crops. When F' is large, the loss can be maintained zero at a sizable population. C: The effect of K has a clear threshold. At smaller K the vicious cycle begins escalating the loss as well as the population. High F' can sustain a stable population with zero loss until K becomes too small. D: When F' is the mitigation focus: Here again a tipping point is observed below which the vicious cycle begins. High F' along with high N_w *is the desirable combination ensuring high population density with little damage. Other parameters for these simulations:* $C_1 = 0.2$, $C_2 = .03$, $C_3 = 0.3$. $N_a = 10$ N_w*(basal) =7, K(basal) = 3.*

Discussion:

Since empirical data on crop damage and on the parameters of the model is fragmentary and collected without any consistent methods across time and areas, we do not expect the quantitative predictions of the model tested as of now. Nevertheless, qualitatively the model can contribute important insights to our understanding of the causes of HWC and the potential effectiveness of the mitigation measures. But before considering the implications for mitigation, we will first examine the robustness of the model outcomes.

The interpretation of the optimum needs to be taken at a population level. If there is an optimum proportion of time spent in *A* and *W* respectively, every animal need not spend the same amount of time. It may be that some proportion of animals spent their entire time in *A* and others in *W*. If some animals move to *A,* the competition in *W* reduces so that individual behaviour can be diverse maintaining the average optimum and distributing the benefit over the population.

Sensitivity analysis: Any model is based on a set of assumptions. We need to see how sensitive are the inferences to the violation of these assumptions. We assumed K_a and K_w to be identical for the simplicity of the model. In reality crops are largely monocultures of edible species which are bred for generations for better nutritive content and fewer secondary metabolites or other repellent properties. Wild forage, on the other hand are mixed species, not all of which might be palatable. Plants produce secondary metabolites as protective mechanisms or evolve thorns, waxes, obnoxious smells etc. owing to which K_w is expected to be larger than K_a. This is likely to make the crops more attractive than the wild forage. Incorporating this difference will slightly shift the positions of the tipping points but otherwise is unlikely to make a qualitative change in the interactions of the parameters and their effect on *L*. K_a can be increased using active measures to discourage crop raiding such as trench-cum-mounds, fences, scare devices and deterrents. A possible effect of increasing the cost of entering the crops, not considered in this model, but suggested by an earlier model is that when the cost of entering a crop increases, the optimum food intake also might increase (Watve *et al* 2016) under some contexts. If this is true, in some parameter space the hurdles might actually increase the loss instead of decreasing it. This is compatible with the anecdotes of some farmers whose crop damage increased after making fences.

We assumed the interrelationships between P, N_w and K_a to be linear for simplicity according to eq 7 to 9. The negative and positive feedback loops among these variables can exist with or without linearity just that the escalation might be slower or faster. Since currently we are only interested in the qualitative outcomes, linearity assumption is not too critical for the purpose.

It is necessary to differentiate between actual risk and perceived risk in our definitions of F_a and F_w. In terms of actual risk the moment the wild life protection act was implemented in India, $F_a < F_w$. If change in animal behaviour was instant, crop raiding would have peaked immediately. But the human avoidance behaviour has been substantially deep rooted in animals and it did not change instantly. Behavioural optimization in animals happens by individual learning, collective intelligence, cultural inheritance and selection on genetic and cultural traits. Unlike learning about food quality and habitat suitability, risk of death cannot be learnt by one's own experience. Therefore, both learning and unlearning of risk needs to happen mainly by selection on culturally and genetically inherited traits. It might take several generations to reach a new optimum in the altered context. The fear of humans appears to be changing notably now as reflected by the minimum flight distance (Price *et al* 2014). Our models incorporate the perceived fear as F. Eventually when the perception catches up with real life risk, the conflict would attain uncontrollable scale. It is also possible that when at the perception level when $F_a < F_w$, crop raiding will happen even when $N_a < N_w$. Animals would stay and breed within the human landscape and feel no need for the wildland. This has already started happening with some species. Attempts to reinstate the avoidance behaviour need to begin before this state is attained. Although the slow change in risk perception kept the farmers in a better state for a few decades, the other side of the coin is that, reinstating human fear would also be a slow process. Substantial time would be needed to regain the behaviour. This might be a simpler and faster process for social animals. Solitary animals would need a longer time. Hunting at a carefully optimized and learning facilitating manner needs to return in the wildlife management policy, but one should not expect immediate reversal of behaviour with a new hunting policy. Nevertheless, the hunting policy needs to be designed so as to maximize learning while minimizing actual killing.

A very fundamental assumption of the model is that of a clear distinction between wildland and agricultural land. This distinction is relatively modern. Human settlements and agriculture must have started within the shared habitat. At a prior stage, human ancestors were prey for large carnivores too (Hart and Sussman 2011). The transition to a predator free species (Watve 1993) and a hunting species must have been a pre-requisite for agriculture. If animals did not avoid humans, growing nutritionally more attractive species as crops and protecting them from other herbivores would have been impossible. Hunting has been a causal factor for the beginning of agriculture and the separation of the habitats. If a cause is removed, the effect is likely to vanish. If hunting stops, animals will start moving freely in the human occupied habitat and agriculture is most likely to collapse. It might be the early stages of this that is being witnessed in India as well as other wildlife rich countries. The habitat separation assumption of the model is itself based on one of the causal hypotheses considered. This strengthens the importance of that causal hypothesis.

An important implication of the model is that for testing the predictions we need reliable, standardized and validated methods of estimation of crop loss. The causal hypotheses can be differentiated mainly based on the relative changes in net loss, loss per unit area, loss per unit population and, spatial patterns of loss. Therefore, developing methods of estimating loss is the first required step. Mitigation attempts without causal understanding are unlikely to be effective and optimum in the long run. In the absence of theoretical development, the importance of reliable damage data was never appreciated. This change in empirical research is the most urgently needed.

So far for mitigation, much emphasis has been on population regulation by culling or by sterilization/contraception. But if population explosion is not the main cause of the problem, population regulation is not only unlikely to be effective; it might turn out to be ecologically dangerous. It is more likely to be detrimental to genetic diversity and increase the local extinction probability. If sufficient time is not given for reinstating the fear response, culling alone is unlikely to resolve the problem immediately (Hoare 2012, Cappa et al 2021). If a crop raiding group is culled or removed, another group is most likely to replace it and the net damage remain unaffected (Plotnik et al 2023). On the other hand, restoring the fear response to a threshold level in the long run can allow a much larger population with minimum conflict and thereby is more compatible with conservation goals.

Our model brings into light the inevitable trade-off between what is desirable for wildlife tourism and what is needed for resolution of HWC. It is possible to have an optimum compromise between the two, which needs much fundamental rethinking and research inputs. If animals are habituated to the presence of noisy tourist vehicles and crowds, they would not respond to farmers' attempts to drive them away. If the level of fear rises, tourists will not be able to view animals as much undisturbed as today. But that is inevitable. Senior tiger activists and experts expressed a concern several decades ago that if tigers become indifferent to tourist presence, they would become more vulnerable to poaching as well (Nature on PBS 2026). The traditional cautious response of animals to human presence needs to return at an optimum level. We haven't specifically examined the carnivore conflict here but it is likely that the same possibility needs to be examined there as well. Although the details may differ the principles behind herbivore and carnivore conflict appear to be similar and the fear key may work for both equally well.

Conclusions:

It is necessary to realize that different causal factors lead to different damage patterns and thereby it is possible to determine the predominant cause of HWC. In the absence of this clarity surreptitious skipping from one hypothesis to another gives an illusion of explaining all patterns in HWC without definitive useful insights helpful in mitigation.

Fear is the key: Even in the absence of empirical data, from theoretical analysis alone it is clear that fear response is the key to resolving HWC. How to reinstate the lost fear is a tricky question and the answer might be different for different species and locations. Hunting appears to be essential to restore the behaviour but just opening up hunting is unlikely to achieve the goals of conservation. Thoughtful hunting protocols need to be evolved specific to species-locations. The objective of hunting needs to be a behavioural change rather than population control or direct financial returns from trophy hunting. A set of behavioural principles decides whether natural resources are handled with prudence or profligacy (Gadgil 1985, Gadgil and Malhotra 1985, Gadgil 1995). Many of the traditional hunting communities had cultural norms that ensured ecological prudence while hunting (Malhotra et al 1983). In the changing global context, it may not be possible to revive the traditional hunting cultures everywhere, but the lessons learnt from them need to be utilized for designing novel systems. On the other hand, understanding the principles of animal learning as well as selection on culturally inherited traits and genetic predispositions will be equally important for the new policy. The learning response of animals might be quick in social species and might be trickier for solitary ones. It would take time and is not expected to happen as soon as the newly designed hunting protocols begin. Although regulated hunting is practiced in many other countries, whether the hunting protocols induced the desired behavioural response needs to be examined. It is likely that the hunting increases F_w more than F_a and thereby is unable to mitigate HWC effectively. Behaviourally optimized system design is a relatively novel concept but has a promise to revolutionize regulatory policy (Chater and Lowenstein 20203, Joshi et al 2021). Conservation policy needs to optimize for animal behaviour and human behaviour simultaneously and a right combination of theoretical and empirical studies are necessary to achieve the goals. Although that is not within the scope of this model, at this stage our model shows that minimum conflict coexistence is certainly possible and restoring a threshold level of mutual fear is the key.

A broader take home message is that even in highly empirical fields theory building is valuable. In its absence, data collection can be incomplete, the most important variables for analytic approaches might be missing from empirical studies. Theory helps in shaping empirical research and in turn real-life data is necessary for completing the theoretical approach. Conservation biology, HWC in particular has been weak in theory building and a simple but comprehensive theory can improve wildlife management substantially.

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