Crop damage by wild herbivores: insights obtained from optimization models

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We constructed a theoretical model of cost–benefit optimization for farmers who face continued economic loss due to crop raiding by wild herbivores, as well as for the wild herbivores that do so. Insights obtained from the model include: (i) In sustenance agriculture, a farmer needs to optimize net benefit rather than benefit-to-cost ratio, whereas herbivores need to optimize the benefit-to-cost ratio. (ii) It is imperative for a farmer to disinvest from agricultural inputs when threatened by depredation. (iii) Many mitigation measures that are highly successful on an experimental scale are most likely to fail when used on a mass scale. (iv) The effectiveness of mitigation measures such as fencing, trenching and culling will be non-monotonic, being counterproductive under certain conditions.

Keywords: Agricultural economics, cost–benefit optimization, crop depredation, optimal foraging, wildlife management.

AGRICULTURE near protected areas has a continued risk of crop depredation by wild herbivores[1–4]. Although this has been recognized as an important issue in conservation[5], empirical and theoretical research in this area is inadequate to answer a number of critical questions. For example, some people believe that wild herbivores come out from the forest cover to raid crops because the sources of nutrition in their natural habitats are depleted, the habitat is substantially fragmented[6–9], or because of the stress of poaching[10]. Others have argued that the crop species are richer in nutrition quality and poorer in secondary metabolites[11]. If the latter is the predominant reason, herbivores are expected to raid crops in spite of good natural habitats being available. The relative contribution of competing causes of crop raiding needs to be addressed on a sound theoretical platform[12]. The efficiency of various protection measures applied can be highly variable[13,14]. To examine the conditions under which a given measure would be effective or not, a baseline theoretical model is needed.

Although crop depredation appears to be a natural phenomenon since prehistoric agriculture, it is unlikely that this loss is borne by farmers without any kind of retaliation[15,16]. Owing to the highly pocketed and dwindling wildlife habitats, the traditional practices employed by people such as culling or trapping may not be advocated[17,18]. Therefore, wildlife management policies specifically addressing these issues are needed. Such policies should be based on a sound theoretical foundation, which could best be built considering cost–benefit optimization for farmers as well as for animals.

Optimization models are based on the assumption that individuals choose behavioural strategies that are most likely to give them maximum benefit in comparison with the cost incurred[19]. Individuals may achieve this through cognitive understanding, experiential learning or through evolved innate behaviours. Generalized optimization models have heuristic function and may use rather abstract quantitative parameters to derive qualitative inference of a given biological problem[20]. These can then be converted to specific models to address a given problem based on empirical data and more specific parameters. General optimization models first developed for animal foraging have been extended to human behaviour[21–24], although the underlying cognitive basis might be different.

An optimum can be defined either based on ratio of benefit to cost (benefit/cost) or subtracting cost from benefit (benefit – cost). Benefit–cost difference is typically termed as net benefit, whereas 'cost–effectiveness' is expressed in the ratio form[25]. Both the approaches have been used in behavioural ecology. For example, models optimizing the amount of movement between foraging bouts maximize the benefit–cost difference, but for optimizing the time spent in a patch they use maximization of the benefit–cost ratio[20]. There are no clear indications as to which of the two is best suited in a given context. This is particularly important since the optimum obtained by difference maximization can be substantially different from that obtained by ratio maximization, as we show below.

Choosing the right optimization model

The cost of agricultural production involves some overhead cost that includes baseline investment in land, equipment and basic land preparation. The produce scales

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linearly or nonlinearly with the cost of seeds/saplings, manure, fertilizers, pesticides, labour and other recurring costs. Since there is an upper limit on the productivity per unit area of any crop, we assume a baseline model in which the benefit increases in a saturation curve beginning with an X-intercept equivalent to the overhead costs (Figure 1). A saturation curve is typically used in optimization models, where some limiting factor decides the upper limit that cannot be exceeded[26–29]. The curve can be captured by a simple mathematical expression (eq. (1)), which is a modified version of the Michaelis–Menten curve

$$Y = \frac{Y_{\max}(C - C_0)}{K + (C - C_0)}, \tag{1}$$

where C_0 is the overhead cost and C the total cost incurred in agricultural inputs. Table 1 provides a list of

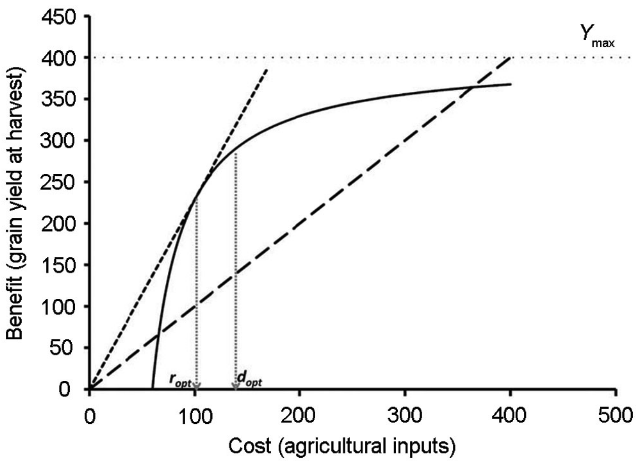

Figure 1. Modified Michaelis–Menten saturation curve. The total agricultural inputs are shown on the X-axis, whereas the Y-axis depicts grain yield obtained at harvest. Since there is an overhead cost, there is an X intercept C_0. Long-dashed line has slope = 1 and short-dashed line is a tangent to the curve. d_{opt} and r_{opt} are optimum inputs by the difference model and ratio model respectively.

Table 1. List of abbreviations used in the models

Parameter	Symbol
Grain yield	Y
Maximum grain yield	$Y_{\max}$
Total cost	C
Overhead cost	C_0
Rate constant	K
Rate constant (forest)	K_1
Rate constant (agriculture)	K_2
Investable amount in agriculture	X
Sustenance cost	S
Probability/frequency of damage	P
Damage (measurable fraction of total land eaten)	F
Damage (measurable fraction of total land eaten) on guarding days	f'
Risk of predation in forest	Pr_1
Risk of predation on farms	Pr_2

abbreviations used in this article. K, the equivalent of Michaelis–Menten constant is a half-saturation cost ignoring the overheads. K will be decided by the default agricultural environment and the specific crop under consideration. Since the relation between cost and yield is a saturating one, it is possible to ask what are the optimum inputs in agricultural practices that can maximize the benefit–cost ratio or their difference. The benefit-to-cost ratio can be maximum where a straight line starting from the origin becomes tangential to the curve (Figure 1). The net benefit (benefit – cost) is maximized where the vertical distance between the curve and the break-even line (benefit = cost) is maximum. This happens where the slope of the curve becomes exactly equal to unity. Since generally the overhead costs are imperative, one can optimize the costs with which the produce scales directly ($C_s = C - C_0$). It can be seen that for the saturation curve starting from a positive X-intercept, the ratio optimum and the difference optimum do not coincide.

The ratio optimization

From eq. (1), the net yield is

$$Y = \frac{Y_{\max}(C - C_0)}{K + (C - C_0)}.$$

Therefore, the benefit-to-cost ratio would be

$$b_{\mathrm{r}} = \frac{Y}{C} = \frac{Y_{\max} C_{\mathrm{s}}}{K + C_{\mathrm{s}}} \times \frac{1}{C_0 + C_{\mathrm{s}}}.$$

The benefit-to-cost ratio scales with C_s; therefore it will be maximum when

$$\frac{\mathrm{d}b_{\mathrm{r}}}{\mathrm{d}c_{\mathrm{s}}} = \frac{Y_{\max}(C_0 K - C_{\mathrm{s}}^2)}{[(K + C_{\mathrm{s}})(C_0 + C_{\mathrm{s}})]^2} = 0.$$

This condition is satisfied when $C_0 K - C_{\mathrm{s}}^2 = 0$, i.e. $C_{\mathrm{s}} = \sqrt{C_0 K}$.

Thus, the optimized total cost will be $C = C_0 + \sqrt{C_0 K}$.

In this model, optimum cost is dependent on both K and C_0, and does not depend on $Y_{\max}$.

The difference optimization

Since the net yield at a given input is

$$Y = \frac{Y_{\max}(C - C_0)}{K + (C - C_0)},$$

the net benefit will be

$$b_{\mathrm{n}} = Y - C = \frac{Y_{\max}(C - C_0)}{K + (C - C_0)} - (C_0 + C_{\mathrm{s}}).$$

Since b_n scales with C_s, this will be maximized when

$$\frac{db_n}{dC_s} = \frac{K \cdot Y_{max}}{(K + C_s)^2} - 1 = 0.$$

This condition is satisfied when $C_s = \sqrt{K \cdot Y_{max}} - K$, which is the optimum input. Thus the total optimum investment will be $C = C_0 + \sqrt{K \cdot Y_{max}} - K$.

In this model the optimum C_s is dependent on Y_{max} and K, but independent of C_0.

Thus, it can be seen that the ratio optimum and its determinants are distinct and different from the difference optimum and its determinants. It is necessary therefore to select the appropriate model for addressing further questions. If an individual has an investable amount X and an investment opportunity whose optimum for both ratio and difference model is known, one can calculate which model gives greater returns on the investment. When $Y_{max} > K + C_0$, i.e. for a sustainable or profitable venture, $\sqrt{K \cdot C_0} < \sqrt{K \cdot Y_{max}} - K$, indicating that in a single venture, at any values of parameters in the sustainable or profitable range, the total cost incurred as well as the total benefit for the difference optimum would be greater than that of the ratio optimum.

$$X + b_{d_{opt}} - C_{d_{opt}} - S > X + b_{r_{opt}} - C_{r_{opt}} - S,$$

where S is the sustenance cost, suffix d_{opt} denotes optimized for the difference model and r_{opt} optimized for the ratio model.

However, if the balance amount from X is invested in another venture with similar parameters, i.e. if multiple investments are possible, then ratio optimization gives better total returns. When X is limiting, $X/C_{d_{opt}}$ different investments of the same type are possible. In that case it is seen that

$$\frac{X}{C_{d_{opt}}}(b_{d_{opt}} - C_{d_{opt}} - S) < \frac{X}{C_{r_{opt}}}(b_{r_{opt}} - C_{r_{opt}} - S).$$

This indicates that whenever alternative investment opportunities are limited, using a difference model is more profitable, but whenever investment opportunities are multiple, a ratio model is more profitable. The ability to invest in multiple ventures is constrained by the nature of the limiting factor. For example, money saved in one enterprise can be invested in another enterprise only when time is not limiting. If the investor cannot manage two or more enterprises due to time or any other limit, then multiple investments are not possible.

Optimization in agriculture: strategies of farmers

In sustenance agriculture, often the piece of land owned by a farmer is limiting and multiple investments in agriculture are not possible. If time spent in agriculture does not allow simultaneously running another enterprise, or limited skillset or any other cultural, social factors make it difficult; then farmers have only one investment opportunity. The protected status of an area may put additional constraints on hunting, gathering or animal grazing as alternative livelihoods. Therefore, farmers close to protected areas should use difference optimization rather than ratio optimization. We show below that farmers indeed use the difference model inadvertently.

The problem of mega-herbivory necessitates two types of changes in the baseline model (Figure 2). One is that the total produce is reduced due to direct damage by animals and the other is the cost of protective measures against crop-raiding needs to be included in the cost–

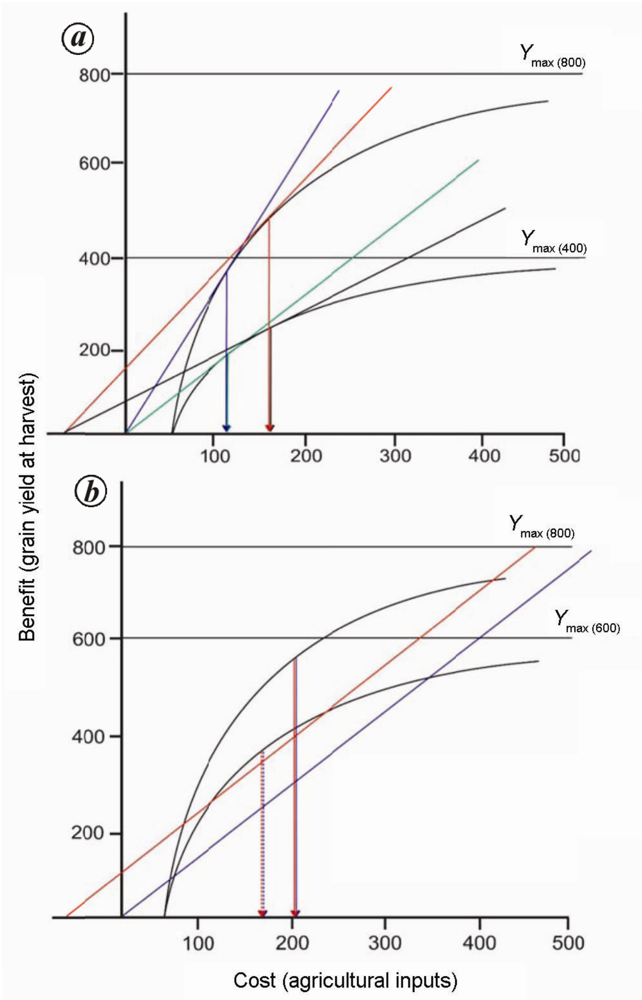

Figure 2. Altered input optima with wild herbivore damage. ***a***, Using ratio model – A change in Y_{max} does not change the position of the optimum. Increased overhead shifts the curve to the right (represented here by shifting the reference to the left). When a tangent is drawn from a point farther away, it moves to the right, meaning that the optimum variable inputs would increase. ***b***, Using difference model – decreasing Y_{max} shifts the optimum to the left, whereas increase in overhead does not affect the shape of the curve and thereby the optimum.

benefit optimization. If we assume that wild herbivores damage some fraction of the total crop, a reduction in Y_{max} is sufficient to represent this change. The guarding efforts can be best considered as an overhead cost, since guarding by itself is not productive and guarding throughout the sensitive period is the only effective strategy. A minimum number of guarding days are needed to ensure no loss, after which the yield will become proportional to the guarding efforts. Similarly, the probability of no loss or that of total loss changes drastically only when the number of guarded days closely approximates total susceptible days (Figure 3).

We will now incorporate the two effects of mega-herbivory in the optimization model. Direct damage by herbivores reduces Y_{max} and protecting–guarding efforts increase the overhead cost as explained above. The ratio and difference optima respond differently for these two changes (Figure 2). As we have seen above, the ratio optimum is independent of Y_{max}, but it increases with C_0. Therefore, when faced with herbivory, the optimum investment increases. As opposed to this in the difference model C_s is not affected by increase in overhead cost, but it decreases with a reduction in Y_{max}. Therefore, one

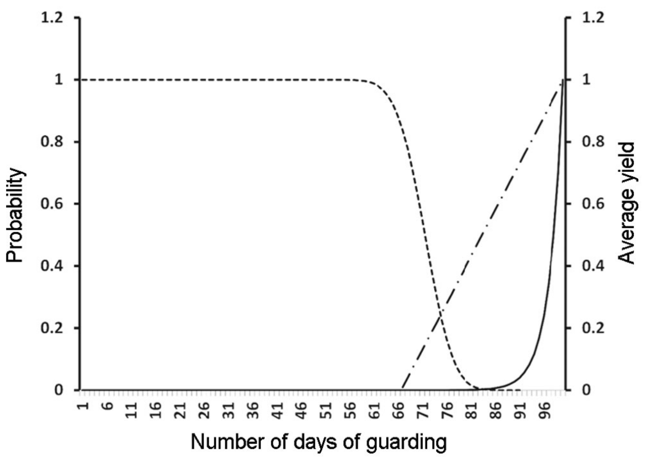

Figure 3. Trend of number of guarding days (d) against probability of no loss (solid line), probability of total loss (dashed line) and average yield (long-dash-and-dot line). The maximum possible yield is assumed to be 1 and the mean per day damage is 0.03. A given crop is visited by wild herbivores with a probability p per day and on an average they cause damage equivalent to a fraction f of the total produce in one day. The total expected damage over the season is $p \cdot f \cdot D$, where D is the total number of days for which the crop is susceptible to damage. If d are the days on which active vigilance is observed and if guarding is highly effective, the total damage would be $p \cdot f \cdot (D - d)$. $D - 1/p \cdot f$ will be the minimum number of days of guarding beyond which such efforts will have some positive effects on the yield. The optimum for benefit-to-cost ratio as well as for benefit–cost difference lies only at $d = D$, i.e. active guarding throughout the susceptible period. Furthermore, it needs to be appreciated that this is a probabilistic process. For an individual farmer, the risk of being at the higher end of the distribution is more threatening than the average damage. The probability of zero damage is given by $(1 - p)^D$. This curve is nonlinear and the only condition to ensure zero damage is $d = D$. The other extreme, i.e. the probability of total loss is also highly nonlinear and works almost like a threshold phenomenon. Therefore, the cost of guarding is best considered as an overhead cost.

should decrease the investment in agricultural inputs when faced with mega-herbivory. Thus in order to optimize the ratio model, one needs to increase agricultural inputs and in order to optimize the difference model one needs to decrease the same. The two models make diametrically opposite predictions. In our study of crop-raiding along the western boundary of the Tadoba–Andhari Tiger Reserve (TATR) in India reported elsewhere (Bayani *et al.*, unpublished), we observed that farmers facing higher risk of herbivory were less likely to use combinations of chemical fertilizers. This observation is compatible with the difference optimization model, and our prediction that farmers should use the difference model over the ratio model. An important implication is that the actual loss due to herbivory is likely to be much greater than direct loss due to damage. The risk of damage induces disinvestment and further brings down the yield. This indirect loss should be counted as due to herbivory. This is an important realization because in the current methods of crop damage assessment, this loss is never accounted for.

If the disinvestment is due to the perceived risk of damage, we expect that an assured realistic damage compensation should reverse the disinvestment trend, i.e. compensating the actual damage would eventually also recover the indirect loss due to disinvestment. An efficient and realistic damage compensation scheme can thus have a dual advantage. On the one hand, it would reduce resentment and anti-conservation attitude among farmers and on the other, it would encourage better agricultural inputs and thereby productivity.

Optimization in foraging: strategies of herbivores

A counterpart of the cost–benefit optimization by the farmer is that by the herbivores. The animals have to take two important decisions, whether to forage in the forest or in the agricultural land, and how much time to spend feeding in an area. We assume that both the decisions are based on cost–benefit optimization. We expect the benefit curve for animals to be similar to the one for farmers, since there is a time and energy cost in moving to and entering a patch, scanning the surroundings for predators and other risks which can be considered as an overhead cost. Further foraging within a patch the tender, nutritious and palatable parts are most likely to be consumed first and therefore, the cost–benefit curve can be visualized as one of diminishing returns. In this curve, Y_{max} is the maximum nutritive benefit that can be obtained from a given patch, C_0 is the cost incurred in moving to the patch and scanning for potential risks, C_s is the time–energy cost incurred in actual feeding, and K is inversely related to the palatability and nutrient density of forage. Unlike farmers who can invest in a limited piece of land, animals have a wide choice in foraging and therefore their optimization would be more appropriately based on benefit–cost ratio. According to the ratio model, the optimum time and energy actually spent in feeding (C_s) would be $C_s = \sqrt{C_0 K}$.

In this time the total nutritive benefit would be

$$\frac{b_{\max} \cdot \sqrt{C_0 K}}{\sqrt{C_0 K} + K},$$

and the benefit-to-cost ratio would be

$$\frac{b_{\max} \cdot \sqrt{C_0 K}}{(\sqrt{C_0 K} + K) \cdot (C_0 + \sqrt{C_0 K})} = \frac{b_{\max} \cdot \sqrt{C_0 K}}{C_0 \cdot \sqrt{C_0 K} + 2C_0 K + K\sqrt{C_0}}.$$

With the risk of predation Pr, the ratio would be

$$\frac{b_{\max} \cdot \sqrt{C_0 K}}{\Pr + (C_0 \cdot \sqrt{C_0 K} + 2C_0 K + K\sqrt{C_0})}$$

$$= \frac{b_{\max}}{\Pr + (C_0 + 2\sqrt{C_0 K} + \sqrt{K})}.$$

Herbivores should choose the forest over agricultural fields, if

$$\frac{b_{\max_1}}{\Pr_1 + (C_{01} + 2\sqrt{C_{01} K_1} + \sqrt{K_1})} > \frac{b_{\max_2}}{\Pr_2 + (C_{02} + 2\sqrt{C_{02} K_2} + \sqrt{K_2})},$$

where the suffix 1 denotes forest and 2 denotes agriculture.

The decision thus should depend upon the relative total nutritional benefit, palatability, overhead costs and predation risk. Since for a given crop the nutritive value and palatability cannot be controlled, increasing the overhead cost by making fences, trenches, etc. can be effective above a threshold increase in C_0, the threshold being decided by the nutritive content and palatability of the crop relative to wild forage. It is not necessary (and perhaps not possible or too expensive) to make a fence that is completely impenetrable to animals. It needs to increase C_0 sufficiently so that the inequality in the above equation is true. Alternatively, the perceived risk in agricultural fields $\Pr_2$ needs to be substantially greater than $\Pr_1$ to make the inequality true. An alternative way of thinking is to increase the natural habitat quality, or wild forage quality and quantity to discourage animals from crop raiding. For this to happen, $b_{\max_1}$ has to increase sufficiently to make the inequality true. From the equation, a change in $b_{\max_1}$ will affect the left-hand-side in direct proportion of the improvement, but a change in C_{02} will have a greater than proportional effect on the relative quantities.

This is important since laws of some countries permit culling of the predominant crop-raiding species[30,31]. However, effect of culling for reducing crop raiding is not widely demonstrated[32]. The inequality suggests that it would work like a threshold phenomenon. There is likely to be a sudden reduction in crop raiding if the perceived $\Pr_2$ is sufficiently greater than the perceived $\Pr_1$ to satisfy the above inequality. If this condition is satisfied, there would be effective deterrence from raiding independent of the population density. However, for this to happen it would be essential that the animals associate the culling risk with the agricultural fields. This is possible if the culling is done only during crop raiding. If it is practised over the wild land, the threshold phenomenon is unlikely to work and reduction in raiding, if any, would only be proportional to the reduction in population. The optimum level of culling $\Pr_2$ should be just sufficient to make the inequality true.

If herbivores chose the agricultural patch, the time they should optimally spend in feeding on a given patch is $\sqrt{C_0 K}$. This means that greater the difficulty in entering a patch, greater should be the time spent in feeding. Therefore, the possible effects of preventive fencing would be complex. Fencing is likely to decrease the probability of herbivores entering a field, but once entered they need to forage more for cost-effectiveness. Thus, the efficiency of fencing would also act as a threshold phenomenon. Below the threshold fencing may actually increase the damage, whereas above the threshold it might suddenly become highly effective (Figure 4).

The above inequality also gives an important insight into the efficiency of a protection measure. If a protection measure is applied to one farm, herbivores certainly have a better benefit-to-cost ratio in the unprotected neighbouring fields and they would avoid the protected field. However, if everyone applies the same protection measure, the

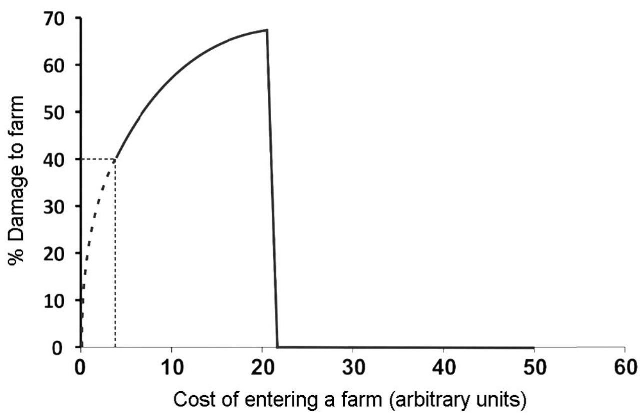

Figure 4. The non-monotonic effect of fencing on expected damage according to the model. The cost of entering is assumed to increase with the quality of the fence. The dotted line denotes cost in the absence of fencing. Contrary to simple belief, the damage increases with the difficulty of crossing the fence up to a threshold, after which it reduces drastically.

inequality or the relative advantage is lost. If this happens animals are likely to resume raiding all fields albeit at a higher cost each. The higher cost may result into greater feeding effort and the actual damage could be more than the unfenced baseline damage, unless the fencing efficiency is above the threshold at which foraging in a forest is more beneficial. Therefore, a measure that is highly effective on an experimental scale is likely to lose its efficiency when applied on a mass scale, and in fact might prove counterproductive.

Discussion

The generalized models provide many qualitative insights into the problem of crop-raiding and raise many novel possibilities that need to be tested empirically. The explicit expression of the conditions when to use ratio model and when to use difference model has wide implications in microeconomics as well as in behavioural ecology and evolution. Apart from the theoretical general principle, the model suggests many practical possibilities. The realization that actual loss of farmers can be greater than the direct damage done by animals is important in providing justice to the farmers[33]. The model warns against many simplistic beliefs such as a protection method that works well on an experimental scale will work equally well on a mass scale. The most important realization is that the effects of fencing or culling can be highly nonlinear and at times non-monotonic. Therefore, any effort to judge the efficacy of a mitigation measure without appropriate modelling may give rise to misleading inferences. In addition to the generalized qualitative inferences, the model makes a foundation on which specialized models can be built[20]. It is unlikely that a single solution would work for mitigating the crop damage problem. An integration of multiple measures might be appropriate[34]. The model can form the right platform on which such an integration can be attempted and evaluated.

Different species of herbivores differ in their population size, gregariousness, activity periods, qualitative and quantitative patters of damage and response to guarding and driving attempts[13,35,36]. In cases where the probability of damage is small, a crop insurance scheme can be a viable proposal even if the extent of damage is large. Insurance schemes are necessarily founded on the principle of small probability of disaster, so that the insurance paid is less than the total premium paid by the pool of people. For smaller but more abundant herbivores, crop insurance schemes are unlikely to be practicable since a large proportion of farmers in a damage-prone area incur actual loss. Also for species which respond well to individual guarding, crop insurance may turn counterproductive since it might cause partial discouragement from active guarding and thereby increase the damage.

In order to make locale and species-specific useful quantitative predictions, more specific models using parameters measurable in the field are needed[20]. The required modifications of the baseline model could be extremely context- and question-driven[20]. They would differ according to the crop species, relevant agricultural practices, microeconomics of farmers, the major damaging herbivore species, their habits, habituation and prevalent laws. The baseline generalized model described above can be used to make such specific quantitative predictive models. An insightful modelling approach is likely to lead towards sustainable solutions.

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