

An evolutionary game theoretic model of rhino horn devaluation

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ABSTRACT

Rhino populations are at a critical level due to the demand for rhino horn and the subsequent poaching. Wildlife managers attempt to secure rhinos with approaches to devalue the horn, the most common of which is dehorning. Game theory has been used to examine the interaction of poachers and wildlife managers where a manager can either 'dehorn' their rhinos or leave the horn attached and poachers may behave 'selectively' or 'indiscriminately'. The approach described in this paper builds on this previous work and investigates the interactions between the poachers. We build an evolutionary game theoretic model and determine which strategy is preferred by a poacher in various different populations of poachers. The purpose of this work is to discover whether conditions which encourage the poachers to behave selectively exist, that is, they only kill those rhinos with full horns.

The analytical results show that full devaluation of all rhinos will likely lead to indiscriminate poaching. In turn it shows that devaluing of rhinos can only be effective when implemented along with a strong disincentive framework. This paper aims to contribute to the necessary research required for informed discussion about the lively debate on legalising rhino horn trade.

1. Introduction

Rhino populations now persist largely in protected areas or on private land, and require intensive protection (Ferreira et al., 2014) because the demand for rhino horn continues to pose a serious threat (Amin et al., 2006). The illegal trade in rhino horn supports aggressive poaching syndicates and a black market (Nowell et al., 1992; Warchol et al., 2003). This lucrative market entices people to invest their time and energy to gain a 'windfall' in the form of a rhino horn, through the poaching of rhinos.

Standard economic theory predicts extinction through poaching alone is unlikely due to escalating costs as the number of remaining species approaches zero (Courchamp et al., 2006). However, the rarity of rhino horn makes it a luxury good, or financial investment for the wealthy (Gao et al., 2016), and thus the increased cost and risk to poach does not increase as rapidly as the increased gain – the anthropogenic Allee effect (Branch et al., 2013; Courchamp et al., 2006). However, the anthropogenic Allee effect was recently revisited (Holden and McDonald-Madden, 2017) to highlight that the relationship is even more complex and pessimistic. The value of rhino horn can inflate, even with a large population size, due to an increase in the cost (i.e. risk) to poach. Therefore measures to protect rhino horn may actually be increasing the gain to poachers. It is not clear whether this relationship

has contributed to the escalation in rhino poaching over recent years. Nonetheless, it is clear that the future existence of rhinos is endangered because of poaching (Biggs et al., 2013; Smith et al., 2013). This rationale leads to debate about legalising rhino horn trade, which in turn may reduce demand. In Biggs et al. (2013) the authors suggest meeting the demand for rhino horn through a legal market by farming the rhino horn from live rhinos. In fact recently the actual quantity of horn that could be farmed was estimated by Taylor et al. (2017). However, Crookes (2016) argues that because the demand for horn is so high, legalising trade may lead to practices that maximise profit, but are not suitable for sustainable rhino populations, and thus rhinos may be 'traded on extinction'. Preventing poaching covers in-country and global issues, and thus legalising rhino horn trade is a controversial and active conversation, which is not limited to rhinos – Harvey et al. (2017) considered ivory and stated that by enforcing a domestic ivory trade ban we can reduce the market's demand.

As it stands, for wildlife managers law enforcement is often one of the main methods to deter poachers. Rhino conservation has seen increased militarisation with 'boots on the ground' and 'eyes in the sky' (Duffy et al., 2015). An alternative method is to devalue the horn itself, one of the main methods being the removal so that only a stub is left. The potential impact of various policies are nicely summarised in Douglas and Blignaut (2016), where de-horning is noted to be

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promising for ‘in-country intervention’. The first attempt at large-scale rhino dehorning as an anti-poaching measure was in Damaraland, Namibia, in 1989 (Milner-Gulland and Leader-Williams, 1992). Other methods of devaluing the horn that have been suggested include the insertion of poisons, dyes or GPS trackers (Gill, 2010; Smith et al., 2013). However, like dehorning, they cannot remove all the potential gain from an intact horn (poison and dyes fade or GPS trackers can be removed and have been found to affect only a small proportion of the horn). In Milner-Gulland and Leader-Williams (1992); Milner-Gulland (1999) they found the optimum proportion to dehorn using mean horn length as a measure of the proportion of rhinos dehorned. They showed, with realistic parameter values, that the optimal strategy is to dehorn as many rhinos as possible. A manager does not need to choose between law enforcement or devaluing, but perhaps adopt a combination of the two; especially given that devaluing rhinos comes at a cost to the manager, and the process comes with a risk to the rhinos.

A recent paper modelled the interaction between a rhino manager and poachers using game theory (Lee and Roberts, 2016). The authors consider a working year of a single rhino manager. A manager is assumed to have standard yearly resources which can be allocated on devaluing a proportion of their rhinos or spent on security. It is assumed that all rhinos initially have intact horns. Poachers may either only kill rhinos with full horns, ‘selective poachers’, or kill all rhinos they encounter, ‘indiscriminate poachers’. This strategy may be preferred to avoid tracking a devalued rhino again, and/or to gain the value from the partial horn. If all rhinos are left by the rhino manager with their intact horns, it does not pay poachers to be selective so they will chose to be indiscriminate since being selective incurs an additional cost to discern the status of the rhino. Conversely, if all poachers are selective, it pays rhino managers to invest in devaluing their rhinos. This dynamic is represented in Fig. 1. Assuming poachers and managers will always behave so as to maximise their payoff, there are two equilibria: either all rhinos are devalued and all poachers are selective; or all horns are intact and all poachers are indiscriminate. Essentially, either the managers win, the top left quadrant of Fig. 1, or the poachers win, the bottom right quadrant of Fig. 1. The paper (Lee and Roberts, 2016) concludes that poachers will always choose to behave indiscriminately, and thus the game settles to the top left quadrant, i.e., the poachers win.

At the extremes, we could consider the game as one of opportunistic exploitation (Branch et al., 2013). That is, consider intact rhinos and devalued rhinos as two species, where one is more valuable than the other. Opportunistic exploitation advances upon the theory of anthropogenic Allee effect to consider two species which are exploited together. Specifically, when a highly valued species becomes rarer, a secondary, less valuable species is then targeted. As with opportunistic exploitation on a larger scale, rhino managers need to account for the multispecies system.

In this manuscript, we explore the population dynamic effects associated with the interactions described by Lee and Roberts (2016). More specifically, the interaction between poachers. In a population full of indiscriminate poachers is there a benefit to a single poacher



Fig. 1. The game between rhino manager and rhino poachers. The system settles to one of two equilibria, either devaluing is effective or not.

becoming selective or vice versa? This notion is explored here using evolutionary game theory (Smith and Price, 1973). The game is not that of two players anymore (manager and poacher) but now the players are an infinite population of poachers. This allows for the interaction between poachers over multiple plays of the game to be explored with the rhino manager being the one that creates the conditions of the population.

Note that poachers are, in practice finite, and each has individual factors that will affect a poacher's behaviour. An infinite population model corresponds to either an asymptotic generalisation or overall descriptive behaviour.

In evolutionary game theory, we assume infinite populations and in our model this is represented by (x_1, x_2) with x_1 being the proportion of the population using a strategy of the first type and x_2 of the second. We assume there are utility functions u_1 and u_2 that map the population to a fitness for each strategy, given by,

$$u_1(x_1, x_2) \text{ and } u_2(x_1, x_2).$$

In evolutionary game theory these utilities are used to dictate the evolution of the population over time, according to the following replicator equations,

$$\begin{cases} \frac{dx_1}{dt} = x_1(u_1(x_1, x_2) - \phi), \\ \frac{dx_2}{dt} = x_2(u_2(x_1, x_2) - \phi), \end{cases} \quad (1)$$

where ϕ is the average fitness of the whole population (Nowak, 2006). In some settings these utilities are referred to as fitness and/or are mapped to a further measure of fitness. This is not the case considered here (it is assumed all evolutionary dynamics are considered by the utility measures).

Here, the overall population is assumed to remain stable thus, $x_1 + x_2 = 1$ and

$$\frac{dx_1}{dt} + \frac{dx_2}{dt} = 0 \Rightarrow x_1(u_1(x_1, x_2) - \phi) + x_2(u_2(x_1, x_2) - \phi) = 0. \quad (2)$$

Recalling that $x_1 + x_2 = 1$ the average fitness can be written as, $\phi = x_1 u_1(x_1, x_2) + x_2 u_2(x_1, x_2)$. (3)

By substituting (3) and $x_2 = 1 - x_1$ in (1),

$$\frac{dx_1}{dt} = x_1(1 - x_1)(u_1(x_1, x_2) - u_2(x_1, x_2)). \quad (4)$$

The equilibria of the differential equation (4) are given by, $x_1 = 0$, $x_1 = 1$, and $0 < x_1 < 1$ for $u_1(x_1, x_2) = u_2(x_1, x_2)$. These equilibria correspond to stability of the population: the differential equation (4) no longer changes.

The notion of evolutionary stability can be checked only for these stable strategies. For a stable strategy to be an evolutionary stable strategy (ESS) it must remain the best response even in a mutated population $(x_1, x_2)_\epsilon$. A mutated population is the post entry population where a small proportion $\epsilon > 0$ starts deviating and adopts a different strategy.

In Section 2, we determine expressions for u_1 , u_2 that correspond to a population of wild rhino poachers and we explore the stability of the equilibria identified in Lee and Roberts (2016). The results contained in this paper are proven analytically, and more specifically it is shown that:

- In the presence of sufficient risk: a population of selective poachers is stable, meaning dehorning is a viable option.
- Full devaluation of all rhinos will lead to indiscriminate poachers.

2. The utility model

As discussed briefly in Section 1, a rhino poacher can adopt two strategies, to either behave selectively or indiscriminately. To calculate

the utility for each strategy, the gain and cost that poachers are exposed to must be taken into account. The poacher incurs a loss from seeking a rhino, and the risk involved. The gain depends upon the value of horn, the proportion of horn remaining after the manager has devalued the rhino horn and the number of rhinos (devalued and not).

Let us first consider the gain to the poacher, where θ is the amount of horn taken. We assume rhino horn value is determined by weight only, a reasonable assumption as rhino horn is sold in a grounded form *Rhino Conservation* (2017). Clearly if the horn is intact, the amount of horn gained is $\theta = 1$ for both the selective and the indiscriminate poacher. If the rhino horn has been devalued, and the poacher is selective, the amount of horn gained is $\theta = 0$ as the poacher does not kill. However, if the poacher is behaving indiscriminately, the proportion of value gained from the horn is $\theta = \theta_r$ (for some $0 < \theta_r < 1$). Therefore, the amount of horn gained in the general case is

$$\theta(r, x) = x(1 - r) + (1 - x)(1 - r + r\theta_r) \quad (5)$$

where r is the proportion of rhinos that have been devalued, and x is the proportion of selective poachers and $1 - x$ is the proportion of indiscriminate poachers. Note that since $\theta_r, r, x \in [0, 1]$, then $\theta(r, x) > 0$, that is, some horn will be taken. Standard supply and demand arguments imply that the value of rhino horn decreases as the quantity of horn available increases (Mankiw, 2010). Thus at any given time the expected gain is

$$H\theta(r, x)^{-\alpha}, \quad (6)$$

where H is a scaling factor associated with the value of a full horn, $\alpha \geq 0$ is a constant that determines the precise relationship between the quantity and value of the horn. Fig. 2, verifies that the gain curve corresponds to a demand curve: we see that as r increases, so that the supply of horn decreases, the value is higher and vice versa. We have chosen a simple function to model the demand (and thus gain) of rhino horn value, relative to the proportion of rhinos devalued. However, demand for illegal wildlife generally involves more factors than simply supply. Additional factors include, but are not limited to, social stigma, tourism revenues, government corruption, and rich countries being willing to pay to ensure species existence (Bulte and Van Kooten, 1999; van and Kooten, 2008).

An individual interacts with the population which is uniquely determined by x , the proportion of selective poachers. Therefore, the gain for a poacher in the population x is either

$$\begin{cases} \theta(r, 1)H\theta(r, x)^{-\alpha} & \text{selective poacher} \\ \theta(r, 0)H\theta(r, x)^{-\alpha} & \text{indiscriminate poacher} \end{cases} \quad (7)$$

depending on the chosen strategy of the individual.

Secondly we consider the costs incurred by the poacher. It is assumed that a given poacher will spend sufficient time in the park to obtain the equivalent of at least a single rhinoceros's horn. For selective poachers this implies searching the park for a fully valued horn and for indiscriminate poachers this implies either finding a fully valued horn or finding N_r total rhinoceroses where $N_r = \lceil \frac{1}{\theta_r} \rceil$.

Fig. 3 shows a random walk that any given poacher will follow in

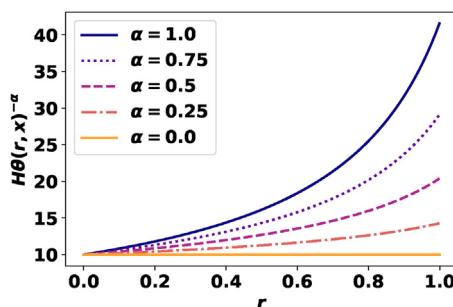


Fig. 2. $H\theta(r, x)^{-\alpha}$ for values $H = 10$, $\theta_r = 0.3$ and $x = 0.2$.

the park. Both types of poacher will exit the park as soon as they encounter a fully valued rhino, which at every encounter is assumed to happen with probability $1 - r$. However, the indiscriminate poachers may also exit the park if they encounter N_r devalued rhinos in a row. Each step on the random walk is assumed to last 1 time unit: during which a rhino is found. To capture the fact that indiscriminate poachers will spend a different amount of time to selective poachers with each rhino the parameter τ is introduced which corresponds to the amount of time it takes to find and kill a rhino (thus $\tau \geq 1$).

Using this, the expected time spent in the park T_1 , T_2 by poachers of both types can be obtained:

For selective poachers:

$$\begin{aligned} T_1 &= (1 - r)\tau + r(1 - r)(1 + \tau) + r^2(1 - r)(2 + \tau) + \dots \\ &= (1 - r) \sum_{i=0}^{\infty} r^i(i + \tau) \\ &= (1 - r) \left(\frac{1}{r} \sum_{i=0}^{\infty} ir^{i+1} + \tau \sum_{i=0}^{\infty} r^i \right) \\ &= (1 - r) \left(\frac{r}{(1 - r)^2} + \frac{\tau}{1 - r} \right) \quad \text{using standard formula for geometric series} \\ &= \frac{r + \tau(1 - r)}{1 - r} \end{aligned} \quad (8)$$

For indiscriminate poachers:

$$\begin{aligned} T_2 &= (1 - r)\tau + r(1 - r)2\tau + r^2(1 - r)3\tau + \dots + r^{N_r-2}(1 - r)(N_r - 1)\tau \\ &\quad + r^{N_r-1}N_r\tau \\ &= (1 - r)\tau \sum_{i=1}^{N_r-1} ir^{i-1} + r^{N_r-1}N_r\tau \\ &= (1 - r)\tau \left(\frac{1}{r(r-1)^2} (N_r rr^{N_r} - N_r r^{N_r} - rr^{N_r} + r) \right) + r^{N_r-1}N_r\tau \\ &= \frac{\tau(1 - r^{N_r})}{(1 - r)} \end{aligned} \quad (9)$$

Fig. 4 shows T_1 and T_2 for varying values of r and τ highlighting that τ has a greater effect on T_2 than T_1 . Also, as r increases the overall time spent in the park by both poachers increases and the value of τ at which T_1 and T_2 are equal increases.

Additionally, the poachers are also exposed to a risk. The risk to the poacher is directly related to the proportion of rhinos not devalued, $1 - r$, since the rhino manager can spend more on security if the cost of devaluing is low. In real life this is not always the case. The cost of security can be extremely high thus it cannot be guaranteed that much security will be added from the saved money. However, our model assumes that there is a proportional and negative relationship between the measures.

$$(1 - r)^\beta, \quad (10)$$

where $\beta \geq 0$ is a constant that determines the precise relationship between the proportion of rhinos not devalued and the security on the grounds. Therefore, at any given time the expected cost (due to the trade off between security and devaluing) for a poacher is,

$$FT_i(1 - r)^\beta \text{ for } i \in \{1, 2\} \quad (11)$$

where F is a constant that determines the precise relationship. Fig. 5 verifies the decreasing relationship between r and the cost. Notice that the cost to indiscriminate poachers remains fairly consistent, irrespective of the proportion of devalued rhinos, until this proportion gets high. Whereas the cost to selective poachers is more sensitive to the proportion of rhinos devalued, especially when the time to kill a rhino is large.

One final consideration given to the utility model is the incorporation of a disincentive to indiscriminate poachers. Numerous interpretations can be incorporated with this:

- more severe punishment for indiscriminate killing of rhinos;
- educational interventions that highlight the negative aspects of indiscriminate killing;

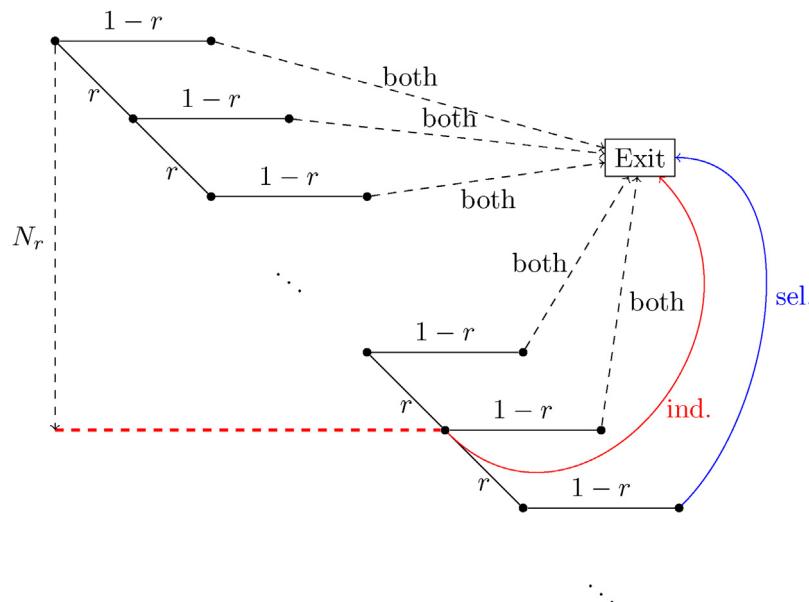


Fig. 3. Illustrative random walk showing the points at which an indiscriminate or a selective poacher will leave the park.

- the possibility of a better alternative being offered to selective poachers.

This will be captured by a constant Γ .

Combining (7) and (11) gives the utility functions for selective poachers, $u_1(x)$, and indiscriminate poachers, $u_2(x)$,

$$u_1(x) = \theta(r, 1)H\theta(r, x)^{-\alpha} - (r + \tau(1 - r))F(1 - r)^{\beta-1}, \quad (12)$$

$$u_2(x) = \theta(r, 0)H\theta(r, x)^{-\alpha} - \tau(1 - r^{N_r})F(1 - r)^{\beta-1} - \Gamma \quad (13)$$

Given a specific individual, let s denote the probability of them behaving selectively. Thus the general utility function for an individual poacher in the population with a proportion of $0 \leq x \leq 1$ selective poachers is

$$u(s, x) = su_1(x) + (1 - s)u_2(x). \quad (14)$$

Substituting (12) and (13) into (14) and using (5) gives,

$$\begin{aligned} u(s, x) = & H(\theta_r r(1 - s) - r + 1)\theta(r, x)^{-\alpha} \\ & - F(sr + s\tau(1 - r) + (1 - s)\tau(1 - r^{N_r}))(1 - r)^{\beta-1} - (1 - s)\Gamma \end{aligned} \quad (15)$$

Fig. 6 shows the evolution of the system over time for a variety of

initial populations and parameters. This is done using numerical integration implemented in Eric et al. (2001). All the source code used for this work has been written in a sustainable manner: it is open source (<https://github.com/Nikoleta-v3/Evolutionary-game-theoretic-Model-of-Rhino-poaching/>) and tested which ensures the validity of the results. The source code has also been properly archived and can be found at Glynatsi and Knight (2018).

A summary of all the parameters and their meanings is given by Table 1.

In Fig. 6 the left column shows parameters sets for which a selective population is stable ($x = 1$). The figures on the right correspond to a decrease in τ which decreases the risk associated with acting indiscriminately: in these cases a population of selective poachers is unstable. In one case ($H = 192$) a mixed population is stable: some poachers will continue to act selectively.

In Section 3, these observations will be confirmed theoretically.

3. Evolutionary stability

By definition, for a strategy to be an ESS it must first be a best response to an environment where the entire population is playing the same strategy. In our model there are three possible stable distributions

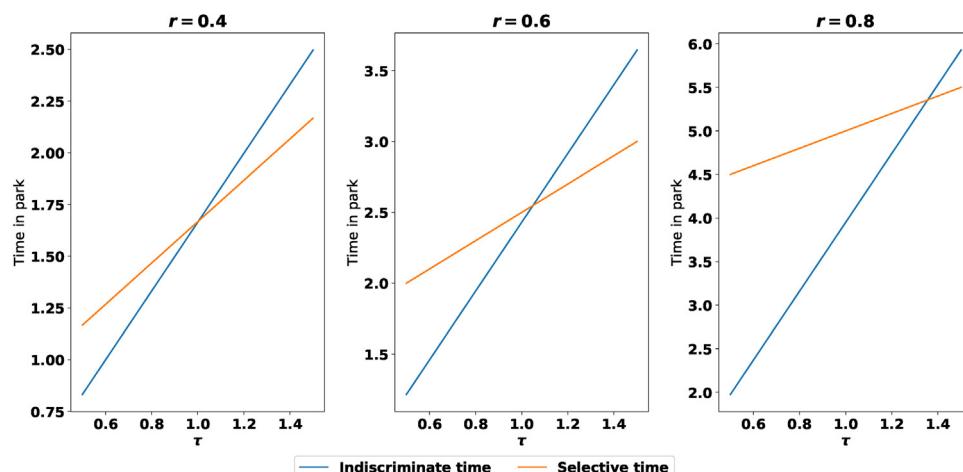


Fig. 4. Expected time spent in the park for selective T_1 and indiscriminate poachers T_2 for $\theta_r = .15$.

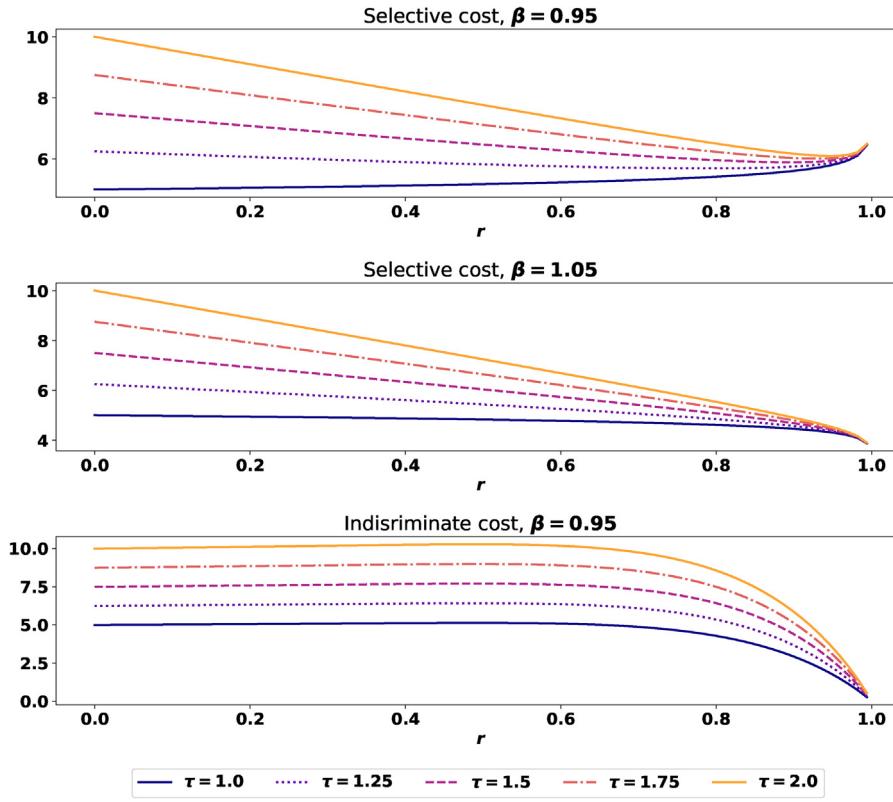


Fig. 5. Costs associated to both poachers for $F = 5$ and varying values of r and τ .

based on the equilibria of equation (4):

- all poachers are selective;
- all poachers are indiscriminate;
- mixed population of selective and indiscriminate poachers.

An ESS corresponds to asymptotic behaviour near the equilibria of (4), this correspond to the concept of Lyapunov stability (Lyapunov,

1992).

For simplicity, denote the right hand side of (4) as f . In this setting, when x is near to some equilibria x^* so that $f(x^*) = 0$ then the evolutionary game can be linearized (using standard Taylor Series expansion) as:

$$\frac{d(x^* + \epsilon)}{dt} = J(x^*)\epsilon \quad (16)$$

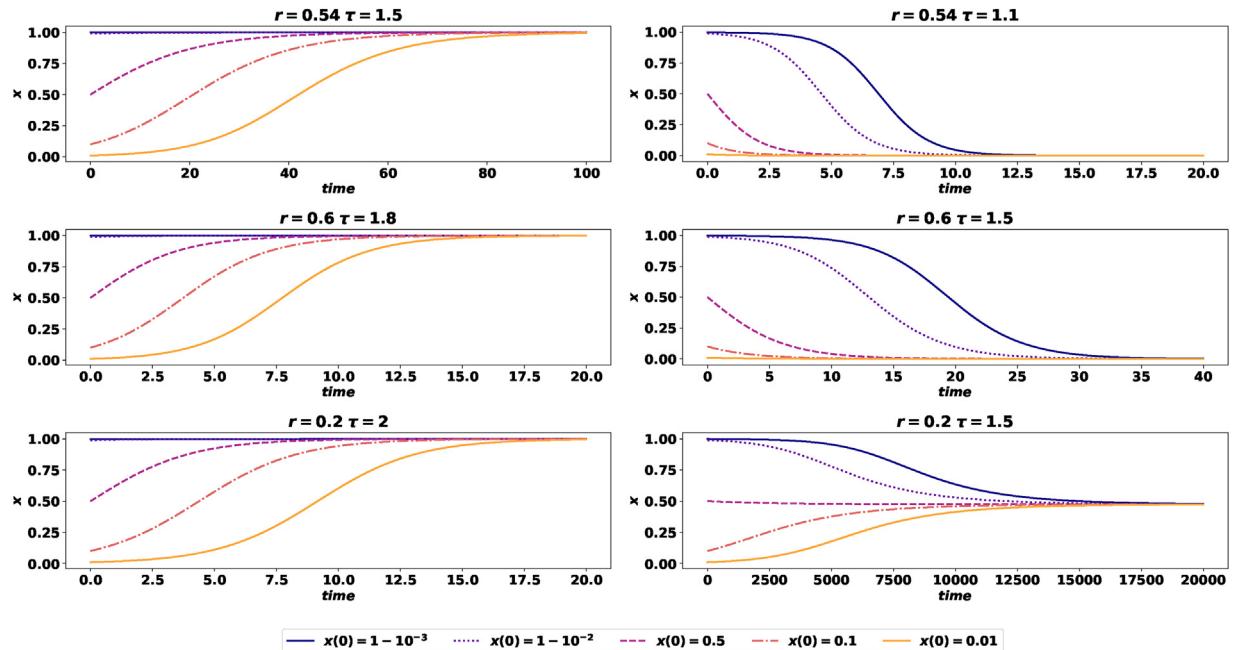


Fig. 6. The change of the population over time with different starting populations. For $F = 5$, $H = 50$, $\alpha = 2$, $\beta = .99$, $\tau = 1.5$, $\theta_r = 0.01$, $\Gamma = 0$.

Table 1
A summary of the parameters used.

Parameter	Interpretation
θ_r	The proportion of value gained from a devalued horn
r	The proportion of rhinos that have been devalued
H	A scaling factor associated with the value of a full horn
α	The relationship between the quantity and value of a horn
F	The cost of retrieving a horn
β	The relationship between the proportion of devalued rhinos and security
τ	The time it takes to find and kill a rhino
Γ	A disincentive only applied to indiscriminate poachers

where:

$$J(a) = \frac{df}{dx} \Big|_{x=a} \quad (17)$$

This gives a standard approach for evaluating equilibria of the underlying game. For a given equilibria x^* , $J(x^*) < 0$ if and only if x^* is an ESS.

Using Eqs. (12) and (13):

$$J(a) = \frac{1}{(r-1)(-a\theta_r + r\theta_r - r + 1)^{\alpha+1}} (J_1 - J_2) + \Gamma(1-2a) \quad (18)$$

where:

$$J_1 = F(-r+1)^\beta(-a\theta_r + r\theta_r - r + 1)^{\alpha+1} \left(2a\tau - 2a\theta_r - 2ar^{[1/\theta_r]} - r\tau + r^{[1/\theta_r]}\tau \right)$$

$$J_2 = H\alpha r^2 \theta_r^2 (-a+1)(r-1) + H\theta_r (2a-1)(r-1)(a\theta_r - r\theta_r + r - 1)$$

Theorem 1. *Using the utility model described in Section 2, a population of selective poachers is stable if and only if:*

$$\tau > \frac{1}{1-r^{[1/\theta_r]-1}} \frac{F + H\theta_r(1-r)^{1-\alpha-\beta} - \frac{\Gamma}{r(1-r)^{1-\beta}}}{F} \quad (19)$$

Proof. Direct substitution gives:

$$J(1) = \frac{1}{(-r+1)^{\alpha+1}(r-1)} (F(-r+1)^\beta(-r+1)^{\alpha+1}(r\tau - r - r^{[1/\theta_r]}\tau) - H\theta_r(r-1)^2 - \Gamma) = (F(1-r)^{\beta-1}(r\tau - r - r^{[1/\theta_r]}\tau) + H\theta_r(1-r)^{-\alpha} - \Gamma)$$

$$F(1-r)^{\beta-1}r + H\theta_r(1-r)^{-\alpha} - \Gamma < F(1-r)^{\beta-1}\tau(r - r^{[1/\theta_r]}) \frac{F + H\theta_r(1-r)^{1-\beta-\alpha} - \frac{\Gamma}{r(1-r)^{1-\beta}}}{F} < \tau$$

which gives the required result. \square

Note that the limit of the right hand side of Eq. (19) tends to infinity as $r \rightarrow 1^-$. This means that devaluing all rhinos is not a valid approach.

Furthermore, we see that the equilibria with poachers acting selectively, predicted in Lee and Roberts (2016) can in fact be obtained in specific settings.

Note that similar theoretic results have been obtained about the evolutionary stability of indiscriminate poachers but these have been omitted for the sake of clarity.

In this section we have analytically studied the stability of all the possible equilibria. We have proven that all potential equilibria are possible. All of these theoretic results have been verified empirically, and the data for this has been archived at Glynatsi et al. (2018). Fig. 7 shows a number of scenarios where $F = 5$, $\beta = 0.99$, $\theta_r = 0.05$ and, unless varied as stated on the x-axis:

- Scenario 1: $H = 50$ $r = 0.45$ $\alpha = 2$, $\tau = 2$, $\Gamma = 0$
- Scenario 2: $H = 50$ $r = 0.4$ $\alpha = 2.5$, $\tau = 1.8$, $\Gamma = 0$
- Scenario 3: $H = 25$ $r = 0.45$ $\alpha = 2$, $\tau = 2$, $\Gamma = 0$
- Scenario 4: $H = 25$ $r = 0.4$ $\alpha = 2.5$, $\tau = 1.8$, $\Gamma = 0$
- Scenario 5: $H = 25$ $r = 0.99$ $\alpha = 2$, $\tau = 2$, $\Gamma = 4$
- Scenario 6: $H = 25$ $r = 0.99$ $\alpha = 2.5$, $\tau = 1.8$, $\Gamma = 4$.

The first plot in Fig. 7 shows that when the value of a full horn is low, and there is no disincentive factor (Scenarios 3 and 4), the poacher strategy can be influenced by the time taken to kill a rhino such that a long time can push the poacher to behave selectively (as there is increased risk associated with acting indiscriminately). The second plot, shows that the disincentive factor has most influence when the value of a full horn is high (Scenarios 1 and 2). Otherwise, poachers will generally be indiscriminate if r is large (Scenarios 5 and 6) or selective otherwise (Scenarios 1, 2, 3 and 4). Most importantly, the third plot confirms Theorem 1. A high value of r forces the population to become indiscriminate even with a high disincentive. Moreover, for all scenarios a value of r does exist for which a selective population will subsist.

This confirms that devaluing alone is not a solution and in fact can potentially have averse consequences: combinations of devaluing and education (creating a disincentive) is needed.

4. Discussion and conclusions

In this work the dynamics of a selective population were explored. It was shown that given sufficient risk associated with killing a rhino, it would be possible for a selective population of poachers to subsist.

We have developed a game theoretic model which examines the specific question for rhino managers: how to deter poachers by devaluing horns? One of the main conclusions of the work presented here is that if there is sufficient risk associated with indiscriminate behaviour then a population of selective poachers can be stable. The model also incorporates wider factors in a general manner such as a disincentive factor. The disincentive factor may be an increase in the monetary fine for poachers. In fact Di Minin et al. (2015), who identify the most important contributors to the number of rhinos illegally killed in South Africa (between 1900 and 2013), found that increasing the monetary fine has a more significant effect than increasing the years in prison. However, the disincentive factor may also include wider influences, such as engaging the rural communities that neighbour wildlife (Biggs et al., 2013), or decreasing the cost of living with wildlife, and supporting a livelihood that is not related to poaching. Zooming out further, it could include global issues such as an increase in ecotourism, which would provide a sustainable income for the community.

Another opportunity for wider factors, such as global issues, to be included in the model is via the supply and demand function. For example, Di Minin et al. (2015) show that one of the three most important contributors to the number of rhinos illegally killed was the GDP in Far East Asia, where the demand for rhino horn is at its greatest. This finding supports (Lawson and Vines, 2014) call for improved law enforcement and demand reduction in the Far East.

Note that the proportion of devalued rhinos r is continuous over $[0, 1]$ in the model. However, standard practice of a given park manager in almost all cases is to either devalue all the animals in a defined enclosed area, or none at all. This is thought to be because partial devaluing tends to disturb rhino social structures. Our results indicate that devaluing all rhinos will only decrease rhino poaching if potential poachers have a viable alternative (even in the case of a large disincentive).

The debate about the effectiveness of devaluation for preventing poachers and, is extensive and ongoing. This model answers one aspect of the topic, but larger questions remain. There are many drivers to account for, many of which are included in a systems dynamics model presented in Crookes (2016) which captures the five most important factors: rhino abundance, rhino demand, a price model, an income

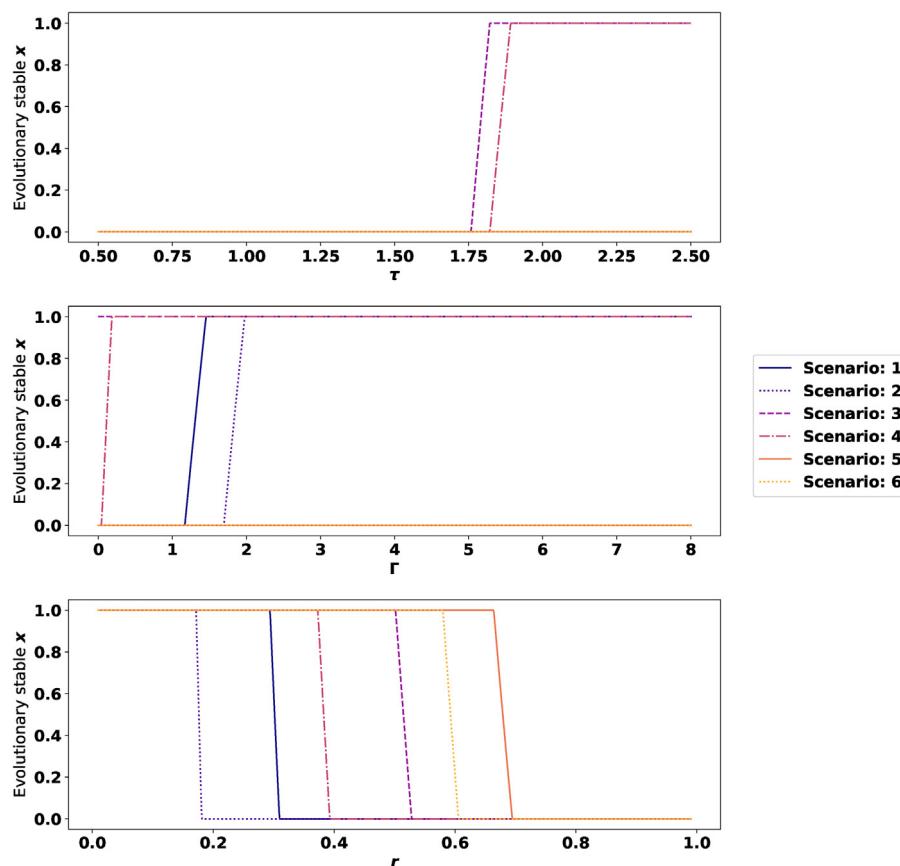


Fig. 7. Evolutionary stable populations for varying values of τ , r , Γ for six different scenarios.

model and a supply model. Using the optimal dehorning model of Milner-Gulland and Leader-Williams (1992), the model (Crookes, 2016) finds that poachers behaving indiscriminately will always prevail, which indicates that the risk associated with indiscriminate behaviour might not have been captured fully.

Following discussions with environmental specialists it is clear that devaluing is empirically thought to be one of the best responses to poaching. This indicates that whilst of theoretic and potential macroeconomic interest, the modelling approach investigated in this work has potential for further work. For example, a detailed study of two neighbouring parks with differing policies could be studied using a game theoretic model, this would require an understanding of the travel times which can be very large and have a non negligible effect. Another interesting study would be to introduce a third strategy available to poachers: this would represent the possibility of not poaching (perhaps finding another source of income) and/or leaving the current environment to poach elsewhere. Finally, the specific rhino population could also be modelled using similar techniques and incorporated in the supply and demand model.

Authors' contributions

All authors conceived the ideas and designed the methodology. NG and VK developed the source code needed for the numerical experiments and generating the data. All authors contributed critically to the drafts and gave final approval for publication.

Conflicts of interest

None.

Data accessibility

The data generated for this work have been archived and are available online (Glynasti et al., 2018).

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A variety of software libraries have been used in this work:
 The Scipy library for various algorithms (Eric et al., 2001).
 The Matplotlib library for visualisation (Hunter, 2007).
 The SymPy library for symbolic mathematics (Meurer et al., 2017).
 The Numpy library for data manipulation (Walt et al., 2011).

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References

- Rhino Conservation – Save the Rhino @ONLINE, 2017.
- Amin, R., Thomas, K., Emslie, R.H., Foose, T.J., Strien, N., 2006. An overview of the conservation status of and threats to rhinoceros species in the wild. *Int. Zoo Yearbook* 40 (1), 96–117.
- Biggs, D., Courchamp, F., Martin, R., Possingham, H.P., 2013. Legal trade of Africa's rhino horns. *Science* 339 (6123), 1038–1039.
- Branch, T.A., Lobo, A.S., Purcell, S.W., 2013. Opportunistic exploitation: an overlooked pathway to extinction. *Trends Ecol. Evol.* 28 (7), 409–413.

Bulte, E.H., Van Kooten, G.C., 1999. Economics of antipoaching enforcement and the ivory trade ban. *Am. J. Agric. Econ.* 81 (2), 453–466.

Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L., Meinard, Y., 2006. Rarity value and species extinction: the anthropogenic Allee effect. *PLoS Biol.* 4 (12), e415.

Crookes, D.J., 2016. Trading on extinction: an open-access deterrence model for the South African abalone fishery. *S. Afr. J. Sci.* 112 (3–4), 1–9.

Crookes, D.J., Blignaut, J.N., 2016. A categorisation and evaluation of rhino management policies. *Dev. South Afr.* 33 (4), 459–469.

Di Minin, E., Laitila, J., Montesino-Pouzols, F., Leader-Williams, N., Slotow, R., Goodman, P.S., Conway, A.J., Moilanen, A., 2015. Identification of policies for a sustainable legal trade in rhinoceros horn based on population projection and socioeconomic models. *Conserv. Biol.* 29 (2), 545–555.

Duffy, R., St John, F.A., Buscher, B., Brockington, D., 2015. The militarization of anti-poaching: undermining long term goals? *Environ. Conserv.* 42 (4), 345–348.

Eric, J., Travis, O., Pearu, P., et al., 2001. SciPy: Open Source Scientific Tools for Python: v0.19.0.

Ferreira, S.M., Pfaf, M., Knight, M., 2014. Management strategies to curb rhino poaching: alternative options using a cost-benefit approach. *S. Afr. J. Sci.* 110 (5–6), 01–08.

Gao, Y., Stoner, K.J., Lee, A.T.L., Clark, S.G., 2016. Rhino horn trade in china: an analysis of the art and antiques market. *Biol. Conserv.* 201, 343–347.

Gill, V., 2010. Rhino Horn GPS Used to Deter Poachers. http://news.bbc.co.uk/earth/hi/earth_news/newsid_9116000/9116106.stm.

Glynatsi, N.E., Knight, V., Lee, T.E., 2018. Data for Evolutionary Game Theoretic Model of Rhino Poaching. <https://doi.org/10.5281/zenodo.1408678>. Available at: <https://doi.org/10.5281/zenodo.1409227>. Available at: <https://doi.org/10.5281/zenodo.1409227>.

Harvey, R., Alden, C., Wu, Y.S., 2017. Speculating a fire sale: options for Chinese authorities in implementing a domestic ivory trade ban. *Ecol. Econ.* 141, 22–31.

Holden, M.H., McDonald-Madden, E., 2017. High prices for rare species can drive large populations extinct: the anthropogenic Allee effect revisited. *J. Theor. Biol.* 429, 170–180.

Hunter, J.D., 2007. Matplotlib: a 2D graphics environment. *Comput. Sci. Eng.* 9 (3), 90–95.

Lawson, K., Vines, A., 2014. Global Impacts of the illegal Wildlife Trade: The Costs of Crime, Insecurity and Institutional Erosion. Chatham House.

Lee, T.E., Roberts, D.L., 2016. Devaluing rhino horns as a theoretical game. *Ecol. Modell.* 337, 73–78.

Lyapunov, A.M., 1992. The general problem of the stability of motion. *Int. J. Control* 55 (3), 531–534.

Mankiw, N.G., 2010. Macroeconomics. Worth Publishers.

Meurer, A., Smith, C.P., Paprocki, M., Čertík, O., Kirpichev, S.B., Rocklin, M., Kumar, A., Ivanov, S., Moore, J.K., Singh, S., Rathnayake, T., Vig, S., Granger, B.E., Muller, R.P., Bonazzi, F., Gupta, H., Vats, S., Johansson, F., Pedregosa, F., Curry, M.J., Terrel, A.R., Roučka, Š., Saboo, A., Fernando, I., Kulal, S., Cimrman, R., Scopatz, A., 2017. Sympy: symbolic computing in python. *PeerJ. Comput. Sci.* 3.

Milner-Gulland, E.J., Leader-Williams, N., 1992. A model of incentives for the illegal exploitation of black rhinos and elephants: poaching pays in Luangwa Valley, Zambia. *J. Appl. Ecol.* 29 (2), 388–401.

Milner-Gulland, E.J., 1999. How many to dehorn? A model for decision-making by rhino managers. *Animal Conservation Forum*, vol. 2. Cambridge University Press, pp. 137–147.

Nowak, M.A., 2006. Evolutionary Dynamics: Exploring the Equations of Life.

Nowell, K., Chyi, W.L., Pei, C.J., 1992. The Horns of a Dilemma: The Market for Rhino Horn in Taiwan: Final Report for WWF Project II3637.03.

Smith, J.M., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.

Smith, R.J., Roberts, D.L., Duffy, R., St John, F.A.V., 2013. New rhino conservation project in South Africa to understand landowner decision-making. *Oryx* 47 (3) 323–323.

Taylor, A., Balfour, D., Brebner, D.K., Coetzee, R., Davy-Moster, H., Lindsey, P.A., Shaw, J., Sas-Rolfs, M., 2017. Sustainable rhino horn production at the pointy end of the rhino horn trade debate. *Biol. Conserv.* 216, 60–68.

van Kooten, G.C., 2008. Protecting the african elephant: a dynamic bioeconomic model of ivory trade. *Biol. Conserv.* 141 (8), 2012–2022.

Walt, S., Colbert, S.C., Varoquaux, G., 2011. The NumPy array: a structure for efficient numerical computation. *Comput. Sci. Eng.* 13 (2), 22–30.

Warchol, G.L., Zupan, L.L., Clack, W., 2003. Transnational criminality: an analysis of the illegal wildlife market in Southern Africa. *Int. Crim. Just. Rev.* 13 (1), 1–27.