POACHING AND THE PROTECTION OF AN ENDANGERED SPECIES: A GAME-THEORETIC APPROACH

Adrian Lopes
Ph.D. Candidate
Dyson School of Applied Economics,
Cornell University

Jon M. Conrad
Professor
Dyson School of Applied Economics,
Cornell University

-DRAFT-

Abstract: The poaching of endangered species like the elephant and the rhino has increased dramatically over the last decade. Anti-poaching patrols must use their limited resources strategically in order to achieve the highest level of protection. We develop a model that views poaching and protection as a repeated game between strategic players. We conceptualize a "space" within which an endangered species is distributed spatially and temporally through migration. Poaching and anti-poaching patrolling are introduced as spatial-temporal activities in the space. We study the long-term effects of different strategies of a poaching unit and an anti-poaching unit on the population dynamics of an endangered species. We solve for a mixed strategy Nash equilibrium in this game and provide a proof for it uniqueness. The model is generally applicable to the protection of spatially distributed species populations that are subject to illegal harvest.

Keywords: *migration, poaching, anti-poaching enforcement, strategies, population dynamics*.

JEL codes: Q57, Q29, Q28, Q24.

(1) Introduction

The protection of endangered species such as the elephant and the rhino has become increasingly difficult in recent times with poaching on the rise in several African countries. International syndicates sponsor poaching units/gangs with aircraft and high-powered weapons, and also arrange for the rapid shipment of tusk and horn to markets in Asia

(Mullen & Zhang, 2012; Sas-Rolfes, 2012; Shukman, 2013; Wassener, 2013; S. K. Wasser et al., 2008). Anti-poaching units/patrols are limited in number, given the area to be covered, and are at a disadvantage given the resources and technology employed by poachers. Anti-poaching units must strategically use their resources to achieve the highest level of protection. Poaching gangs and anti-poaching patrols are essentially engaged in a repeated game of poaching and protection.

Economic models are used to study poaching behavior under open access settings with the assumption that poachers have no incentive to preserve a natural resource (E. H. Bulte & van Kooten, 1999a; E. H. Bulte & van Kooten, 1999b; A. Johannesen & Skonhoft, 2005; Kremer & Morcom, 2000; Messer, 2010; Milner-Gulland & Leader-Williams, 1992; Skonhoft & Solstad, 1998). These models predict equilibrium levels of endangered populations under different conservation policies. When studying systems in which a resource is distributed heterogeneously in space (Sanchirico & Wilen, 1999a) note that a considerable amount of interesting behavior is unaccounted for when a model aggregates out the spatial aspects of economic activity. The literature has given inadequate attention to the effects of spatial variability on resource harvesting and management. (E. Bulte, Damania, Gillson, & Lindsay, 2004) note that models that link ecological theory and natural resource economics should expand their scope beyond the notion of steady state equilibrium by incorporating variability, complexity, scale, and uncertainty into economic models. The interaction between ecological variability and the economic behavior of individuals engaged in poaching and protecting endangered species requires further research (E. Bulte et al., 2004; Skonhoft, 2007).

This paper develops a simple, yet novel, model of *strategic* poaching and protection for an endangered species that is spatially and temporally distributed across interconnected habitats. Uncertainty is introduced through strategic spatial-temporal location choices of poaching gangs and anti-poaching patrols. This causes the population harvested illegally to become a stochastic process, and in turn causes a stochastic evolution in the species' population dynamics. Our simple model links the spatial dynamics of species migration with the economic game of poaching and protection. This research asks the following questions: (1) "What anti-poaching strategy can best combat the best strategy of a poaching gang?" and (2) "How do these strategies affect the population dynamics of an endangered species?" In the next section we provide an overview of the relevant literature. In section 3 we lay out the components of the model, the payoffs and potential strategies of the players, a solution for a Nash equilibrium, and numerical simulations. In section 4 we discuss the numerical results of the model. Section 5 provides some caveats and a conclusion.

(2) Overview and Background for the Model

The incentive to poach has been studied under various conservation policies such as trade bans (E. H. Bulte & van Kooten, 1999a; E. H. Bulte & van Kooten, 1999b; Burton, 1999), fines for poaching (E. H. Bulte & van Kooten, 1999a; E. H. Bulte & van Kooten, 1999b; Damania, Milner-Gulland, & Crookes, 2005; Damania, Stringer, Karanth, & Stith, 2003; Milner-Gulland & Leader-Williams, 1992; Skonhoft & Solstad, 1998), alternative livelihoods when there is conflict between land use and species conservation (Fischer, Muchapondwa, & Sterner, 2011; A. Johannesen & Skonhoft, 2005; Skonhoft, 2007), price-control through supply restrictions (Brown & Layton, 2001; Kremer & Morcom, 2000; Mason C.F., Bulte E.H., & Horan R.D., 2012), and the controversial "shoot-poachers-on-sight" policy (Messer, 2010). Models of illegal harvest assume open access conditions under which poachers myopically maximize short-run profit, and entry and exit occur until rents are dissipated.

Models of anti-poaching enforcement on the other hand study the optimization problem for park managers who maximize long-term revenue from tourism and hunting permits, and from which they net out enforcement costs (E. H. Bulte & van Kooten, 1999b; Muchapondwa & Ngwaru, 2010; Skonhoft & Solstad, 1998). Such studies of poaching and anti-poaching enforcement predict how the steady-state equilibrium stock, harvest, and enforcement levels change with economic parameters such as harvest prices, poaching costs, and the detection probability of anti-poaching patrols (E. H. Bulte & van Kooten, 1999b; A. Johannesen & Skonhoft, 2005; A. B. Johannesen & Skonhoft, 2004; Milner-Gulland & Leader-Williams, 1992; Skonhoft & Solstad, 1998). (Messer, 2010) contends that low wages in developing countries impose limits on the potential economic costs for poachers of fines and imprisonment. Messer infers that increasing the economic cost to poachers through tough anti-poaching policy, such as increasing the risk of detection, might be an effective way to curb poaching.

With ecosystems continually changing, models should incorporate the ecological variability of interconnected habitats and the opportunity costs of protecting them (E. Bulte et al., 2004). In a spatial econometric study (Frank & Maurseth, 2006) find that elephant population changes in one country positively affect population changes in neighboring countries. Frank and Maurseth contend that poachers may account for varying levels of anti-poaching enforcement in different countries. Resource harvesting models allow for spatial heterogeneity of the resource and connectivity between its sub-populations through migration (Conrad & Smith, 2012; Sanchirico & Wilen, 1999a; Skonhoft, 2007). The dispersal of meta-populations can be modeled in a variety of ways. These include fully integrated system, a closed system, a sink-source system, and finally a spatially linear system (Sanchirico & Wilen, 1999a). In a fully integrated system biomass disperses directly from one patch to any other patch in the system. In a closed system the maintenance of biomass density within each region is only determined by its own production and no dispersal occurs anywhere in the system. In a sink-source system one or more patches provide unidirectional biomass movement to other patches. In a spatially linear system one can have dispersal in a pairwise fashion between adjacent patches. (Skonhoft, 2007) notes that density-dependent dispersal is often not observed empirically and usually dispersal is of the sink-source type. Seasonal migration, which is a form of sink-source dispersal, has been documented for several animal species such as the African savannah elephant (Muchapondwa & Ngwaru, 2010; Van Aarde et al., 2008), the wildebeest (A. B. Johannesen & Skonhoft, 2004), reindeer and moose (Skonhoft, 2007) amongst others.

(Sanchirico & Wilen, 1999b) model an open access system with a spatially distributed resource over interconnected patches. They study the effects of profitability of a particular patch on the decision to harvest from that patch. Their model determines steady state equilibrium effort levels for each of the interconnected patches. Effort is shown to flow to patches with higher biomass and therefore higher profitability; the effort flows continue until a steady state is attained under open access and all rent is dissipated. (Muchapondwa & Ngwaru, 2010) model park managers' choices of anti-poaching enforcement levels in neighboring parks between which there is population migration. The park manager maximizes expected tourism benefits net of anti-poaching enforcement costs. Through comparative static exercises Muchapondwa and Ngwaru determine theoretical conditions under which unified park management is feasible given expected poaching levels and institutional heterogeneity in the constituent parks.

In this paper we consider the strategic interaction between a poaching unit and an anti-poaching unit in a manner that is different from previous studies in the literature. We develop a game-theoretic model of poaching and protection in the presence of a spatially and temporally distributed resource. The leaders of a poaching unit and an anti-poaching unit act strategically by choosing locations (patches/habitats) to poach and patrol. Uncertainty is introduced into the model through location choice strategies for poaching and patrolling. The number of animals killed versus the number of animals protected will be the stochastic outcome of a game that is played repeatedly between a poaching unit and an anti-poaching unit. We focus on the interactions between strategic players and determine the long-term effects of different strategies on the population dynamics of an endangered species.

(3) A Model of Poaching and Protection

Consider a "space" represented by a three-by-three grid as shown in Figure 1. The protected species population is distributed spatially and temporally across the nine patches or cells as and when seasonal migration takes place. In season one of the first year the population is distributed over seasonal patches 1, 2, & 3 in the row denoted season $s = 1$. In season two migration of the sub-populations in the three seasonal patches takes place from row $s = 1$ to row $s = 2$, when the sub-populations flow to the subsequent three seasonal patches. Migration routes follow a northward direction from season one through season three, and then turn southward in season four, returning to the seasonal patches 1, 2, & 3 at the beginning of season one in the subsequent year. Migration coefficients determine the population distribution across the grid, over the four seasons, in each year. Thereby the sub-populations are distributed in the seasonal patches 1, 2, & 3 in seasons one, two, three, and four in the rows denoted by season $s = 1$, $s = 2$, $s = 3$, and $s = 4$ respectively. The migration cycle continues year after year.

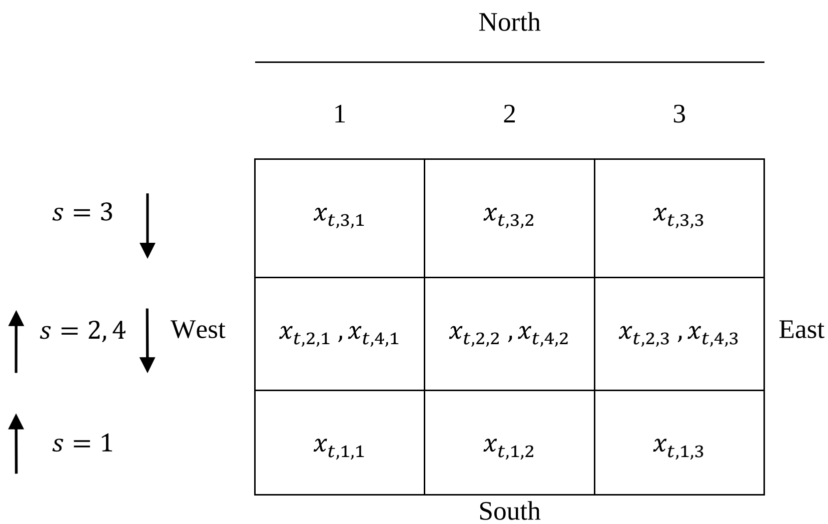


Figure 1: Space within which seasonal migration, poaching and anti-poaching patrolling take place.

Let us assume that there is one anti-poaching patrol/unit and one poaching unit operating per season. The poaching unit leader wants to choose a patch that has no patrol in it. At the same time the anti-poaching patrol leader wants to intercept the poaching unit by choosing the same patch, and thereby avoid losing a portion of the resident population to poaching. If the poaching unit selects a different patch from the patrol leader, the poaching unit kills some proportion of the resident patch's animal population. If both choose the same patch then the poaching unit is "decommissioned" for the rest of that year, but a new poaching unit forms in season one of the next year. In each season both unit leaders know the population distribution in the three seasonal patches. In season one of each year the population is augmented by the birth of juveniles from females that survive poaching and natural mortality in the previous year. We use the following notation for our model:

$i, j = 1, 2, 3$: seasonal patch index,
$\text{s} = 1, 2, 3, 4$: number of seasons within a year,
$t = 1, 2, \ldots, T$: year index,
$x_{t,s,i}$: species sub-population in time period t, in season s, in patch i.

$m_{s,j,i}$: migration coefficient for sub-population flowing from patch j in season s, to patch i in season $s+1$; $0 \leq m_{s,j,i} \leq 1$, $\sum_{i=1}^{3} m_{s,j,i} = 1$,
$0 < q \leq 1$: kill rate of the poaching unit,
$k_{t,s,i} = qx_{t,s,i} \geq 0$: population lost to poaching in year t, in season s, in patch i,
$x_{t,s+1,i} = m_{s,i,i}\left(x_{t,s,i} - k_{t,s,i}\right) + \sum_{j \neq i} m_{s,j,i}\left(x_{t,s,j} - k_{t,s,j}\right)$: species sub-population in year t, in season $s+1$, in patch i,
$x_{0,1,i}$: initial population distribution in $t = 0$, in $s = 1$, in patch i,

The surviving sub-populations at the end of season four of year t is augmented by the birth of juveniles in season one of the next year $t+1$ as per an *iterative map* (I) with $F(\cdot)$ denoting a population growth function:

$$x_{t+1,1,i} = \left\{m_{4,i,i}\left[x_{t,4,i} + F(\cdot) - k_{t,4,i}\right] + \sum_{j \neq i} m_{4,j,i}\left[x_{t,4,j} + F(\cdot) - k_{t,4,j}\right]\right\} \qquad \text{(I)}$$

Given the seasonal location of the species' sub-populations, the poaching unit leader and the patrol unit leader must make binary decisions $G_{t,s,i} = \{0, 1\}$ and $P_{t,s,i} = \{0, 1\}$ in season $s =$ 1, 2, 3, and 4, in patch $i =$1, 2, & 3. With only one patch chosen by the gang and the patrol we impose the requirement that $\sum_i G_{t,s,i} = 1$ and $\sum_i P_{t,s,i} = 1$.

(3.1) Payoffs and Strategies

The model can be viewed as a repeated game between smart opponents, with strategies potentially depending on the population distribution in the seasonal patches. We assume the poaching unit leader is a myopic poacher who maximizes the *expected* payoff in each season given the chosen strategy of the patrol leader. With myopic poaching in each season the anti-poaching patrol leader maximizes his own *expected* payoff, or minimizes the *expected* loss to poaching for a given population distribution. This brings us to the question of whether randomization might be optimal when the game is repeated. Antagonistic interactions between hosts and parasites have been modeled as *zero-sum games* to study the evolutionary fitness of strategies (Adami C, Schossau J, & Hintze A, 2012; Cohen & Newman, 1989; Kerr, Riley, Feldman, & Bohannan, 2002; Kirkup & Riley, 2004). A parasite may favor one distribution of possible strategies so as to maximize the mean change in its net reproductive rate. The host, in defending itself from the parasite, will favor a different distribution, one that minimizes the net reproductive rate of the parasite (Cohen & Newman, 1989). The value of the host-parasitic interaction may be defined as the mean change in net reproductive rate when evolutionary fitness forces the parasite to maximize the mean change in its net reproductive rate, given that the host is evolving (choosing strategies) by minimizing the net reproductive rate that the parasite can achieve. (Cohen & Newman, 1989) find that the best mean change in the parasite's net reproductive rate results from the randomization of strategies from stable distributions for parasites and hosts. For potential strategies in our poaching and protection game the poaching unit leader might consider randomizing using the population in the seasonal patches to generate a discrete distribution for selecting a patch in which to poach. The patrol leader might similarly generate a discrete distribution for selecting a patch in which to patrol. For ease of notation we drop the season (s) and time (t) subscripts of the sub-populations in the seasonal patches, and simply refer to $x_{t,s,1}$, $x_{t,s,2}$, $x_{t,s,3}$ as x_1, x_2, x_3 in **Figure 2**.

Seasonal patch 1	Seasonal patch 2	Seasonal patch 3
$x_{t,s,1} = x_1$	$x_{t,s,2} = x_2$	$x_{t,s,3} = x_3$

Figure 2: Population distribution in the seasonal patches shown in **Figure 1**.

As payoffs let us consider the following. If, for instance, in a given season the poaching unit leader chooses seasonal patch 1 and the patrol leader chooses another seasonal patch j ($\neq$ 1) then the gang leader achieves a payoff of qx_1, which is the population killed since the gang would have successfully evaded the anti-poaching patrol. The patrol leader therefore loses qx_1 of the population to poaching. If however both choose the same patch then the poaching unit is destroyed and there is no loss of that patch's resident population to poaching. Consequently the gang is destroyed and there are no gains for the poaching unit leader.[1] We assume that the cost of choosing a patch is zero for both the poaching unit and the patrol. We further assume that the gain to the patrol leader when choosing the same patch as the gang leader is only the amount of the resident species population that is not lost to poaching, i.e. zero. We can thereby formulate the payoffs and losses, to the gang and patrol respectively, as a zero-sum game. Since the kill rate of the poaching gang (q) is a common term we can ignore it in the payoff matrix shown in Figure 3.

		Patrol leader		
		Patch 1 (p_1)	Patch 2 (p_2)	Patch 3 (p_2)
Poaching unit leader	Patch 1 (g_1)	$0, 0$	$x_1, -x_1$	$x_1, -x_1$
	Patch 2 (g_2)	$x_2, -x_2$	$0, 0$	$x_2, -x_2$
	Patch 3 (g_3)	$x_3, -x_3$	$x_3, -x_3$	$0, 0$

Figure 3: Payoff matrix of the seasonal game.

[1] We ignore any monetary cost (such as poaching fines) to the poaching unit when decommissioned since this could be considered as a transfer from the poaching unit to the patrol with the same property of a zero-sum payoff in the game.

We denote the set of possible actions (patch choices of the poaching unit and the patrol leaders) as $L = \{1, 2, 3\}$. We denote $\Delta G = \{(g_1, g_2, g_3) \in \mathbb{R}^3 | (g_1, g_2, g_3) \geq 0 \,\&\, \sum_{i=1}^{3} g_i = 1\}$ as the set of probability distributions of the poaching unit/gang leader on L. Similarly we denote $\Delta P = \{(p_1, p_2, p_3) \in \mathbb{R}^3 | (p_1, p_2, p_3) \geq 0 \,\&\, \sum_{i=1}^{3} p_i = 1\}$ as the set of probability distributions of the patrol leader on L. $\pi_G(l_G, l_P)$ is the gang leader's payoff associated with the action pair $(l_G, l_P) \in L \times L$. The gang leader's expected payoff for a pair of mixed strategies $(g, p) \in \Delta G \times \Delta P$ would equal $E[\pi_G(g, p)] = \sum_{(l_G, l_P) \in L \times L} g(l_G) p(l_P)\, \pi_G(l_G, l_P)$. Similarly the patrol leader's expected payoff for a pair of mixed strategies $(p, g) \in \Delta P \times \Delta G$ would equal $E[\pi_P(p, g)] = \sum_{(l_P, l_G) \in L \times L} p(l_P) g(l_G)\, \pi_P(l_P, l_G)$.

The payoff matrix in Figure 3 shows that there are no dominant strategies for either the gang leader or the patrol leader. We use the property that any two-player game must have at least one Nash equilibrium (Gibbons, 1992) to derive a solution to the game. With no dominant strategies for either player the solution is that of a mixed strategy Nash equilibrium. We list the associated Nash equilibrium probabilities over the action spaces for the poaching unit leader and the patrol leader. The derivation of the mixed strategy Nash equilibrium and a proof of its uniqueness are provided in the Appendix.

$$g_1^* = \frac{x_2 x_3}{x_1 x_2 + x_2 x_3 + x_1 x_3}\,,\ g_2^* = \frac{x_1 x_3}{x_1 x_2 + x_2 x_3 + x_1 x_3}\,,\ g_3^* = \frac{x_1 x_2}{x_1 x_2 + x_2 x_3 + x_1 x_3}\,,$$

$$p_1^* = \frac{x_1 x_2 + x_1 x_3 - x_2 x_3}{x_1 x_2 + x_2 x_3 + x_1 x_3}\,,\ p_2^* = \frac{x_1 x_2 + x_2 x_3 - x_1 x_3}{x_1 x_2 + x_2 x_3 + x_1 x_3}\,,\ p_3^* = \frac{x_1 x_3 + x_2 x_3 - x_1 x_2}{x_1 x_2 + x_2 x_3 + x_1 x_3}\,.$$

In a system with *two seasonal patches* we can similarly derive the associated mixed strategy Nash equilibrium probabilities over the action spaces for the leaders of the poaching unit and the anti-poaching unit. The derivation and the uniqueness proof are provided in the Appendix.

$$g_1^* = \frac{x_2}{x_1 + x_2}\,,\ g_2^* = \frac{x_1}{x_1 + x_2}\,,$$

$$p_1^* = \frac{x_1}{x_1 + x_2}\,,\ p_2^* = \frac{x_2}{x_1 + x_2}\,.$$

In order to derive the intuition behind this result we turn to the two-player game of rock-paper-scissors. In the two player zero-sum game of rock-paper-scissors (Nouweland, 2007) analytically proves that, with equal payoffs for each of the three actions, the unique mixed strategy Nash equilibrium is to play each action with equal probability, i.e. one-third each. If however one were to modify the game of rock-paper-scissors with unequal payoffs then it can be shown that on average the players will each choose an action depending on the chances of that action defeating their opponent's chosen action in such a way that expected payoffs for each action tend towards zero in equilibrium.[2] Drawing from the zero-sum game of rock-paper-scissors with uneven payoffs we can infer an interpretation of the mixed strategy Nash equilibrium $\left((g_1^*, g_2^*, g_3^*), (p_1^*, p_2^*, p_3^*)\right)$ in the economic game of poaching and protection. The poaching unit leader's probability of choosing a location depends on how often he expects the patrol leader to choose the other location(s), given the seasonal population distribution. The patrol leader's probability of choosing a location to patrol depends on how often he expects the gang leader to choose that location, thereby minimizing the expected loss of population to poaching given the seasonal population distribution. We note that if the sub-populations were to be evenly distributed in a season then the mixed strategy Nash equilibrium values would be exactly $\left(({}^1/_3, {}^1/_3, {}^1/_3), ({}^1/_3, {}^1/_3, {}^1/_3)\right)$ in the three seasonal patches system, and $\left(({}^1/_2, {}^1/_2), ({}^1/_2, {}^1/_2)\right)$ in the two seasonal patches system.

(3.2) Numerical Analysis

Having derived a mixed strategy Nash equilibrium in our game of poaching and protection we proceed to study the effect of this strategy on the population dynamics of an endangered species. The model is applied to the case of the migratory savannah elephant (*Loxodonta africana*). The logistic growth function is often used to model elephant population dynamics (E. H. Bulte & van Kooten, 1999b; Milner-Gulland & Leader-Williams, 1992). Following (Milner-Gulland & Leader-Williams, 1992) we adopt a skewed-logistic specification for the population growth function $F(x) = x + rx(1 - (x/c)^z)$. x is the population, r is the intrinsic net growth rate of population, c is the habitat carrying capacity, and z is a skew parameter. The surviving adult population at the end of season four of year t is augmented by the birth of juveniles in season one of the next year $t + 1$ as per the *iterative map* previously defined in (I):

$$x_{t+1,1,i} = \Big\{ m_{4,i,i} \left[x_{t,4,i} \left(1 + r\left(1 - \left(x_{t,4,i}/c_i\right)^z\right)\right) - k_{t,4,i} \right] + \sum_{j \neq i} m_{4,j,i} \left[x_{t,4,j} \left(1 + r\left(1 - \left(x_{t,4,j}/c_j\right)^z\right)\right) - k_{t,4,j} \right] \Big\}$$

Adult female elephants give birth to approximately one offspring every three years, which implies a population pregnancy rate of approximately 0.33 per year (Armbruster & Lande, 1993). The average natural mortality rate of elephants has been estimated at 0.27, which implies a net intrinsic growth rate of $r = 0.06$ (Armbruster &

[2] For example if the wining payoffs to rock, paper, and scissors are 1, 3, and 5 (i.e. rock beating only scissors with a payoff of 1, paper beating only rock with a payoff of 3, and scissors beating only paper with a payoff of 5), then it can be shown that players would choose to play rock with 5/9th probability, paper with 1/9th probability, and scissors with 3/9th probability.

Lande, 1993). A skew parameter greater than one ($z > 1$) is used to model population dynamics of large mammals (Cromsigt, Hearne, Heitkonig, & Prins, 2002); (E. H. Bulte & van Kooten, 1999b; Milner-Gulland & Leader-Williams, 1992) set $z = 7$. We normalize the carrying capacity of the seasonal "space" to one (i.e. $\sum_i c_i = 1$), and assume it to be equally divided between the seasonal patches.

Using the data of (E. H. Bulte & van Kooten, 1999b) on illegal off-take of elephants in African range states we calculate the off-take rates as varying between 0.03% and 3.8% of the resident elephant population in the mid-1990s. Noting the reports of organized criminal syndicates involved in elephant and rhino poaching in African range states (Mullen & Zhang, 2012; Sas-Rolfes, 2012; Shukman, 2013; Wassener, 2013; S. K. Wasser et al., 2008) it is likely that the scale and intensity of poaching has increased since the 1990s. A 2006-07 report (Blanc, 2007) of savannah elephant population totals by region listed the elephant population in Southern Africa at approximately 300,000. Based on data from seizures of illegal ivory shipments amounting to roughly 24 tons in the year 2006 Wasser *et. al.* (2007) use DNA analysis to estimate that approximately 23,000 savannah elephants were illegally harvested from the southern African range states. This evidence suggests an illegal off-take rate of approximately 7% to 8% in the year 2006. For the base-case set of parameters in the model we assume a poaching off-take/ kill rate of $q = 0.07$. Table 1 lists the base-case values of the model's parameters.

Table 1: Model base-case parameter values

Parameter		Value	Source
Intrinsic growth rate	$r =$	0.06	(Armbruster & Lande, 1993)
Logistic growth skew parameter	$z =$	7	(E. H. Bulte & van Kooten, 1999b; Milner-Gulland & Leader-Williams, 1992)
Poaching/off-take rate	$q =$	0.07	Based on data from Wasser *et. al.* (2007)
Initial sub-populations	$x_{0,1,i} =$	0.15 ($i = 1,2,3$)	
Carrying capacity	$\sum_i c_i =$	1	
Number of time periods	$T =$	100	

We assume an evenly distributed initial elephant population of $E_{0,1,1} = 0.15$, $E_{0,1,2} = 0.15$, and $E_{0,1,3} = 0.15$, and the following migration coefficients for the spatial-temporal dispersal of the sub-populations in the space of Figure 1.

Table 2: Seasonal migration coefficients

$s = 1$:	$m_{1,1,4} = 0.4$	$m_{1,1,5} = 0.3$	$m_{1,1,6} = 0.3$
	$m_{1,2,4} = 0.3$	$m_{1,2,5} = 0.5$	$m_{1,2,6} = 0.2$
	$m_{1,3,4} = 0.1$	$m_{1,3,5} = 0.3$	$m_{1,3,6} = 0.6$
$s = 2$:	$m_{2,4,7} = 0.2$	$m_{2,4,8} = 0.5$	$m_{2,4,9} = 0.3$
	$m_{2,5,7} = 0.1$	$m_{2,5,8} = 0.4$	$m_{2,5,9} = 0.5$
	$m_{2,6,7} = 0.1$	$m_{2,6,8} = 0.4$	$m_{2,6,9} = 0.5$
$s = 3$:	$m_{3,7,4} = 0.5$	$m_{3,7,5} = 0.3$	$m_{3,7,6} = 0.2$
	$m_{3,8,4} = 0.4$	$m_{3,8,5} = 0.5$	$m_{3,8,6} = 0.1$
	$m_{3,9,4} = 0.2$	$m_{3,9,5} = 0.3$	$m_{3,9,6} = 0.5$
$s = 4$:	$m_{4,4,1} = 0.6$	$m_{4,4,2} = 0.2$	$m_{4,4,3} = 0.2$
	$m_{4,5,1} = 0.4$	$m_{4,5,2} = 0.5$	$m_{4,5,3} = 0.1$
	$m_{4,6,1} = 0.1$	$m_{4,6,2} = 0.2$	$m_{4,6,3} = 0.7$

As noted previously in the setup of the game the poaching unit leader wants to choose a patch with no patrol, and the anti-poaching patrol leader wants to choose the same patch. If different patches are selected the poaching unit kills some proportion (q) of the resident population. If both choose the same patch then the poaching unit is “de-commissioned” for the rest of that year, but a new poaching unit forms in season one of the next year. Given initial conditions, the model parameters in Table 1, and the set of migration coefficients the stochastic process of poaching and protection will cause the elephant population to evolve stochastically over T years. We simulate approach paths for a period of $T = 100$ years, i.e. 400 seasons, to provide insight into the long-term effects of location strategies on the population dynamics. Qualitatively different approach paths would arise depending on the type of strategy chosen by the poaching unit/gang and patrol leaders.

We first study the effect on elephant population dynamics when the gang leader and the patrol leader randomize their seasonal location choices based on their respective mixed strategy Nash equilibrium probabilities.

Mixed strategy Nash equilibrium randomness:

$$\big((g_1, g_2, g_3), (p_1, p_2, p_3)\big) = \big((g_1^*, g_2^*, g_3^*), (p_1^*, p_2^*, p_3^*)\big)$$

Next we study the effect on elephant population dynamics when the gang leader and the patrol leader randomize their location choices uniformly with equal probability of choosing any of the seasonal locations.

Mixed strategy uniform randomness:

$$\big((g_1, g_2, g_3), (p_1, p_2, p_3)\big) = \big((1/3\,, 1/3\,, 1/3), (1/3\,, 1/3\,, 1/3)\big)$$

Given the previous two sets of strategies we consider two possible combinations of them. This can be used to determine if there is incentive for either the patrol leader or the gang leader to deviate from the Nash equilibrium. In the first combination the patrol leader chooses the mixed Nash equilibrium strategy and the gang leader deviates by choosing the uniform mixed strategy. In the second combination we look at the opposite case where the patrol leader deviates by choosing the uniform mixed strategy and the gang leader plays the Nash mixed strategy.

Mixed strategy: *Uniform and Nash equilibrium randomness*

$$\big((g_1, g_2, g_3), (p_1, p_2, p_3)\big) = \big((1/3\,, 1/3\,, 1/3), (p_1^*, p_2^*, p_3^*\,)\big)$$

or

$$\big((g_1, g_2, g_3), (p_1, p_2, p_3)\big) = \big((g_1^*, g_2^*, g_3^*\,), (1/3\,, 1/3\,, 1/3)\big)$$

Lastly we consider the effect on population dynamics when the strategy of the patrol leader is to patrol the patch with the highest species sub-population. The strategy of the gang leader is to select in the patch with the next highest sub-population.

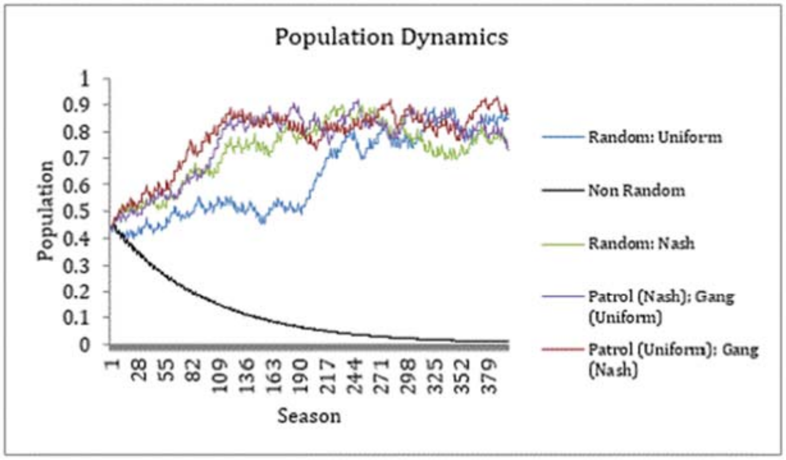
Non-random strategy:

$$l_P = i, \qquad E_{t,s,i} \geq E_{t,s,j}\ (i \neq j)$$
$$l_G = j, \qquad E_{t,s,i} \geq E_{t,s,j}\ (i \neq j)$$

Population dynamics and the average payoffs to the patrol and gang leaders under the different strategies as listed are compared with that of the mixed strategy Nash equilibrium. Figure 4 charts the results of a single simulation for each of the strategy sets over the one hundred year time horizon for the set of base-case model parameters. The simulations are repeated one thousand times and the average population and poaching levels are reported on the right-hand side panel of Figure 4. The mixed Nash strategy is shown in green; the uniform random strategy is shown in blue; the combination of the patrol leader playing the Nash mixed strategy and the gang leader playing the uniform random mixed strategy is shown in purple; the combination of the gang leader playing the Nash mixed strategy and the patrol leader playing the uniform random mixed strategy is shown in red; and finally the non-random strategy is shown in black. Each of the random strategies appear to have the effect of leading to higher elephant population over time when compared with the non-random strategy. For each of the strategy sets we list the average values of population and poaching from season two hundred to season four hundred, or the period of time when a stable distribution of population is attained. This reduces the effect of the initial conditions on the average values.

Let us study the average values of population and poaching of Figure 4 a little more closely. The average values of population and poaching are 0.82516 and 0.00745 in the mixed strategy Nash equilibrium. This is what the patrol leader and the gang leader can expect on average. Now we ascertain if there is incentive for either party to deviate from playing the Nash mixed strategy. If the gang leader deviates by playing the uniform strategy while the patrol leader continues playing the Nash strategy we note that the average poaching level declines to 0.00739 and the average population increases to 0.82657 which is statistically greater than the Nash equilibrium value at the ten percent error level. There is therefore no incentive for the gang leader to deviate from playing the Nash strategy. If the patrol leader deviates from playing the Nash strategy by playing the uniform random strategy, while the gang leader continues to play the Nash strategy the patrol leader is better off since the average population increases to 0.83374 and the average poaching level declines to 0.00724. The average population level is also statistically greater than the Nash equilibrium value at the one percent error level. Since the gang leader is worse off he will consider playing the uniform random strategy as well and increase his average payoff- poaching value- to 0.00761. The average population value declines to 0.81551, which is statistically lower than the Nash equilibrium value at the one percent error level. This creates a disincentive for both the patrol leader and the gang leader to deviate from playing the mixed strategy Nash equilibrium.

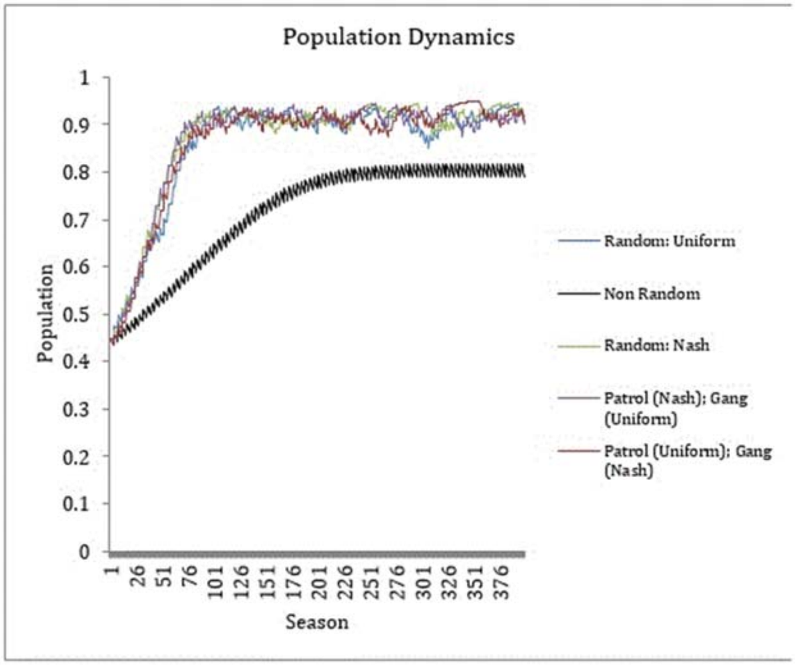
We carry out further numerical analyses by varying the poaching gang's kill rate, q, between 3% and 12% to account for a wide range of poaching efficiency rates. The simulation results are plotted in Figures 5 through 9 for $q = 3\%$, 5%, 8%, 10%, and 12%. We note that for q between 3% and 8% the broad results are similar to the base-case when $q = 7\%$. The differences in average population levels are statistically different from the Nash equilibrium average values. Apart from $q = 3\%$ we note that the random strategies achieve higher average payoffs for both the patrol leader and the gang leader. Similar to the results in Figure 4 the simulated average values of population and poaching in Figure 5, Figure 6, and Figure 7 suggest that the Nash mixed strategy is a unique equilibrium on average. When the poaching off-take/ kill rate is increased to $q \geq 10\%$ we begin to notice that the differences in average poaching become statistically significant when compared with the average Nash equilibrium values. The population distributions are no longer stable and the variance increases dramatically. One thing that we do note is that the uniform random strategy does worse than the Nash for both leaders. When $q = 12\%$ we see that the elephant sub-population begin a slow decline towards extinction for each of the random strategies. The non-random strategies always results a very quick decline towards extinction.



	Average Population $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{g=200}^{400} E_g}{400-200}\right)_n}{1000}$	Average Poaching $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{g=200}^{400} K_g}{400-200}\right)_n}{1000}$
Random: Uniform	0.81551 (9.0997)***	0.00761 (-0.4540)
Random: Nash	0.82516	0.00745
Patrol (Nash); Gang (Uniform)	0.82657 (-1.3756)*	0.00739 (0.1409)
Patrol (Uniform); Gang (Nash)	0.83374 (-8.4142)***	0.00724 (0.5557)
Non Random	0.02395 (649.97)***	0.00059 (26.89)***

Figure 4: Population and poaching dynamics with initial population set at 0.45, and poaching off-take set at $q = 0.07$

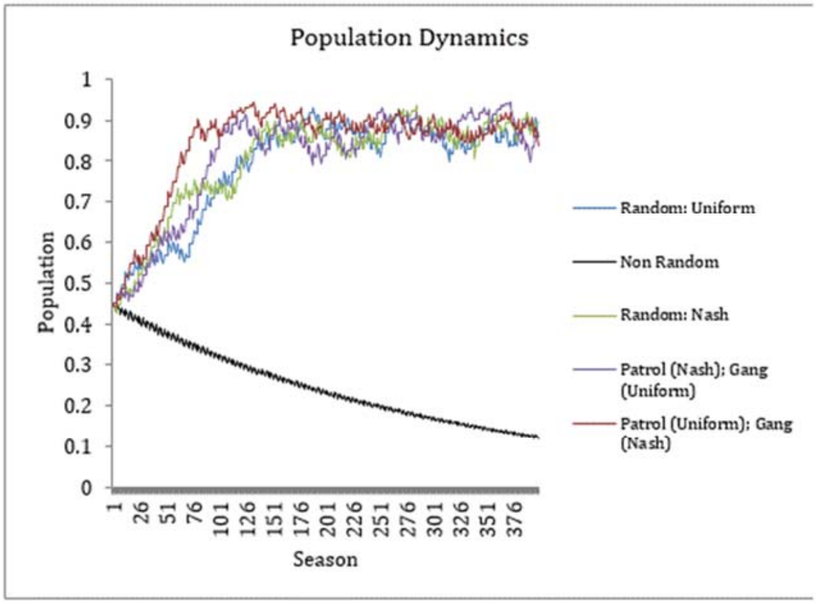
t-statistics of difference of means between Nash equilibrium value and other strategy's equilibrium value in (parentheses). *** statistically significant mean difference at 1% error level; ** statistically significant mean difference at 5% error level; * statistically significant mean difference at 10% error level.



	Average Population $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=200}^{400} E_s}{400-200}\right)_n}{1000}$	**Average Poaching** $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=200}^{400} K_s}{400-200}\right)_n}{1000}$
Random: Uniform	0.91152 (1.7298)**	0.00363 (-0.4554)
Random: Nash	0.91234	0.00355
Patrol (Nash); Gang (Uniform)	0.91317 (-1.7636)**	0.00350 (0.2926)
Patrol (Uniform); Gang (Nash)	0.91349 (-2.4717)***	0.00346 (0.5369)
Non Random	0.80046 (123.8)***	0.00856 (-35.94)***

Figure 5: Population and poaching dynamics with initial population set at 0.45, and poaching off-take set at $\boldsymbol{q = 0.03}$

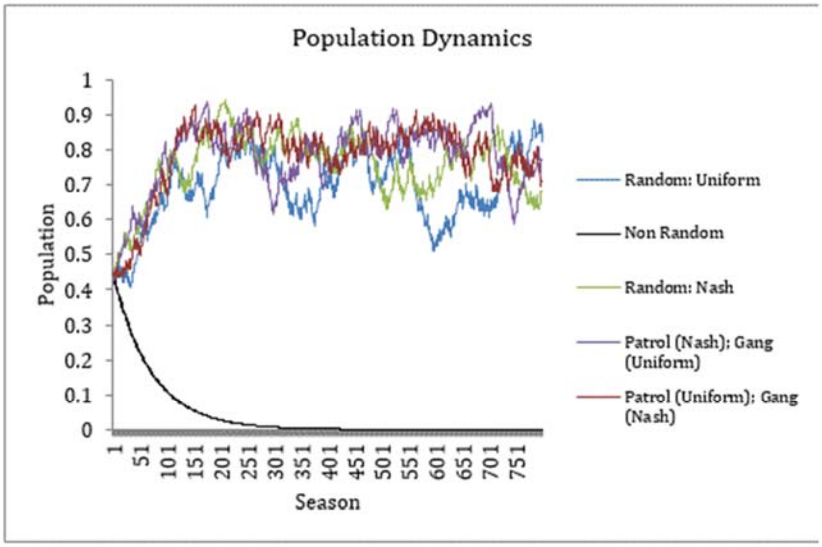
t-statistics of difference of means between Nash equilibrium value and other strategy's equilibrium value in (parentheses). *** statistically significant mean difference at 1% error level; ** statistically significant mean difference at 5% error level; * statistically significant mean difference at 10% error level.



	Average Population $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=200}^{400} E_s}{400-200}\right)_n}{1000}$	Average Poachin $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=200}^{400} K}{400-20}\right.}{1000}$
Random: Uniform	0.87432 (4.3353)***	0.00582 (-0.5483)
Random: Nash	0.87764	0.00568
Patrol (Nash); Gang (Uniform)	0.87913 (-1.9778)**	0.00559 (0.3412)
Patrol (Uniform); Gang (Nash)	0.88081 (-4.2492)***	0.00551 (0.5989)
Non Random	0.17331 (298.3)***	0.00309 (13.22)***

Figure 6: Population and poaching dynamics with initial population set at 0.45, and poaching off-take set at $q = 0.05$

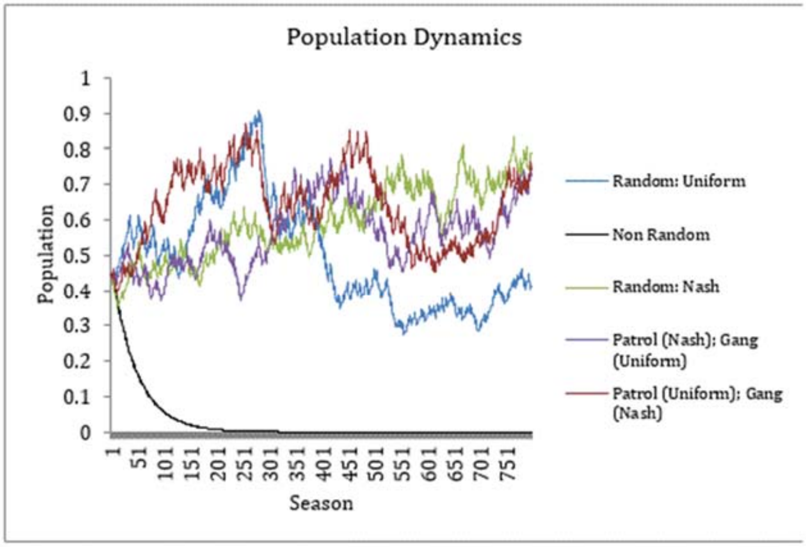
t-statistics of difference of means between Nash equilibrium value and other strategy's equilibrium value in (parentheses). *** statistically significant mean difference at 1% error level; ** statistically significant mean difference at 5% error level; * statistically significant mean difference at 10% error level.



	Average Population $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=800}^{1000} E_s}{1000-800}\right)_n}{1000}$	**Average Poachin** $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=800}^{1000} K}{1000-8}\right.}{1000}$
Random: Uniform	0.7786 (8.4741)***	0.00819 (-0.0535)
Random: Nash	0.7879	0.00817
Patrol (Nash); Gang (Uniform)	0.7918 (-3.6103)***	0.00806 (0.2664)
Patrol (Uniform); Gang (Nash)	0.7998 (-10.998)***	0.00799 (0.4408)
Non Random	0.0000 (1030.9)***	0.0000 (29.41)***

Figure 7: Population and poaching dynamics with initial population set at 0.45, and poaching off-take set at $q = 0.08$

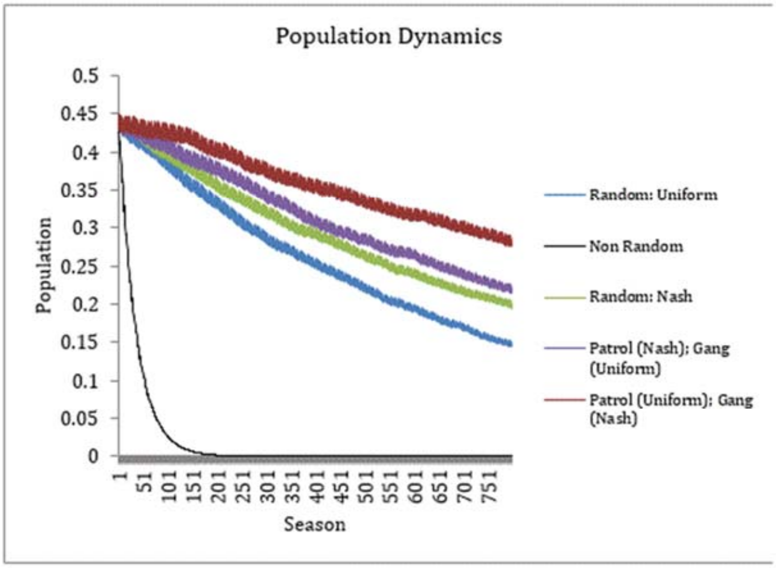
t-statistics of difference of means between Nash equilibrium value and other strategy's equilibrium value in (parentheses). *** statistically significant mean difference at 1% error level; ** statistically significant mean difference at 5% error level; * statistically significant mean difference at 10% error level.



	Average Population $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=800}^{1000} E_s}{1000-800}\right)_n}{1000}$	Average Poaching $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=800}^{1000} K_s}{1000-800}\right)}{1000}$
Random: Uniform	0.56298 (59.032)***	0.00746 (1.6930)**
Random: Nash	0.62530	0.00809
Patrol (Nash); Gang (Uniform)	0.63735 (-10.923)***	0.00816 (-0.1502)
Patrol (Uniform); Gang (Nash)	0.66922 (-39.65)***	0.00838 (-0.6697)
Non Random	0.00000 (825.1)***	0.00000 (29.0)***

Figure 8: Population and poaching dynamics with initial population set at 0.45, and poaching off-take set at $q = 0.10$

t-statistics of difference of means between Nash equilibrium value and other strategy's equilibrium value in (parentheses). *** statistically significant mean difference at 1% error level; ** statistically significant mean difference at 5% error level; * statistically significant mean difference at 10% error level.



	Average Population $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=800}^{1000} E_s}{1000-800}\right)_n}{1000}$	**Average Poaching** $\frac{\sum_{n=1}^{1000}\left(\frac{\sum_{s=800}^{1000} K_s}{1000-800}\right)_n}{1000}$
Random: Uniform	0.13063 (50.05)***	0.00205 (6.013)***
Random: Nash	0.18026	0.00279
Patrol (Nash); Gang (Uniform)	0.20532 (-25.22)***	0.00310 (-2.036)**
Patrol (Uniform); Gang (Nash)	0.26669 (-82.98)***	0.00398 (-6.512)***
Non Random	0.00000 (243.6)***	0.00000 (28.18)***

Figure 9: Population and poaching dynamics with initial population set at 0.45, and poaching off-take set at $q = 0.12$

t-statistics of difference of means between Nash equilibrium value and other strategy's equilibrium value in (parentheses). *** statistically significant mean difference at 1% error level; ** statistically significant mean difference at 5% error level; * statistically significant mean difference at 10% error level.

(4) Discussion and Conclusion

The numerical analysis provides some key results in this paper. We observe that when both the anti-poaching unit/patrol leader and the poaching unit/gang leader play their mixed strategy Nash equilibrium strategies they achieve higher payoffs on average as compared with the uniform random strategy. This holds true for a wide range in values for the poaching efficiency parameter, q. The numerical analysis also reveals that on average there is no incentive for either the patrol leader or the gang leader to deviate from the Nash equilibrium. This occurs in the range $3\% \leq q \leq 8\%$, i.e. when we observe stable distributions of population over a long time horizon. This corroborates the analytical proof of the uniqueness of the mixed strategy Nash equilibrium. The base-case value of $q = 7\%$ is estimated from secondary data in the literature. We have considered what would occur if q were to increase i.e. poaching units/gangs become more effective. The population distributions are no longer stable, the variances in the distributions increase significantly, and the sub-populations start to descend towards extinction over time.

The different random strategies achieve higher payoffs for both the leaders compared to the non-random strategy. This result mirrors findings from other studies on evolutionary fitness of strategies in zero-sum antagonistic games between strategic opponents (Adami C et al., 2012; Cohen & Newman, 1989; Kerr et al., 2002; Kirkup & Riley, 2004). The numerical results also suggest that non-random strategies lead to extinction of sub-populations when q increases. The incentive for both the patrol leader and the gang leader to deviate from playing the Nash strategy is stronger once the poaching off-take rate increases beyond eight percent. The differences in average payoffs between the Nash strategies and other random strategies become statistically significant. At the same time however we observe that the population stocks decline rapidly, and that population distributions are no longer stable.

We noted earlier that the mixed strategy Nash equilibrium probabilities would be identical to those of the uniform random strategy if the sub-populations were evenly distributed across seasonal patches in the conceptual space. The probabilistic nature of choosing patches by both the patrol leader and the gang leader, in conjunction with the set of migration coefficients, leads to uneven seasonal population distributions in our numerical analyses. We have confirmed that the Nash strategy is superior to the uniform random strategy for both the patrol leader and the gang leader. The superiority of the Nash strategy stems from the nature of the game of poaching and protection, in that the players behave strategically with each other. Deviations from the Nash for either player would merit careful consideration.

This paper has considered the theoretical implications of optimal strategies on the population dynamics of an endangered species. The model is generally applicable to other species, and it can also be scaled up for more realistic analysis. Different growth functions and biological parameters can be used in the model to better suit the modeling of different species' population dynamics. The set of migration coefficients in Table 2 can be modified to reflect different proportions of the sub-populations that migrate from one patch to another. For simplicity we assumed a costless choice of patch to poach and patrol in the conceptual space. The model can be modified to account for heterogeneity in patrolling and poaching costs in the different seasonal patches. The model can be applied to an empirical setting if data were to be made available on poaching and patrolling. In scaling up this model one could think about adding more seasonal patches in the space, adding more anti-poaching units/patrols, and adding more poaching units/gangs to reflect a more realistic setting.

As we noted earlier (E. Bulte et al., 2004)state that models which link ecological theory and natural resource economics should expand their scope beyond the notion of steady state equilibrium by incorporating variability, complexity, scale, and uncertainty into economic models. Our paper has considered purely the strategic aspects of poaching and protection when smart opponents face each other. We introduced uncertainty into our model through the strategic location choices of a poaching unit and an anti-poaching patrol. Spatial-temporal strategic decisions by the poaching unit and the anti-poaching patrol caused the number of elephants killed to become a stochastic process. The model provides insight into the effects of different strategies on the long-term population dynamics of an endangered species, and thereby links the spatial-temporal dynamics of species migration with the economic game of poaching and protection.

Acknowledgements

Adrian Lopes gratefully acknowledges the Joseph L. Fisher Dissertation Award from Resources for the Future, and the Andrew W. Mellon Student Grant from the Cornell University Graduate School, both of which have supported this research.

Appendix: Derivation of the mixed strategy Nash equilibrium, and a proof of its uniqueness

(Nouweland, 2007) lists three conditions for the existence of a mixed strategy Nash equilibrium in two-player zero-sum games.

Condition 1: A pair of mixed strategies (g, p) is a mixed Nash equilibrium if and only if the strategy of one player (gang leader) is a best response to the strategy of the other player (patrol leader) and vice-versa.

Condition 2: If (g, p) $\left((p, g)\right)$ is a strategy profile and every action $l_G \in L$ $(l_P \in L)$ that the gang (patrol) leader plays with positive probability $g(l_G) > 0$ $(p(l_P) > 0)$ is at least as good a response to p (g) as every other action, then g (p) is a best response to p (g). For the gang (patrol) leader this would mean $E[\pi_G(l_G, p)] \geq E[\pi_G(l'_G, p)]$ $(E[\pi_P(l_P, g)] \geq E[\pi_P(l'_P, g)])$ for all $l'_G \in L$ $(l'_P \in L)$.

Condition 3: If $g \in \Delta G$ $(p \in \Delta P)$ is a best response to $p \in \Delta P$ $(g \in \Delta G)$ and the gang (patrol) leader plays action $l_G \in L$ $(l_P \in L)$ with a positive probability, i.e. $g(l_G) > 0$ $(p(l_P) > 0)$, then l_G (l_P) is at least as good a response to p (g) as every other action. For the gang (patrol) leader this would mean $E[\pi_G(l_G, p)] \geq E[\pi_G(l'_G, p)]$ $(E[\pi_P(l_P, g)] \geq E[\pi_P(l'_P, g)])$ for all $l'_G \in L$ $(l'_P \in L)$.

Using *Condition 1* we can state that a pair of mixed strategies (g, p) is a mixed strategy Nash equilibrium if, for the gang (patrol) leader and every alternative mixed strategy $g' \in \Delta G$ $(p' \in \Delta P)$ of the gang (patrol) leader, it holds that $E[\pi_G(g', p)] \leq E[\pi_G(g, p)]$ $(E[\pi_P(p', g)] \leq E[\pi_P(p, g)])$. This entails that at a Nash equilibrium a player in the game will be indifferent between the action choices when the expected payoffs from these actions are equal to each other i.e. $E[\pi_G(i, p)] = E[\pi_G(j, p)]$ and $E[\pi_P(g, i)] = E[\pi_P(g, j)]$ where $i, j = 1,2, \ldots, n$ and $i \neq j$. Given the payoff matrix in Figure 3 we can define the associated expected payoffs to the gang leader and the patrol leader for the individual location choices or actions. When there are two seasonal patches i.e. $n = 2$, we have the expected payoffs for the gang leader of choosing patches 1 and 2.

$$\mathrm{E}[\pi_G(1, p)] = p_1.0 + p_2.x_1 \quad (1)$$
$$\mathrm{E}[\pi_G(2, p)] = p_1.x_2 + p_2.0 \quad (2)$$

Similarly we define the expected payoffs for the patrol leader of choosing patches 1 and 2.

$$\mathrm{E}\big[\pi_p(g, 1)\big] = g_1.0 - g_2.x_2 \quad (3)$$
$$\mathrm{E}[\pi_P(g, 2)] = g_2.0 - g_1.x_1 \quad (4)$$

Setting (1) = (2) and (3) = (4) we solve for the Nash equilibrium values of the system with *two* seasonal patches.

$$g_1^* = \frac{x_2}{x_1+x_2},\ g_2^* = \frac{x_1}{x_1+x_2},\ p_1^* = \frac{x_1}{x_1+x_2}, \text{ and } p_2^* = \frac{x_2}{x_1+x_2}.$$

When there are three seasonal patches i.e. $n = 3$, we have the expected payoffs for the gang leader of choosing patches 1, 2, and 3.

$$E[\pi_G(1, p)] = p_1.0 + p_2.x_1 + p_3.x_1 \quad (5)$$
$$E[\pi_G(2, p)] = p_1.x_2 + p_2.0 + p_3.x_2 \quad (6)$$
$$E[\pi_G(3, p)] = p_1.x_3 + p_2.x_3 + p_3.0 \quad (7)$$

Similarly we define the patrol leader's expected payoffs for his actions of choosing seasonal locations a, b, & c.

$$E[\pi_P(g,1)] = -g_2.x_2 - x_3 + g_1.x_3 + g_2.x_3 \quad (8)$$
$$E[\pi_P(g,2)] = -g_1.x_1 - x_3 + g_1.x_3 + g_2.x_3 \quad (9)$$
$$E[\pi_P(g,3)] = -g_1.x_1 - g_2.x_2 \quad (10)$$

Setting (5) = (6) = (7), and (8) = (9) = (10), and using that $g_3 = 1 - g_1 - g_2$ and $p_3 = 1 - p_1 - p_2$ we solve for the Nash equilibrium values of the system with *three* seasonal patches.

$$g_1^* = \frac{x_2x_3}{x_1x_2+x_2x_3+x_1x_3},\ g_2^* = \frac{x_1x_3}{x_1x_2+x_2x_3+x_1x_3},\ g_3^* = \frac{x_1x_2}{x_1x_2+x_2x_3+x_1x_3},$$

$$p_1^* = \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3},\ p_2^* = \frac{x_1x_2+x_2x_3-x_1x_3}{x_1x_2+x_2x_3+x_1x_3},\ p_3^* = \frac{x_1x_3+x_2x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}.$$

First we prove the uniqueness of the Nash equilibrium for the system with *two* seasonal patches. We use the approach followed by (Nouweland, 2007) who uses *Condition 2* and *Condition 3* to show that a mixed strategy, which is not the Nash equilibrium, cannot be a best response to any strategy that is a best response to it. We derive the following useful identities, which equal zero at the Nash equilibrium values. Any deviations from the Nash equilibrium values would mean that the identities would no longer equal zero.

(1) – (2): $E[\pi_G(1,p)] - E[\pi_G(2,p)] = p_2.x_1 - p_1.x_2$
(3) – (4): $E[\pi_P(g,1)] - E[\pi_P(g,2)] = g_1.x_1 - g_2.x_2$

Consider the first case of the gang leader deviating from the Nash equilibrium: $g_1 > \frac{x_2}{x_1+x_2}$, $g_2 < \frac{x_1}{x_1+x_2}$. We will accordingly have (3) – (4) $>$ 0, and by *Condition 2* we know that $p_2 = 0$. But if $p_2 = 0$ then we will have (1) – (2) $<$ 0, and by *Condition 3* we know that $g_1 = 0$, which contradicts $g_1 > \frac{x_2}{x_1+x_2}$ for $x_1, x_2 > 0$. In the second case of the gang leader deviating from the Nash equilibrium we consider $g_1 < \frac{x_2}{x_1+x_2}$, $g_2 > \frac{x_1}{x_1+x_2}$. We will accordingly have (3) – (4) $<$ 0, and by *Condition 2* we know that $p_1 = 0$. But if $p_1 = 0$ then we will have (1) – (2) $>$ 0, and by *Condition 3* we know that $g_2 = 0$, which contradicts $g_2 > \frac{x_1}{x_1+x_2}$ for $x_1, x_2 > 0$. The other two cases of the gang leader deviating from the Nash equilibrium i.e. $g_1 > \frac{x_2}{x_1+x_2}$ & $g_2 > \frac{x_1}{x_1+x_2}$, and $g_1 < \frac{x_2}{x_1+x_2}$ & $g_2 < \frac{x_1}{x_1+x_2}$ are mathematically not feasible since $g_1 + g_2 = 1$ by definition, and the latter two cases violate this condition.

Let us now consider the first case of the patrol leader deviating from the Nash equilibrium: $p_1 > \frac{x_1}{x_1+x_2}$, $p_2 < \frac{x_2}{x_1+x_2}$. We will accordingly have (1) – (2) < 0, and by *Condition 2* we know that $g_1 = 0$. But if $g_1 = 0$ then we will have (3) – (4) < 0, and by *Condition 3* we know that $p_1 = 0$, which contradicts $p_1 > \frac{x_1}{x_1+x_2}$ for $x_1, x_2 > 0$. In the second case of the patrol leader deviating from the Nash equilibrium we consider $p_1 < \frac{x_1}{x_1+x_2}$, $p_2 > \frac{x_2}{x_1+x_2}$. We will accordingly have (1) – (2) > 0, and by *Condition 2* we know that $g_2 = 0$. But if $g_2 = 0$ then we will have (3) – (4) > 0, and by *Condition 3* we know that $p_2 = 0$, which contradicts $p_2 > \frac{x_2}{x_1+x_2}$ for $x_1, x_2 > 0$. The other two cases of the patrol leader deviating from the Nash equilibrium i.e. $p_1 > \frac{x_1}{x_1+x_2}$ & $p_2 > \frac{x_2}{x_1+x_2}$, and $p_1 < \frac{x_1}{x_1+x_2}$ & $p_2 < \frac{x_2}{x_1+x_2}$ are mathematically not feasible since $p_1 + p_2 = 1$ by definition, and the latter two cases violate this condition. This proves that a mixed strategy other than the Nash equilibrium is not a best response to any mixed strategy that is a best response to it. Using *Condition 1* we have shown that there is no mixed strategy Nash equilibrium in which the patrol leader and gang leader plays a strategy that is different from $\left((g_1^*, g_2^*), (p_1^*, p_2^*)\right)$ in a system with *two* seasonal patches. ■

Now we prove the uniqueness of the Nash equilibrium for a system with *three* seasonal patches. Again we make use of the following identities that equal zero at the Nash equilibrium values.

(5) – (6): $E[\pi_G(1,p)] - E[\pi_G(2,p)] = x_1 - x_2 - p_1.x_1 + p_2.x_2$
(5) – (7): $E[\pi_G(1,p)] - E[\pi_G(3,p)] = x_1 - p_1.x_1 - p_1.x_3 - p_2.x_3$
(8) – (9): $E[\pi_P(g,1)] - E[\pi_P(g,2)] = g_1.x_1 - g_2.x_2$
(8) – (10): $E[\pi_P(g,1)] - E[\pi_P(g,3)] = g_1.x_1 - g_3.x_3$

Consider the first case of the gang leader deviating from the Nash equilibrium: $g_1 > \frac{x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$, $g_2 > \frac{x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$, & $g_3 < \frac{x_1x_2}{x_1x_2+x_2x_3+x_1x_3}$. The sign of (8) – (9) is ambiguous, while the sign of (8) – (10) is unambiguously greater than zero. Suppose (8) – (9) ≥ 0 and (8) – (10) > 0. Then by *Condition 2* we know that $p_2 = 0$ and $p_3 = 0$. This would imply that (5) $= 0$, (6) > 0, & (7) > 0. This in turn would imply that (5) – (6) < 0 and (5) – (7) < 0. Using *Condition 3* we know that $g_1 = 0$, which contradicts $g_1 > \frac{x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$. Now suppose (8) – (9) < 0 and (8) – (10) > 0. By *Condition 2* we know that $p_1 = 0$ and $p_3 = 0$. This implies that (5) > 0, (6) $= 0$, & (7) > 0. This would imply that (5) – (6) > 0, and using *Condition 3* we would have $g_2 = 0$, which contradicts $g_2 > \frac{x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$.

The proof by contradiction in the case of $g_1 > \frac{x_2 x_3}{x_1x_2+x_2x_3+x_1x_3}$, $g_2 < \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$, & $g_3 > \frac{x_1 x_2}{x_1x_2+x_2x_3+x_1x_3}$ holds by symmetry. The case of $g_1 > \frac{x_2 x_3}{x_1x_2+x_2x_3+x_1x_3}$, $g_2 < \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$, & $g_3 < \frac{x_1 x_2}{x_1x_2+x_2x_3+x_1x_3}$ is straightforward since the signs of (8) – (9) and (8) – (10) would be unambiguously greater than zero.

Consider next the case of $g_1 < \frac{x_2 x_3}{x_1x_2+x_2x_3+x_1x_3}$, $g_2 > \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$, & $g_3 < \frac{x_1 x_2}{x_1x_2+x_2x_3+x_1x_3}$. The sign of (8) – (9) is unambiguously less than zero, but the sign of (8) – (10) is ambiguous. Suppose (8) – (9) < 0 and (8) – (10) ≥ 0. Then by *Condition 2* we know that $p_3 = 0$ and $p_1 = 0$. This would imply that (5) > 0, (6) $= 0$, & (7) > 0. This in turn would imply that (5) – (6) > 0, and by *Condition 3* $g_2 = 0$, which contradicts $g_2 > \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$. Now suppose (8) – (9) < 0 and (8) – (10) < 0. By *Condition 2* this implies $p_1 = 0$ and $p_2 + p_3 = 1$, and thereby (5) $= p_2.x_1 + p_3.x_1 = x_1$. We also derive (6) $= p_3.x_2 \geq 0$, and (7) $= p_2.x_3 \geq 0$.[3] Thereby we derive (5) – (6) $= 0$,[4] and we can infer from *Condition 3* that $g_2 = 0$, which contradicts $g_2 > \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$.

The proof by contradiction in the case of $g_1 < \frac{x_2 x_3}{x_1x_2+x_2x_3+x_1x_3}$, $g_2 < \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$, & $g_3 > \frac{x_1 x_2}{x_1x_2+x_2x_3+x_1x_3}$ holds by symmetry. The case of $g_1 < \frac{x_2 x_3}{x_1x_2+x_2x_3+x_1x_3}$, $g_2 > \frac{x_1 x_3}{x_1x_2+x_2x_3+x_1x_3}$, & $g_3 > \frac{x_1 x_2}{x_1x_2+x_2x_3+x_1x_3}$ is straightforward since the signs of (8) – (9) and (8) – (10) would be unambiguously less than zero. We have shown that $(g_1, g_2, g_3) \neq (g_1^*, g_2^*, g_3^*)$ is not a best response to (p_1^*, p_2^*, p_3^*). Next we prove that any deviation from (p_1^*, p_2^*, p_3^*) is not optimal for the patrol leader.

Let us begin with the case of $p_1 > \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$, $p_2 > \frac{x_1x_2+x_2x_3-x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$, $p_3 < \frac{x_1x_3+x_2x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}$. The sign of (5) – (7) is unambiguously less than zero while the sign of (5) – (6) is ambiguous.[5] Suppose (5) – (6) ≥ 0 and (5) – (7) < 0. Then by *Condition 2* we know that $g_2 = 0$ and $g_1 = 0$. This would imply that (8) $= -z$, (9) $= -z$, and (10) $= 0$. This is turn implies that (8) – (10) ≤ 0 and (9) – (10) ≤ 0. Using *Condition 3* we can infer that $p_1 = 0$ and $p_2 = 0$, which contradicts $p_1 > \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$ and $p_2 > \frac{x_1x_2+x_2x_3-x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$. Now suppose (5) – (6) < 0 and (5) – (7) < 0. Then by *Condition 2* we know that $g_1 = 0$ or that $g_2 + g_3 = 1$. This would imply that (8) $= -g_2.x_2 - x_3 +$

[3] Note that since $p_1^* = \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3} = 0$ is only possible when $x_1x_2 + x_1x_3 = x_2x_3$, we will have $p_3.x_2 = \frac{x_1x_3+x_2x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}.x_2 = \left(\frac{x_1x_2+x_1x_3+x_1x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}\right).x_2 = \frac{2x_1x_2x_3}{x_1x_2+x_2x_3+x_1x_3} \geq 0$.

[4] (5) – (6) $= x_1 - \frac{2x_1x_2x_3}{x_1x_2+x_2x_3+x_1x_3} = \frac{x_1(x_1x_2+x_2x_3+x_1x_3)-2x_1x_2x_3}{x_1x_2+x_2x_3+x_1x_3} = \frac{x_1(x_2x_3+x_2x_3)-2x_1x_2x_3}{x_1x_2+x_2x_3+x_1x_3} = 0$ (see footnote 3).

[5] Note that the sign and magnitude of p_3 does not matter since it drops out of identities (5) – (6) and (5) – (7).

$g_2.x_3$, (9) $= -x_3 + g_2.x_3$, and (10) $= -g_2.x_2$. Therefore (8) – (9) < 0, and (8) – (10) < 0. Using *Condition 3* we can infer that $p_1 = 0$, which contradicts $p_1 > \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$. In the case of $p_1 > \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$, $p_2 < \frac{x_1x_2+x_2x_3-x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$ and $p_3 < \frac{x_1x_3+x_2x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}$, we note that (5) – (7) < 0 always and that since p_2 enters as a positive term in (5) – (6) we have the same case of ambiguity in the sign of (5) – (6).

Next we consider the case of $p_1 < \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$, $p_2 > \frac{x_1x_2+x_2x_3-x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$ and $p_3 < \frac{x_1x_3+x_2x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}$. The sign of (5) – (6) is unambiguously greater than zero while the sign of (5) – (7) is ambiguous. Suppose (5) – (6) > 0 and (5) – (7) ≥ 0. Then by *Condition 2* we know that $g_2 = 0$ and $g_3 = 0$ or that $g_1 = 1$. This in turn implies that (8) $= 0$, (9) $= -x_1$, and (10) $= -x_1$. Therefore we would have (8) – (9) $= x_1 \geq 0$, and (10) – (9) $= x_1 \geq 0$. Using *Condition 3* we can infer that $p_2 = 0$, $p_3 = 0$, and $p_1 = 1$. Now suppose (5) – (6) > 0 and (5) – (7) < 0. Then by *Condition 2* we know that $g_2 = 0$ and $g_1 = 0$ or that $g_3 = 1$. This in turn implies that (8) $= x_3$, (9) $= -x_3$, and (10) $= 0$. Therefore we would have (8) – (10) ≤ 0 and (10) – (9) ≥ 0. Using *Condition 3* we can infer that $p_2 = 0$.

Finally we consider the case of $p_1 < \frac{x_1x_2+x_1x_3-x_2x_3}{x_1x_2+x_2x_3+x_1x_3}$, $p_2 < \frac{x_1x_2+x_2x_3-x_1x_3}{x_1x_2+x_2x_3+x_1x_3}$ and $p_3 > \frac{x_1x_3+x_2x_3-x_1x_2}{x_1x_2+x_2x_3+x_1x_3}$. The signs of both (5) – (6) and (5) – (7) are unambiguously greater than zero. By *Condition 2* we know that $g_2 = 0$ and $g_3 = 0$ or that $g_1 = 1$. This implies (8) $= 0$ and (10) $= -g_1.x_1$. We now have (8) – (10) > 0 and by *Condition 3* we know that $p_3 = 0$. ■

We have shown that a mixed strategy other than the Nash equilibrium is not a best response to any mixed strategy that is a best response to it. Using *Condition 1* we have shown that there is no mixed strategy Nash equilibrium in which the patrol leader and gang leader plays a strategy that is different from $\left((g_a^*, g_b^*, g_c^*), (p_a^*, p_b^*, p_c^*)\right)$ for the system with *three* seasonal patches.

References

Adami C, Schossau J, & Hintze A. (2012). Evolution and stability of altruist strategies in microbial games. *Physical Review.E, Statistical, Nonlinear, and Soft Matter Physics, 85*(1)

Armbruster, P., & Lande, R. (1993). A population viability analysis for african elephant (*Loxodonta africana*): How big should reserves be? *Conservation Biology, 7*(3)

Blanc, J. J. (2007). *African elephant status report 2007 : An update from the african elephant database.* Gland, Switz.: IUCN.

Brown, G., & Layton, D. F. (2001). A market solution for preserving biodiversity: The black rhino. In J. Shogren, & T. Tschirhart (Eds.), *Protecting endangered species in the united states: Biological needs, PoliticalRealities, economic choices* (pp. 32-50).

Cambridge: Cambridge University Press. doi:http://dx.doi.org/10.1017/CBO9780511625916.004
Bulte, E. H., & van Kooten, G. C. (1999a). Economic efficiency, resource conservation and the ivory trade ban. *Ecological Economics*, *28*(2), 171-181.
Bulte, E. H., & van Kooten, G. C. (1999b). Economics of antipoaching enforcement and the ivory trade ban. *American Journal of Agricultural Economics, 81*(2), 453-466.
Bulte, E., Damania, R., Gillson, L., & Lindsay, K. (2004). Space--the final frontier for economists and elephants. *Science, 306*(5695), 420-421. doi:10.1126/science.1105392
Burton, M. (1999). An assessment of alternative methods of estimating the effect of the ivory trade ban on poaching effort. *Ecological Economics*, *30*(1), 93.
Cohen, J. E., & Newman, C. M. (1989). Host-parasite relations and random zero-sum games: The stabilizing effect of strategy diversification. *The American Naturalist, 133*(4)
Conrad, J. M., & Smith, M. D. (2012). Nonspatial and spatial models in bioeconomics. *Natural Resource Modeling, 25*(1), 52-92. doi:10.1111/j.1939-7445.2011.00102.x
Cromsigt, J. P. G. M., Hearne, J., Heitkonig, I. M. A., & Prins, H. H. T. (2002). Using models in the management of black rhino populations. *Ecological Modelling., 149*(1), 203.
Damania, R., Milner-Gulland, E. J., & Crookes, D. J. (2005). A bioeconomic analysis of bushmeat hunting. *Proceedings of the Royal Society B: Biological Sciences, 272*(1560), 259-266.
Damania, R., Stringer, R., Karanth, K. U., & Stith, B. (2003). The economics of protecting tiger populations: Linking household behavior to poaching and prey depletion. *Land Economics, 79*(2), 198.
Fischer, C., Muchapondwa, E., & Sterner, T. (2011). A bio-economic model of community incentives for wildlife management under CAMPFIRE. *Environmental and Resource Economics*, *48*(2), 303-319.
Frank, B., & Maurseth, P. B. (2006). The spatial econometrics of elephant population change: A note. *Ecological Economics, 60*(1), 320-323. doi:10.1016/j.ecolecon.2005.12.007
Gibbons, R. (1992). *Game theory for applied economists*. Princeton, N.J.: Princeton University Press.
Johannesen, A., & Skonhoft, A. (2005). Tourism, poaching and wildlife conservation: What can integrated conservation and development projects accomplish? *Resource and Energy Economics, 27*(3), 208-226.
Johannesen, A. B., & Skonhoft, A. (2004). Property rights and natural resource conservation. A bio-economic model with numerical illustrations from the serengeti-mara ecosystem. *Environmental and Resource Economics, 28*(4), 469-488.
Kerr, B., Riley, M. A., Feldman, M. W., & Bohannan, B. J. M. (2002). Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors. *Nature, 418*(6894), 171-174.
Kirkup, B. C., & Riley, M. A. (2004). Antibiotic-mediated antagonism leads to a bacterial game of rock–paper–scissors in vivo. *Nature*, *428*(6981), 412-414.
Kremer, M., & Morcom, C. (2000). Elephants. *The American Economic Review, 90*(1), 212-234.

Mason C.F., Bulte E.H., & Horan R.D. (2012). Banking on extinction: Endangered species and speculation. *Oxford Review of Economic Policy, 28*(1), 180-192.

Messer, K. D. (2010). Protecting endangered species: When are shoot-on-sight policies the only viable option to stop poaching? *Ecological Economics, 69*(12), 2334-2340.

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. *Journal of Applied Ecology, 29*(2), 388-401.

Muchapondwa, E., & Ngwaru, T. (2010). *Modelling fugitive natural resources in the context of transfrontier parks: Under what conditions will conservation be successful in africa?* (Working Paper ed.). Cape Town, South Africa: University of Cape Town.

Mullen, J., & Zhang, D. (2012). *Booming illegal ivory trade taking severe toll on africa's elephants.* Retrieved February 6, 2013, from http://www.cnn.com/2012/09/05/world/africa/africa-ivory-elephant-slaughter

Nouweland, A. v. d. (2007). Rock-paper-scissors: A new and elegant proof. *Economics Bulletin, 3*(43), 1-6.

Sanchirico, J. N., & Wilen, J. E. (1999a). Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environmental Economics and Management, 37*(2), 129-150.

Sanchirico, J. N., & Wilen, J. E. (1999b). Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environmental Economics and Management, 37*(2), 129-150. doi:http://dx.doi.org/10.1006/jeem.1998.1060

Sas-Rolfes, M. '. (2012). *The rhino poaching crisis: A market analysis.* Retrieved November/2, 2012, from http://www.rhinoresourcecenter.com/pdf_files/133/1331370813.pdf

Shukman, D. (2013). *Lab bids to combat species smuggling.* Retrieved March, 5, 2013, from http://www.bbc.co.uk/news/science-environment-21618345

Skonhoft, A. (2007). Economic modeling approaches for wildlife and species conservation. *Ecological Economics, 62*(2), 223-231.

Skonhoft, A., & Solstad, J. T. (1998). The political economy of wildlife exploitation. *Land Economics, 74*(1), 16-31.

Van Aarde, R. J., Ferreira, S. M., Jackson, T., Page, B., deBeer, Y., Gough, K., . . . Trimble, M. J. (2008). Elephant population biology and ecology. In R. J. Scholes, & K. G. Mennell (Eds.), *Elephant managment: A scientific assessment for south africa* (pp. 84-145). Johannesburg: Wits University Press.

Wassener, B. (2013, July 19). Hong kong seizes smuggled elephant tusks. *New York Times,*

Wasser, S. K., Mailand, C., Booth, R., Mutayoba, B., Kisamo, E., Clark, B.,Stephens, M.,. (2007). Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban. *Proceedings of the National Academy of Sciences Proceedings of the National Academy of Sciences, 104*(10), 4228-4233.

Wasser, S. K., Joseph Clark, W., Drori, O., Stephen Kisamo, E., Mailand, C., Mutayoba, B., & Stephens, M. (2008). Combating the illegal trade in african elephant ivory with DNA forensics. *Conservation Biology, 22*(4), 1065-1071.