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The Economic Implications of A Multiple Species Approach to Bioeconomic Modelling

CHRISTOPHER M. FLEMING AND ROBERT R. ALEXANDER

Department of Applied and International Economics
Massey University
New Zealand

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ABSTRACT

Ecologists frequently note the importance of modelling entire ecosystems rather than single species, but most bioeconomic models in the current literature focus on a single species. While the mathematical difficulty of multiple species may quickly become overwhelming, sometimes making the single species option necessary, it is important to recognise the significance of the single species assumption to the model results. In this paper, the authors address the economic significance of this assumption through the development of a multiple species model and demonstrate, using African Wildlife as an example, the importance of interrelationships and economic values to the survival of endangered species.

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1. INTRODUCTION

Conservation efforts have traditionally focussed on the identification and preservation of a small number of charismatic species. This approach has increasingly been challenged as our knowledge of the many and varied interactions among species, their habitats, and the environment have improved. While the ecological implications of modelling single species in isolation, rather than as part of an ecosystem, are well documented (Pimm, 1991; Begon et al., 1996; Milner-Guilland and Mace, 1998), little attention has been paid to the economic implications. In an earlier paper (Fleming and Alexander, 2002) we seek to redress this imbalance by exploring analytically the introduction of multiple species to the traditional bioeconomic modelling framework. This paper extends this concept with the addition of an empirical analysis of southern African wildlife species.

The bioeconomic modelling of species extinction has grown out of the literature of fisheries economics. Working from Gordon's (1954) seminal fisheries model, Clark (1973) develops a model to analyse the decision-making of a sole owner seeking to maximise the present value of his harvests. He identifies the conditions under which the owner has an economic incentive to harvest the species to extinction.

Many extensions have been made to Clark's original model. Clark et al. (1979) study the effects of irreversible capital investment, concluding a short-run situation exists during which a fishery faces an over-capacity of harvesting resources, before leading to a long-run equilibrium situation of optimum sustainable yield. Swanson (1994) recognises that, unlike marine species, terrestrial species compete with humans for the use of land resources. He seeks to bring the literature 'onshore' by including land resources as an additional control variable.

Further, such models are increasingly applied to empirical issues of terrestrial conservation. For example, Bulte and van Kooten (1996) offer a model of the African Elephant to analyse the effects of the Convention on International Trade in Endangered Species (CITES) trade ban on optimal elephant stocks for the range state of Kenya. The authors present an empirical model with terms for harvest revenue, tourism revenue and elephant damage to crops and wildlife habitat.

They conclude, as long as the societal discount rate is greater than 3.5 percent (highly likely in the case of a developing nation), a trade ban would result in higher elephant stocks than would be likely under a controlled harvest policy. However, their model generates an optimal stock level, irrespective of the discount rate, of 15,700, three hundred less than actual stock at the time of the study. Given the perceived need to devote resources to elephant conservation, and the dramatically declining populations in Kenya over the past few decades, this result may seem somewhat surprising. One must carefully consider the meaning of *optimal* means in such a case. Within the bioeconomic framework, the ‘optimal’ outcome is a reflection of incentives faced by resource owners, not necessarily an indication of the best outcome for society as a whole.

Considering both the harvest and non-harvest case, Skonhoft (1999) analyses the optimal management of species when land use costs, non-consumptive benefits and nuisance costs are taken into account. Skonhoft concludes, in each case, that an increase in the profitability of alternative land use activities (such as farming) will lead to a long-run loss of habitat and consequently animal numbers.

A notable feature of the aforementioned models is their single species focus. Though many authors acknowledge the shortcomings of such an approach (Ragozin and Brown, 1985; Bulte and van Kooten, 1996) the bioeconomic literature remains dominated by single species models.

This paper compares the single and the multiple species results of terrestrial bioeconomic models, paying particular attention to the potential consequences of misapplying a single species model to a multiple species situation. Three cases of species interaction are considered: ecological independence, predator-prey interaction and inter-specific competition. Species independence is illustrated using the African Elephant *(Loxodonta africana)* and the Southern White Rhinoceros *(Ceratotherium simum simum)*. The African Wild Dog *(Lyacon pictus)* and the Impala *(Aepyceros melampus)* serve as an example of a predator-prey interaction, while the Impala and Greater Kudu *(Trageelaphus scriptus)* illustrate the case of inter-specific competition.

The economic theory underlying the multiple species approach is examined in Section 2 with reference to the theory of joint production. The generalised multi-species model is developed in Section 3 and necessary functional forms introduced. Empirical results are presented and discussed in Section 4. Finally, some implications of the multiple species approach are drawn in Section 5.

2. DEALING WITH MULTIPLE SPECIES WITHIN A BIOECONOMIC FRAMEWORK

a. Multiple Species as Joint Products

The production economics literature makes clear the distinction between firms producing single outputs and those producing multiple outputs (Beattie and Taylor, 1985). A single species model clearly assumes the former to be the case. However, to the extent that the allocation of land resources for conservation of one species necessarily provides habitat to other species which share that land, conservation management may be more properly viewed as a multiple product production process.

In multiple product production, a distinction is drawn between joint and non-joint production. Joint production is said to exist when more than one output emerges from a single productive activity. Two classes of joint production are distinguished in the literature: the case where all joint products are desirable, and the case where one product is desirable while another is undesirable (Baumgartner et al, 2001). The latter case is well documented in the environmental economics literature. Early authors, including Johann Heinrich von Thumen, William Jevons and Karl Marx, all address the phenomenon of pollutants arising as joint products of desired goods (Baumgartner, 2000).

While well studied in production economics, the case where all joint products are desirable has received little attention in the natural resource, environmental and ecological economics literature. However, Baumgartner et al (2001) have recently suggested joint production, though not recognised as such, is in fact a fundamental concept in ecology. They argue that ecosystems "…as open, self-organising systems, necessarily take in several inputs and generate several outputs…" (p.367). Although it is by no means the case that all species are at all times desirable, it is a working assumption in this article that the conservation problem is one in which that assumption may hold. Thus, we will not address the case of undesirable species in this work.

A further distinction found in the literature is between allocable and non-allocable factors of production. Allocable factors are those for which the amount of the factor of production used in producing a given output, $y_{1,}$ can be distinguished from the amount of that factor used in producing another output, y_2 (Beattie and Taylor, 1985). Non-allocable factors are those for which such a distinction cannot be made.

Where the factor under consideration is conservation land, clearly we have a case of a non-allocable factor, as illustrated in Figure 1,

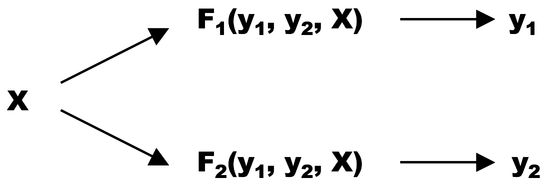

Figure 1. A non-allocable factor of production. (Adapted from: Beattie and Taylor, 1985)

where X represents the total quantity of input (land), and $F_1(\cdot)$ and $F_2(\cdot)$ represent the production functions through which X is converted into outputs y_1 and y_2 (species 1 and 2) respectively.

b. Specifying Functional Form

Within a bioeconomic framework, the production functions of Figure 1 are represented by the growth functions of the renewable resource stocks. To develop the multiple species growth functions, we begin with a basic single species form and adapt that to the multiple species case.

The logistic growth function first proposed as a population model by P.F. Verholst in 1838 (Clark, 1976) is often used in bioeconomic models,

$$F(x) = \frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) \tag{1}$$

where r is the intrinsic growth rate of the resource, $x = x(t)$ is the population of the species in time t and K is the carrying capacity of the habitat. This formulation characterises the concept of density-dependence, in which populations are self-limiting as the density of a population increases and competition for available resources limits net growth. In a logistic growth function, population grows rapidly at first and then, upon reaching a maximum growth rate, begins to decline such that

$$F'(x) > 0, F''(x) < 0 \text{ for all } x < \frac{K}{2}, \text{ and}$$

$$F'(x) < 0, F''(x) > 0 \text{ for all } x > \frac{K}{2}.$$

This function provides for smooth and continuous population adjustments to exogenous forces and easy recovery from low population levels. Alternative functional forms are often used to model species that exhibit non-continuous population adjustments and less resilient recovery from low population levels (Clark, 1976), however the logistic function is used throughout this paper as it creates the most parsimonious models with which to demonstrate the distinction between single and multiple species models.

An assumption of fixed habitat size is implicit in the Verholst function. However, habitat loss is the principal threat facing the majority of the worlds endangered species[1]. Any loss of habitat effectively reduces the carrying capacity of the species, making it necessary to amend the Verholst equation to acknowledge potential variation in habitat size. Following the work of Alexander and Shields (2002), this is done through the introduction of an additional variable, L, where, L, represents a unit of land resource available to species.

This yields a modified logistic growth function as follows,

$$F(x) = \frac{dx}{dt} = rx\left(1 - \frac{x}{K \cdot L}\right). \tag{2}$$

under this growth function, effective carrying capacity now varies with the allocation of land. If land allocation falls, $\frac{x}{K \cdot L}$ increases, dampening growth. Conversely, enhanced growth is obtained through the additional allocation of land.

The Verholst growth function applies to a single species. Ecological communities, however, are composed of many populations of distinct species interacting to varying degrees. The potential interactions range from essentially neutral interactions in which two populations are jointly part of each other's habitat but not part of each other's environment, to interactions with some direct influence on the ability of the individuals in one or both populations to survive and reproduce. Clearly these interactions must be considered when attempting to build models within a multiple species framework.

Following the approach of Lotka (1925) and Volterra (1926), it is possible to incorporate a variation of equation (2) to represent the effects of inter-specific interaction. Denoting the first species x_1 and the second species x_2 , and adding α to represent the effects of interaction (either positive or negative) between the two, our equation for population growth of species 1 and 2 now become:

$$F\left(x_{1,} x_2, L\right) = \frac{dx_1}{dt} = r_1 x_1 \left[1 - \frac{x_1}{K_1 \cdot L} + \alpha_{1,2} \frac{x_2}{K_1 \cdot L}\right] \tag{3}$$

$$G\left(x_{1,} x_2, L\right) = \frac{dx_2}{dt} = r_2 x_2 \left[1 - \frac{x_2}{K_2 \cdot L} + \alpha_{2,1} \frac{x_1}{K_2 \cdot L}\right]. \tag{4}$$

In the growth function for species 1 (equation (3)), K_1 appears in the denominator throughout since we are interested in the effects of both intra-specific and inter-specific competition on resources used by species 1. The interaction coefficient $\alpha_{1,2}$ represents the relative impact of one individual of species 2 on the population growth rate of species 1. If $\alpha_{1,2}$ is greater than one, an individual of species 2 has more influence on the growth rate of species 1 than does a single individual of species 1. The growth function for species 2 (equation (4)) follows the same logic.

These equations can be extended to accommodate interactions with more than one interacting species. Terms may be added to represent the effects of additional species, however we will only use the two-species case in this paper.

Simply altering the sign of the coefficient may represent the various relationships through which the various members of a community might interact. A mutually beneficial relationship results in two positive interaction coefficients, a predator–prey relationship as one positive (predator) and one negative (prey), and inter-specific competition as two negative coefficients.

3. THE GENERALISED MODEL

In this section, we introduce a simple two-species analytical model to demonstrate the effect of adding additional species to the single species bioeconomic framework (Fleming and Alexander, 2002). Suppose society wishes to maximise the present value of net returns from harvesting both species[2]. The objective function may be specified as:

$$\max_{h} \int_0^{\infty} e^{-\delta t}\{[p_1 - c_1(x_1)]h_1 + [p_2 - c_2(x_2)]h_2 - \delta p_L L\} \qquad (5)$$

where the subscripts denote species 1 and 2, p_i is average revenue (price) received for harvesting one member of species i, $x_i = x_i(t)$ is the population of species i in time t, $c_i(x_i) = c_i(x_i(t))$ is the marginal cost of harvesting species i as a function of population, $h_i = h_i(t)$ is the harvest of species i in time t, $L = L(t)$ is a unit of terrestrial resource (land) allocated collectively to all species in time t, and p_L is the unit price of a base unit of that land

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[1] Habitat loss or degradation affect 89% of all threatened birds, 83% of mammals and 91% of plants (IUCN, 2000).

[2] The authors recognise that non-consumptive values, such as tourism and existence values, play an important role in the conservation of wildlife. In this model, we restrict our attention to consumptive (harvest) values as they amply demonstrate the distinction between single and multiple species models without adding the undue complexity of additional market relationships.

resource. Following Swanson (1994), the land term is multiplied by the social discount rate, δ, to indicate that the returns from our species must meet the opportunity cost of alternative returns available from use of the same land.

The dynamics defining the change in stock of each species are represented by the state equations:

$$\dot{x}_1 = F(x_1, x_2, L) - h_1 \tag{6}$$

$$\dot{x}_2 = G(x_1, x_2, L) - h_2 \tag{7}$$

where $F\left(x_1, x_2, L\right)$ and $G\left(x_1, x_2, L\right)$ are the joint production functions of species 1 and 2.

Using the Pontryagin necessary conditions for maximisation of this problem, and simplifying the notation by allowing $R_1 = R_1(x_1) = p_1 - c_1(x_1)$ and $R_2 = R_2(x_2) = p_2 - c_2(x_2)$ to represent net revenues from harvest, the following conditions are derived:

$$\delta = \frac{R_1 F_L}{p_L} + \frac{R_2 G_L}{p_L} \tag{8}$$

$$\delta = F_1(x_1, x_2, L) - \frac{c_1'(x_1) F(x_1, x_2, L)}{R_1} + \frac{R_2}{R_1} G_1(x_1, x_2, L) \tag{9}$$

$$\delta = G_2(x_1, x_2, L) - \frac{c_2'(x_2) G(x_1, x_2, L)}{R_2} + \frac{R_1}{R_2} F_2(x_1, x_2, L)\,. \tag{10}$$

Equation (8) reflects the impact of the land control term in the objective function, and is a multiple species version of the result found by Swanson (1994). This condition implies that society will allocate land only to the extent that the species supported by it are able to generate a competitive rate of return from their use of the resource. In a single species model, it would appear that this return must be generated entirely by the species under consideration. However, when the conservation of a wilderness area provides benefits to many species, the returns generated by all species may contribute to meeting the required returns from the land resource.

Although we restrict our intention to the two species case, the extension to multiple species will simply lead to additional terms, resulting in a further reduction of individual species burden. This relationship holds regardless of the nature of any interdependence between the species.

Equations (9) and (10) are modified 'golden rule' equations for species 1 and 2. The LHS and the first term on the RHS indicate that the resource must be maintained at a stock level such that the marginal productivity of the resource stocks, $F_1(\cdot)$ and $G_2(\cdot)$, equate to the returns available from other assets, δ. All other terms on the RHS modify that relationship.

The second terms on the RHS of Equations (9) and (10) reflect the stock-dependent harvest costs ($c'(x) < 0$), expressed proportionately to the unit net revenue of harvesting the resource. The only change in these terms from the single species case is that the growth functions, $F(\cdot)$ and $G(\cdot)$, are potentially interdependent. This term acts to increase the marginal productivity of the resource, making the resource a more attractive investment. While these terms exhibit potential interdependence between species, they arise directly from the harvest activity and are strongly dependent on the ratio of marginal costs to marginal revenues.

The third terms on the RHS of Equations (9) and (10) reflect the biological interdependence of the two species, modified by the relative marginal profitability of each. Each equation indicates that returns for one species are modified by the marginal affect that species has on the other, multiplied by the proportional revenue of the second species to the first. Whether this makes a species more or less desirable depends upon both the ecological relationship between the species and the relative values of the species. We shall henceforth refer to these as the *interdependence terms*.

4. Considering Species Interdependence

We consider three cases of species interdependence: (i) independent species, (ii) a predator-prey relationship, and (iii) species competition.

a. Independent Species

(i) Analytical

In the independent case, each species' state equation is a function only of its own population and the land resource so that $G_1(x_1, x_2, L) = F_2(x_1, x_2, L) = 0$. Equations (6) and (7) become:

$$\dot{x}_1 = F(x_1, L) - h_1 \tag{11}$$

$$\dot{x}_2 = G(x_2, L) - h_2 . \tag{12}$$

Consequently, the interdependence terms of Equations (9) and (10) become zero, and the second and third conditions revert to a pair of modified golden rule harvest conditions from a standard single species model. Equation (8) remains unchanged.

$$\delta = F_1 - \frac{c_1'(x_1)F(x_1, L)}{R_1} \tag{13}$$

$$\delta = G_2 - \frac{c_2'(x_2)G(x_2, L)}{R_2} \tag{14}$$

The implication of equations (13) and (14) are that harvest decisions for each species are made without regard to the existence of the other species. In this respect, a two species model would yield the same results as two independently developed single species models if we failed to consider the constraint on returns to land. However, equation (8) is still a necessary condition, and each species is still dependent on the same land input for its production.. Thus, both species still contribute to returns to the land resource. In developing the single species version of this condition, Swanson (1994) makes a compelling argument for considering returns to land in terrestrial species conservation. This model supports that argument and extends it by demonstrating the need to consider all relevant species in an ecosystem, even when they appear to be ecologically independent.

(ii) Empirical – The Case of the African Elephant and the White Rhinoceros

The plight of both the elephant and the rhinoceros is well documented. The ivory trade has reduced elephant numbers from a population of nearly 1,700,000 in the late 1970's to less than 500,000 today (Barnes et al, 1999). Similarly, the rhinoceros' horn, used as dagger handles and goblets in the Middle East, and as traditional medicine in Asia, has been the principle agent of its decline. On a positive note, the southern White Rhino stands as one of the world's greatest conservation success stories. From a population of just 20 in 1885, there are now nearly 10,000 rhino in the wild (Emslie and Brooks, 1999).

Nevertheless both species remain vulnerable. In addition to poaching pressure, rapid growth of human population in Africa is putting these species into competition with humans for useable land, resulting in severe habitat loss. Although single species bioeconomic models of the elephant exist (see for example, Bulte and van Kooten, 1996), the fact that both species share a habitat, have considerable harvest value, and are often the focus of joint conservation efforts, suggests there is a strong case for modelling the species together.

Available data suggest the intrinsic rate of growth (r) for rhino and elephant are 9.0% and 6.5% respectively (Owen-Smith, 1988). Owen-Smith (1988) suggests that in favourable habitats, both rhino and elephant are capable of reaching densities of 5 animals per km^2, this figure serves as an estimate of carrying capacity (K). Harvest value (p) is calculated using information from African Safari Consultants (2002). Estimates are obtained by multiplying the per-person daily rate by the minimum number of days needed to hunt each particular species plus the appropriate trophy fee. The elephant attracts a daily rate of $650[3] for a minimum of ten days, plus a trophy fee of $8,000, yielding a harvest value of $14,500. The rhinoceros attracts a daily rate of $750 again for a minimum of ten days, plus a trophy fee of $30,000, yielding a harvest value of $37,500. Initial cost of harvest (c_0) is taken to be harvest value less the trophy fee, this is considered to be an overestimate as a level of profit is undoubtedly built into the daily hunting rate. The advantage of this approach however, is that it allows cost to be calculated in a consistent manner across all species in question. Current population densities are taken from the Kruger National Park year 2000 census (TOURSAA, 2002). A discount rate of 5.0% is used, though this is viewed as conservative. The value of land resource p_L is based upon the estimated start up cost of a typical game ranch of $15,000 per km^2 (Hearne and Swart, 2000).

The model is solved in discrete form, for 150 periods, using the General Algebraic Modeling System (GAMS)[4]. Societal objective function and constraints were defined as in equations (5), (6) and (7). Schaefer's (1957) function for cost of harvest was chosen and specified as follows:

$$c(x) = \frac{c_0 x_0}{x_t} \tag{15}$$

where c_0 is initial cost of harvest, and x_0 the initial stock level. In seeking to reflect the threat of species loss within the model, additional constraints were imposed upon the allocation of land. Land is given an initial parameter (and upper bound) of 1.0 to represent land currently devoted to the species, with any value below this point representing a scenario whereby further habitat loss is likely.

In the single species result (Figure 2), the harvesting of elephant alone generates an insufficient return to ensure the survival of the species. The model predicts an immediate harvest of elephants back to 5% of initial density (from an initial stock of 9,152 to 540), and thereafter harvesting to keep numbers at this level. The continued presence of elephants (albeit at critically low levels) probably owes more to the specification of a cost function,

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[3] All figures are in US dollars.

[4] For a copy of the GAMS program contact the author.

which makes harvesting small populations prohibitively expensive, than to the value derived from the elephant themselves.

In contrast, the inclusion of the more valuable rhinoceros affords the elephant access to the resources necessary for its continued survival, with periodic harvesting approximately every 35 periods. Keeping the elephant within a stock limit cycle of 50 and 330 times initial density (a stock range of 4,500 to 30,400). In effect the value generated from the continued existence and harvest of the rhinoceros subsidises continued existence and harvest of the elephant. This result underlines the potential for misapplication of single species results and, illustrates the importance of considering all species of value in management decisions, even in the absence of any direct ecological relationship.

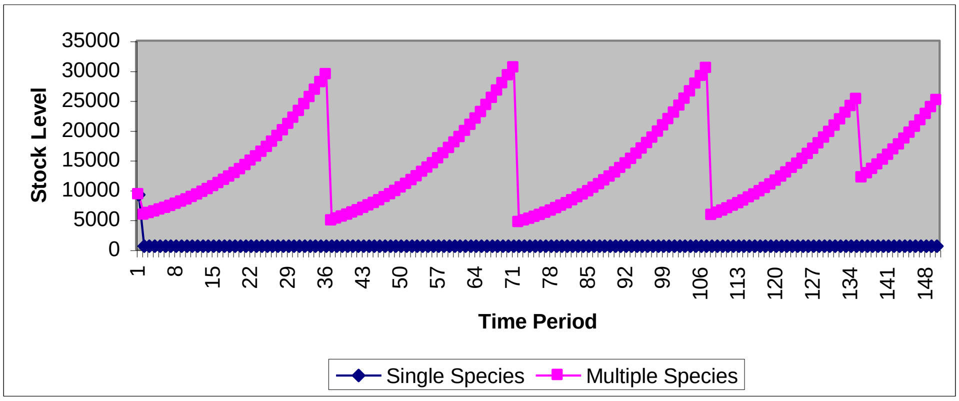

Fig 2: Optimal Stock Levels for the African Elephant under a Single and a Multiple Species (independent) Model

As the high value species, the stock level of the rhinoceros (Figure 3) is relatively unaffected by the presence of the elephant in the model, though the multiple species case generates a more stable long run stock and harvest level, with a fractionally larger average harvest over the time period in question. This result arises from the relationship shown in equation (8), which acts to 'charge' each species for the entire value of the land in the single species case, but which allows them to share the burden in the multiple species situation.

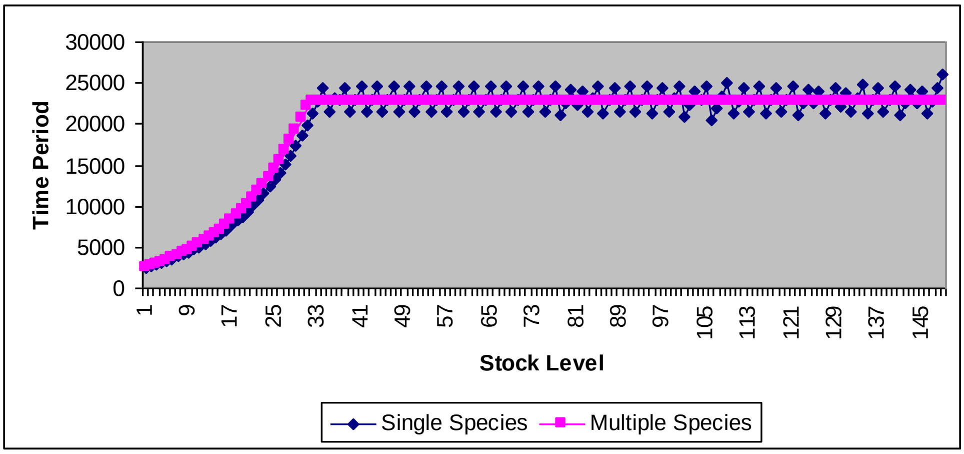

Fig 3: Optimal Stock Levels for the White Rhinoceros under a Single and a Multiple Species (independent) Model

The high value rhinoceros generates sufficient return in the long run to allow the initial allocation of land resources to continue (Figure 4), though the multiple species case, with the addition of revenue from the elephant, is able to provide this return more quickly. The elephant alone however, is unable to generate sufficient return to justify the continued allocation of land resource, and it is this, not the value of the harvested products per se, which motivates the harvesting decision discussed above.

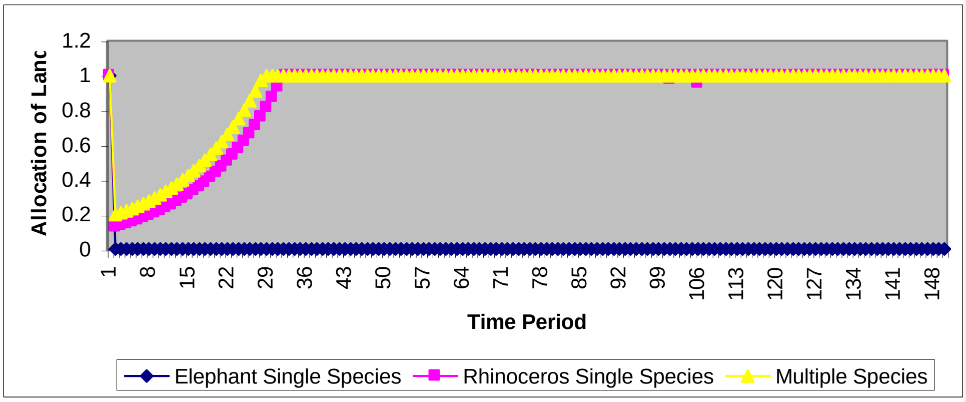

Fig 4: Optimal Land Resource Allocation to the White Rhinoceros and African Elephant under Single and Multiple Species (independent) Models

b. Predator-Prey Species

(i) Analytical

The predator-prey relationship is defined as one in which the growth of one species is positively affected by the presence of the second, but in which the growth of the second species is adversely affected by the presence of the first. In the generalised model, this implies $G_1(x_1, x_2, L) < 0,\ F_2(x_1, x_2, L) > 0$ or $G_1(x_1, x_2, L) > 0,\ F_2(x_1, x_2, L) < 0$. Suppose species 1 is a predator ($G_1(x_1, x_2, L) < 0$) and species 2 is its prey ($F_2(x_1, x_2, L) > 0$). Then the interdependence term of Equation (9), works against the predator (makes it less valuable), while the corresponding term in Equation (10), works in favour of the prey species. If both species have a harvest value, the predator, by reducing the growth of its prey, is reducing the potential returns to the land resource. Conversely, the prey is increasing potential returns by increasing the growth of the predator. The result of these interactions are dependent upon the relative value of the two species. In the case where the predator has a high value relative to the prey, there will exist healthy populations of both species, the predator for it harvest value, the prey as a source of food. If both have equal value, again healthy populations of both will exist. The potential for extinction will only arise in the case where the prey is of significantly greater value than the predator. As the harvest value of the predator approaches zero, given the prey has some positive net value, then the resource owner has the incentive to harvest the predator to extinction. This is the behaviour exhibited by livestock owners around the world as they seek to eliminate all predation of their stock, and is a principle cause of the decline of wild predators. The policy prescription for those wishing to conserve both species is clear, increase the value of the predator.

(ii) Empirical – The Case of the African Wild Dog and the Impala

The African Wild Dog has become severely endangered in recent times. They are extinct in most countries in West and Central Africa, and in the East and the South they are confined to a few areas where human population density remains low. Today, Africa’s wild dog population numbers between 3,000 and 5,500. The ultimate cause of the wild dogs’ decline has been a combination of persecution and habitat loss. Wild dogs kill livestock, and have therefore been shot, snared and poisoned in most livestock areas. However, in the last two decades, awareness of the wild dogs’ plight has grown, and conservation efforts are underway. Breeding programmes have been established, but with limited success (Woodroffe et al, 1997). In stark contrast, impala are among the most numerous mammal species in southern Africa. Kruger National Park alone has an estimated impala stock of 100,000, and the impala is numerically the most important single species available for game hunting in the majority of the region's game ranches (Fairall, 1982). In addition to being a target of game hunters, impala are the preferred prey of wild dog, Mills and Biggs (1993) suggest impala make up 52% of prey taken by wild dogs in the Kruger National Park.

Data suggests the intrinsic rate of growth (r) for wild dog and impala are 5.50% and 35.00% respectively (Woodroffe et al, 1997; Falkena, 2000). In favourable habitats impala are able to reach considerable densities of up to 20 animals per km^2, this figure serves as an estimate of carrying capacity (K). The wild dog requires large home ranges, much larger than would be expected on the basis of their body size. Outside the denning period, existing packs within Kruger National Park have a range of in excess of 885km^2 (Gorman et al, 1992). The home ranges of different wild dog packs may overlap considerably, but they rarely enter another pack's core area. As a result, wild dogs' large home ranges translate into very low population densities, and a figure of 1 animal per km^2 is used as an estimate of (K) (Woodroffe et al, 1997). A Harvest value (p) for impala is calculated in the same manner as for elephant and rhinoceros, yielding a value of $600. Wild dogs are assumed to have no harvest value. The initial cost of harvest for both species (c_0) is taken to be one fifth of the cost of a single day's plains game hunting. The interaction coefficients $\alpha_{1,2}$ and $\alpha_{2,1}$ are determined by the mid-point of the possible bounds (determined by the relative values of each species carrying capacity), between which coexistence is possible. In order to generate meaningful stock and harvest dynamics, given the relatively low harvest values of each species, it is necessary to adjust the value of land resource parameter. If left at $15,000 per km^2, the model simply harvests both species to extinction in the first period. The impala and the wild dog themselves do not generate sufficient return to justify the continued use of the valuable land resource, a predictable result that reinforces the necessity of taking into account the value of all relevant species in this type of model. Accordingly, p_L is taken to be US$1,500 per km^2 in order to observe the interaction dynamics between the species. As the purpose of the model is to investigate the variations inherent in single versus multiple species models, the arbitrary adjustment of land values should not adversely affect our results. All other parameters are consistent with the earlier models.

Comment [c1]: Some authors (for eg Bulte an van Kooten, 1996) discuss parameter selection in the appendix, which do you think is better?

In the predator-prey scenario, we use the extreme case where the prey has some positive value and the predator's value approaches zero. As such, the wild dog single species and predator-prey multiple species result are somewhat similar (Figure 5). In the single species case, the wild dog is heavily cropped in the first period and numbers kept to a minimum thereafter (less than 20 individuals), whereas, the multiple species follows a pattern of periodic harvesting, at all times keeping populations at less than half of initial density. The difference lies in the motivations underlying the responses. In the single species case, the wild dog is continually harvested due to its inability to generate sufficient revenue to justify the continued allocation land. Yet in the multiple species case, land resource's remain available (due to the value of the impala), and harvest of the wild dog is motivated by both its lack of harvest value and a desire to protect valuable prey. In both cases, the wild dogs extinction is probably prevented in the model by the choice of cost function.

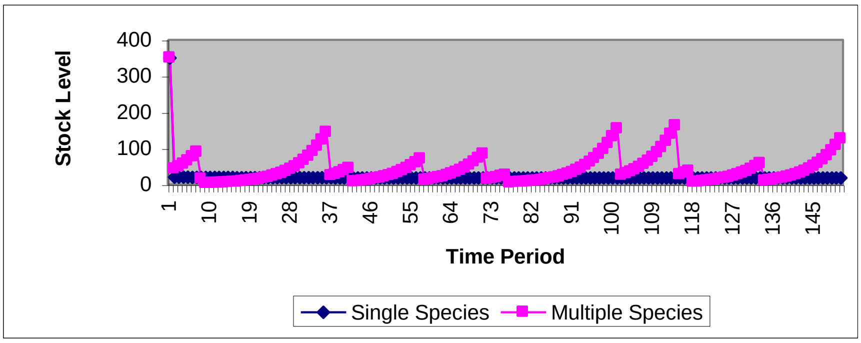

Fig5: Optimal Stock Levels for the African Wild Dog under a Single and a Multiple Species (predator-prey) Model

As a species of high value, impala is able to reach strongly positive steady state stock levels under both the single species and multiple species models (Figure 6). Again, multiple species is the significantly more stable case. Unlike the independent case where the multiple species steady state stock level bisected the bounds of the oscillating single species stock level, due to the dampening effect of predation, the multiple species level lies towards the lower bound of these oscillations.

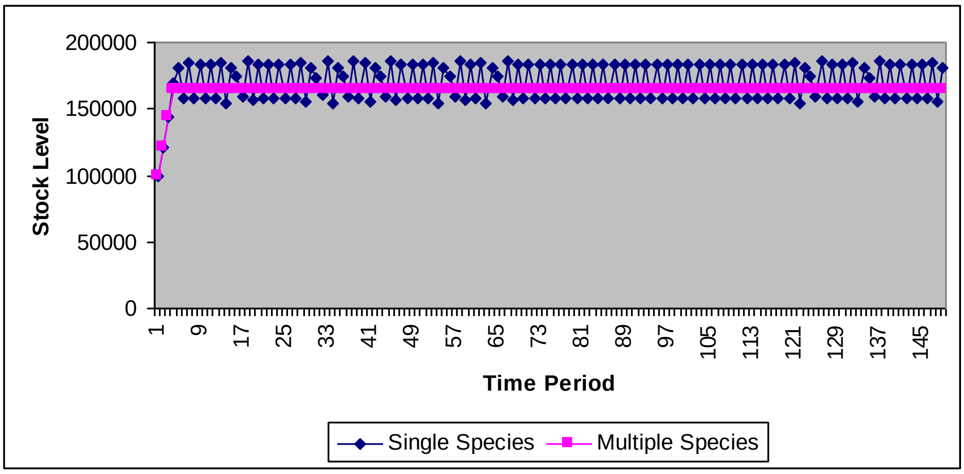

Fig 6: Optimal Stock Levels for the Impala under a Single and a Multiple Species (predator-prey) Model

The Land allocation (Figure 7) is much the same as for independent species. The high value species justifies the continued provision of land resources (at the lowered value) for both the single and multiple species case, while the lesser-valued species, when modelled alone, suggests habitat conversion is the optimal policy.

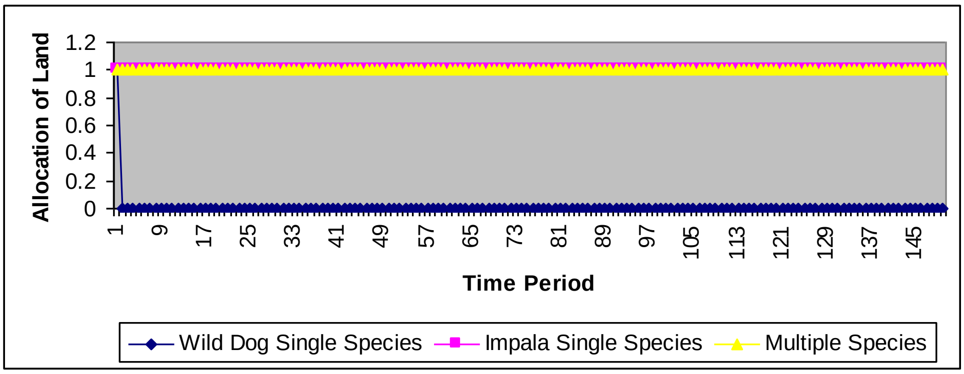

Fig 7: Optimal Land Resource Allocation to the African Wild Dog and the Impala under Single and Multiple Species (predator-prey) Models

c. Competition

(i) Analytical

The distinguishing characteristic of this case is that each species acts against the interests of the other, so that $G_1\left(x_1, x_2, L\right) < 0,\ F_2\left(x_1, x_2, L\right) < 0$. One again, the outcome is determined by the relative values of the species. If species 1 is of greater (lesser) value than species 2, then the magnitude of the term working against species 1 in Equation (10) is reduced (increased), and the magnitude of the term working against the second species in Equation (11) is increased (reduced). If competition exists between two species, the resource owner has the incentive to reduce populations of the lower value species, in favour of retaining the species with higher value. At moderate ratios of net revenue, the resource owner has insufficient incentive to exterminate the less valuable species, and populations of both species will be retained.

However, as one species gains significantly greater value than the other, the resource owner has an incentive to harvest the less valued species to extinction, so as to devote all of the land resources to production of the more valuable species. Livestock husbandry is the extreme manifestation of this behaviour.

(ii) Empirical – The Case of the Impala and Greater Kudu

Where the Impala, with its high rate of growth and carrying capacity, has become a favourite of the burgeoning game ranch industry, the Greater Kudu remains conservation dependent. In southern Africa, greater Kudu have been hunted for many years. The meat is highly valued and the horns of the male Kudu are a trophy for many game hunters. Natural jumpers, they prefer lower densities than the Impala, and while more valuable are more difficult to manage, especially on smaller ranches. Both species favour a similar habitat; impala are mixed grazer browsers, while kudu are browsers. Evidence suggests a degree of competition between the two, especially in times of drought (Huffman, 2002).

Data suggests the intrinsic rate of growth (r) for the kudu is 20.00% (Falkena, 2000). In favourable habitats kudu are able to reach densities of up to 15 animals per km^2, this figure serves as an estimate of carrying capacity (K). A Harvest value (p) for kudu is calculated in the same manner as for impala, yielding a value of \$1,350. Initial cost of harvest for both species (c_0), remains one fifth of the cost of a single day's plains game hunting. Again the interaction coefficients $\alpha_{1,2}$ and $\alpha_{2,1}$ are determined by the mid-point of the possible bounds

Comment [c2]: Some authors (for eg Bulte and van Kooten, 1996) discuss parameter selection in the appendix, which do you think is better?

(determined by the relative values of each species carrying capacity), between which competitive coexistence is possible. Following the approach taken in the predator-prey model, the value of land resource, p_L is taken to be $1,500 per km^2 to generate meaningful stock and harvest dynamics. All other parameters are consistent with the earlier models.

The effect of inter-specific competition is clear both in the steady state stock and harvest levels (Figure 8). The effect of impala on the greater kudu is to reduce the steady state stock and harvest levels. The greater the level of competition, the further the multiple species outcome falls below the single species result.

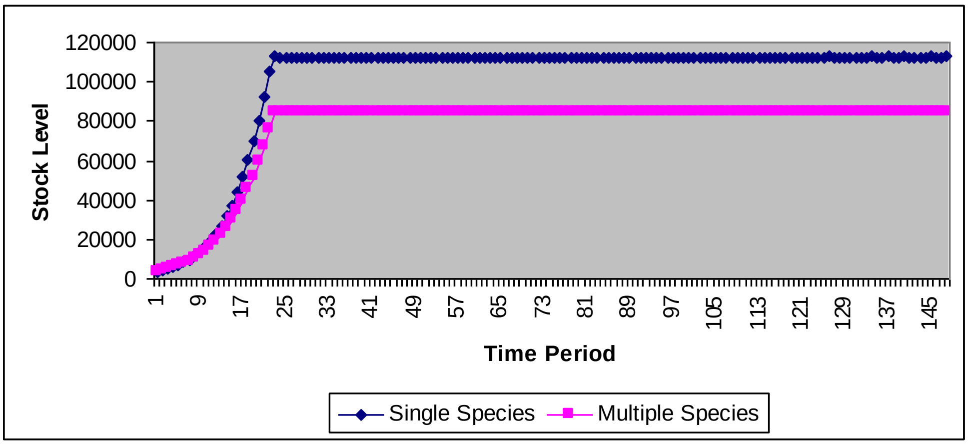

Fig 8: Optimal Stock Levels for the Greater Kudu under a Single and a Multiple Species (competition) Model

Similarly, the impala's steady state stock level falls below the bounds of the oscillating single species levels (Figure 9). However, unlike the greater kudu, the average level of harvest of impala is greater under a multiple species framework.

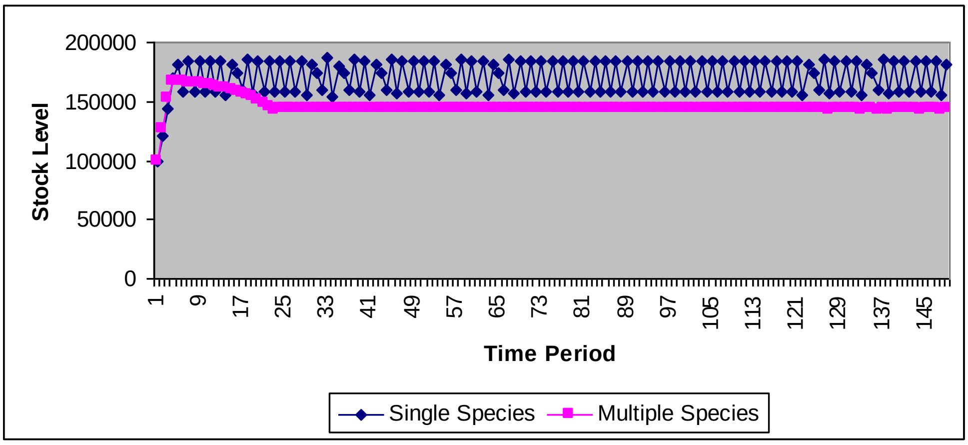

Fig 9: Optimal Stock Levels for the Impala under a Single and a Multiple Species (competition) Model

Under the unrealistic land value specified, the impala and the kudu alone, and as a pair, are capable of retaining use of their land at the initial level. As aforementioned, this result is unlikely to hold if the true opportunity cost of land is considered.

5. CONCLUSION

While the importance of taking an ecosystem approach to species conservation is well documented in the ecological and conservation biology literatures, the economic implications have been less thoroughly addressed. Working from within the existing bioeconomic framework, we have developed a multiple species model that allows several economic implications to be drawn, and in part illustrates the incentives behind observable human actions.

The model demonstrates that the addition of species to the single species framework spreads the burden of generating a competitive return to land resources across all species, which otherwise may appear to fall solely on an individual species. The empirical analyses undertaken suggests there exists significant quantitative implications for the estimation of optimal species stocks, such as those calculated by Bulte and van Kooten (1996) for the African Elephant. It further illustrates that this result holds independently of the relationship between the species.

Where interdependencies between species exist, the model demonstrates more complex behavioural relationships. The predator-prey case highlights the importance a species relative value has on its ultimate fate. The case in which the prey is of high value and the predator of little value is particularly revealing. Here the incentive exists for the resource owner to harvest the predator species to extinction. The decline of wild predators throughout the world can largely be traced to behaviour consistent with that predicted by the model. When the predator is of relatively higher value, the incentives act to preserve both species. Though this case is less common than the former, it can be observed in many areas of the world, such as in African game parks where the presence of predators is critical to the success of the operations.

Relative values also have implications for competing species. In this case each species acts against the economic interest of the other and resource owners have the incentive to reduce stocks of low value species in favour of retaining species of high value, though this tendency is often buffered from extremes by the presence of stock-dependent harvest costs.

An important outcome of the model is that one can use it to infer the conditions under which a single species model may be appropriate, at least in general terms. If species are independent, and either the opportunity cost of capital or the value of wilderness land is very low, then a single species model may yield results similar to that of a multiple species model. In this case the burden on species, as given by Equation (8), is negligible while Equations (9) and (10) become similar to the single species modified golden rule.

Similarly, if the relative value of one species is significantly greater than that of all others in the ecosystem, then a single species model may also approximate the results of a multiple species approach. In this case, the interdependent terms are negligible for all except the species of value. Even when this occurs, the valid use of a single species model is not certain as the ecological interdependencies in the species' growth functions may still introduce additional effects not considered here. Such effects must be considered on a case-by-case basis.

Clearly, in the absence of these conditions, the model demonstrates that the inclusion of at least all economically valuable species in an ecosystem is important. Using single species models where multiple species are economically significant may lead to misleading results and ultimately to incorrect policy decisions.

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