



An approach to determine the extinction risk of exploited populations

D.J. Crookes^{a,*}, J.N. Bignaut^{a,b}

^a School for Public Leadership, Stellenbosch University, Stellenbosch, Western Cape, South Africa

^b South African Environmental Observation Network, Pretoria, Gauteng, South Africa

ARTICLE INFO

Keywords:

IUCN
Sustainability assessment
White rhino
Ceratotherium simum
South African abalone
Haliotis Midiae

ABSTRACT

We propose a method for assessing the persistence of species where the resource is harvested. Four sustainability measures are employed, namely a population measure, a harvest measure, a profitability measure and a catchability measure. These are used to assess the sustainability of two natural resources representing terrestrial and aquatic species, namely White Rhino (*Ceratotherium simum*) and South African abalone (*Haliotis Midiae*) species, respectively. The framework is used to evaluate these two resources against relevant local and international protected species listings. The results show that the proposed framework produces a more conservative approach to listing threatened species, consistent with the precautionary principle. The framework provides a way of conducting a precautionary assessment of extinction risk under conditions of exploitation, across a range of aquatic and terrestrial species. Once developed, we also apply this framework to seven additional species using a scenario analysis. The results highlight the importance of taking into consideration institutional factors under conditions of overexploitation.

1. Introduction

The sustainability of the world's natural resources is a cause for concern (Barnosky et al., 2011). Not only are there risks of 'empty forests' (Nasi, Taber, & Van Vliet, 2011) and 'empty savannas' (Lindsey et al., 2013), but also of 'empty oceans'. Seafood, which once was abundant, is now much scarcer (Pauly, Watson, & Alder, 2005). A major cause of the decline of many species is overexploitation, resulting in the possibility of the risk of extinction in some cases (see Purvis, Gittleman, Cowlshaw, & Mace, 2000; Milner-Gulland & Bennett, 2003; Dulvy et al., 2004; Robinson & Bennett, 2004; Cowlshaw, Mendelson, & Rowcliffe, 2005; Wilkie et al., 2005; Bignaut & Aronson, 2008; Bignaut, De Wit, & Barnes, 2008; Fa & Brown, 2009; Hoffmann et al., 2010; Allebone-Webb et al., 2011; Abernethy, Coad, Taylor, Lee, & Maisels, 2013; Crookes & Bignaut, 2015; Saayman & Saayman, 2017). A recent review of 37 economic values across agricultural, water, natural vegetation and wildlife sectors indicates that the greatest threat to national security arises through declines in wildlife species (Crookes & Bignaut, 2019).

One of the main tools to assess the extinction risk of species is the International Union for Conservation of Nature (IUCN) Red List (see Akçakaya et al., 2000; Akçakaya & Ferson, 2001; Mace et al., 2008; IUCN, 2012). Milner-Gulland and Akçakaya (2001) state that there are benefits to promoting cross-fertilisation between the fisheries literature

and the red-listing of threatened species; they argue that this would lead to an improvement in the assessment and management of specifically exploited species. The fisheries literature (see Wilen, 1976; Bjørndal & Conrad, 1987; Opsomer & Conrad, 1994) is one such an example, and it provides a means of determining the extinction risk of exploited species. The fisheries literature has been applied to terrestrial species as well (see Milner-Gulland & Leader-Williams, 1992; Milner-Gulland & Clayton, 2002). However, to date the tools proposed in the fisheries literature have not been fully utilised in IUCN Red List assessments.

Drawing upon the fisheries literature, we propose a tool for assessing exploited species. We use four different measures to assess sustainability, namely a population measure, a harvest measure, a profitability measure and a catchability measure. We then apply the framework to nine species across a range of ecosystems, with the primary focus of analysis on White Rhino (*Ceratotherium simum*) and South African abalone (*Haliotis Midiae*). Next, we use the framework to score the different species to determine their overall sustainability. The results of our assessment are then compared to existing IUCN Red List classifications in order to assess the extent to which our tool aligns with the current tools used in the IUCN Red List classification, to see which tool provides the most conservative assessment. According to the IUCN Red List methodology, for multiple assessments of extinction risk, the tool that provides the most conservative assessment of extinction risk

* Corresponding author.

E-mail address: dcrookes@outlook.com (D.J. Crookes).

should be used.

2. Materials and methods

2.1. Gordon-Schaefer fisheries model

The method proposed for the assessment is extremely simple. First, a simple dynamic bio-economic model is constructed based on the Gordon Schaefer fisheries model (more details on these equations are given in [Appendix A](#)):

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{k}\right) - qEx \quad (1)$$

$$\frac{dE}{dt} = n'E(qx - c/p) \quad (2)$$

where n' is an adjustment parameter, r is the intrinsic growth rate, x are the stocks (or population), k is the carrying capacity, q is the catchability coefficient, E is the harvesting effort and p is the price of the resource and c is the cost per unit effort. This model has been widely applied to wildlife subject to harvesting, for example bushmeat hunting in West and Central Africa ([Damania, Milner-Gulland, & Crookes, 2005](#)). Elephant poaching and bushmeat hunting in East Africa ([Holden et al., 2018](#)), rhino poaching in Zambia ([Bulte, 2003](#); [Milner-Gulland & Leader-Williams, 1992](#)), in India ([Lopes, 2014](#)) and in South Africa ([Crookes & Blignaut, 2016a](#)), and predicting extinction risk of over-exploited species ([Courchamp et al., 2006](#); [Holden & McDonald-Madden, 2017](#)).

Following the fisheries literature, the prey is the resource population and the predator is the harvesting effort. The model, although simple, takes into consideration multiple threats resulting from harvesting, profitability and stock dynamics, as well as feedback between the different elements of the model, which is important in conservation ([Larrosa, Carrasco, & Milner-Gulland, 2016](#)).

This model may be constructed in a number of software programs, such as Microsoft Excel or Matlab. However, we prefer system dynamics modelling software such as Vensim® since it provides a number of other tools that facilitate the validation of the model. Furthermore, if the model contains missing parameter values that need to the estimated, Vensim® provides a better optimisation routine compared to Microsoft Excel solver (see [Appendix B](#) for proof of this). Therefore, it is preferable to use this software instead of Microsoft Excel. Although more advanced versions of the software are sold to customers, a free version (Vensim® PLE) is available for constructing simple models such as those proposed here. A stock flow diagram is constructed (see [Fig. 1](#)), with each link containing an embedded mathematical equation, describing the nature of the link.

2.2. System dynamics modelling

System dynamics modelling is a tool for modelling complex systems. It is characterised by non-linear feedback between the components in the system ([Bester, Blignaut, & Crookes, 2019](#); [Mudavanhu, Blignaut, Vink, Crookes, & Nkambule, 2017](#); [Sternman, 2000](#); [Vundla, Blignaut, & Crookes, 2017](#)). System dynamics models are usually extremely complicated, with many interacting and counter-balancing loops. Often the problem with these complicated models is over-fitting, meaning that these models are not suitable for forecasting ([Butterworth, Plagányi, Robinson, Moosa, & De Moor, 2015](#)). However, if simple predator-prey models are constructed, these may provide good predictions in the short- to medium-term ([Crookes & Blignaut, 2016b](#); [Crookes, 2017](#); [Swart, 1990](#)). These models form the initial modelling tool for the classification framework.

The system dynamics model is then constructed in a software program such as Vensim®, using known values (as far as possible) for the following parameters: the intrinsic growth rate of the species (r), the

carrying capacity (k), the cost per unit effort (c), the price of the resource (p), and the catchability coefficient (q). However, it is not essential that all parameter values in the model are known. The calibration of the data with historical trends in population abundance and trends in effort data may enable the modeller to determine the value of these missing parameters (see [Fig. 2](#)). The system dynamics model is therefore used to generate the values for r , c , p , q and k that are used in the sustainability assessment.

2.3. Sustainability assessment

In steady state, the resource stock (x) as a proportion of carrying capacity under harvesting is given as:

$$\frac{x}{k} = \frac{c}{pqk} \quad (3)$$

where c is the cost of the resource in question and p is the price of the harvestable stock, q is the catchability coefficient, k represents the carrying capacity, and q is the catchability coefficient.

Based on this simple equation, and the literature, we can derive four sustainability measures representing unitless measures of assessment (see [Appendix A](#) for a derivation of Eq. (3), properties, and more details on these measures). These measures are based on whether the measure increases the equilibrium stock level or decreases it, and are as follows:

- Population measure ($\frac{x}{k}$)

We use this measure to assess whether or not stock in equilibrium exceed maximum sustainable yield (biomass at Maximum Sustainable Yield, hereafter B_MSY). In this analysis we use a very crude measure of B_MSY, namely $0.5k$ for all species, where k is the carrying capacity of the resource. In reality, B_MSY may differ across species, but we use this measure to ensure uniformity across studies. B_MSY is not always a good measure for sustainability, though. [Ling and Milner-Gulland \(2006\)](#) show that, in certain cases, if $h > MSY$ then the resource is not sustainable.

- Harvest measure (h)

Given the weakness identified in the first measure, the harvest measure assesses whether $h > MSY$ (note this this is yield at Maximum Sustainable Yield and not Biomass at Maximum Sustainable Yield as in the previous measure). Following [Milner-Gulland and Rowcliffe \(2007\)](#), MSY is $r_{max} * k / 4$, where r_{max} is the maximum intrinsic rate of increase of the resource.

The last two measures of sustainability are not absolute measures of sustainability, but rather they indicate whether the measure increases sustainability or decreases sustainability.

- Profitability measure ($\frac{c}{p}$)

Profitability is proposed as a sustainability measure by [Milner-Gulland and Rowcliffe \(2007\)](#). Here the profitability measure is c/p , where a value of greater than 1 increases the sustainability of the resource.

- Catchability measure (qk)

The catchability measure is the carrying capacity (k) multiplied by the catchability coefficient (q). If this is less than 1 (in other words the species is difficult to capture), the sustainability of the resource increases. On the other hand, if $qk > 1$ then the sustainability of the resource decreases.

If a resource passes a particular sustainability assessment measure, then a score of 1 is given. The sustainability measures are then summed to generate a “sustainability score” (Sus score). The score (out of 4) is

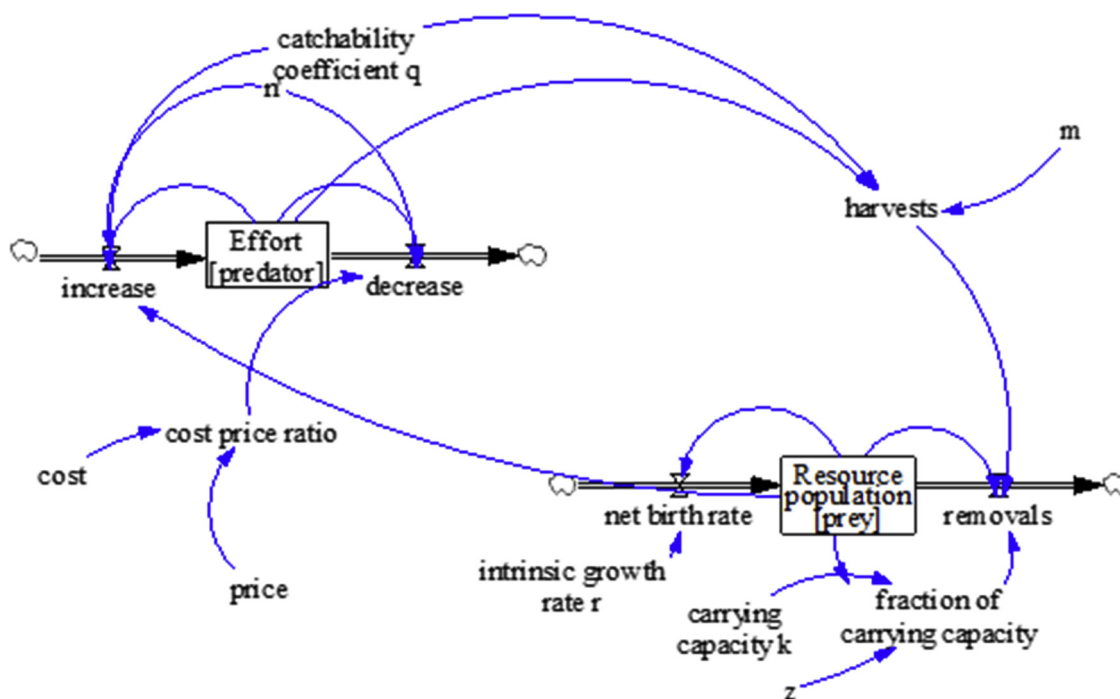


Fig. 1. Simple stock flow diagram developed in Vensim® to model the predator-prey system.

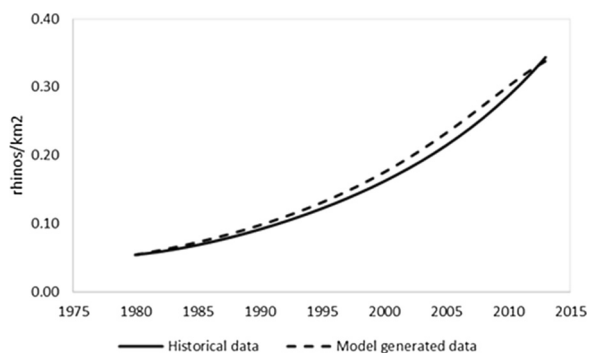


Fig. 2. An example of calibration, in this case a rhino population trajectory, whereby the model-generated data are matched to the historical data in order to estimate unknown parameter values for the sustainability assessment.

then converted to a threat status as follows: Sus score = 4 – Extinction risk: Least concern; Sus score = 3 – Extinction risk: Near threatened; Sus score = 2 – Extinction risk: Vulnerable; Sus score = 1 – Extinction risk: Endangered; Sus score = 0 – Extinction risk: Critically endangered.

In order to test the framework, we apply these four sustainability measures to the two species as mentioned, namely rhino and abalone. The data for these species came from two separate system dynamic models (Crookes, 2016, 2017). The results of the assessment are then compared to IUCN Red List assessments for those species.

2.4. Scenario planning

Scenario planning is a tool used in conservation under conditions of excessive uncertainty which are not controllable (Peterson, Cumming, & Carpenter, 2003). Under certain circumstances there may be too much uncertainty to conduct a full assessment of extinction risk using the aforementioned framework. Scenario planning may be more preferable in these instances. In order to demonstrate this, we extend our analysis to include the following seven species: Minke whale (*Balaenoptera acutorostrata*), Japanese common squid (*Todarodes pacificus*), African civet (*Civettictis civetta*), Mona monkey (*Cercopithecus mona*),

African elephant (*Loxodonta africana*) and Buru babirusa (*Babyrousa babyrussa*). These species were chosen because good data were available to populate all the parameters in the model. The parameters for the various species were obtained from various published research studies (Amundsen, Bjørndal, & Conrad, 1995; Damania et al., 2005; Hoshino, Milner-Gulland, & Hillary, 2012; Milner-Gulland & Clayton, 2002; Milner-Gulland & Leader-Williams, 1992; see also supplementary material S1 for data used and further references). In this instance, rather than comparing the data to the IUCN Red List classification, we used scenario planning as proposed by Cartwright et al. (2013).

For scenario planning, instead of a threat status, a scenario descriptor is assigned to the sustainability score. Box 1 describes the different scenarios in more detail and the implications in terms of protecting the species. For example, if no sustainability assessments are failed (Sus score = 4), then the scenario assessment is plain sailing; if only one of the four sustainability tests is failed (Sus score = 3), then the scenario classification is ‘ready for the storm’; for Sus score = 2 the scenario classification is ‘even keel but going south’; for Sus score = 1, the scenario classification is ‘dangerous waters’; and for Sus score = 0 the scenario classification is ‘Leaky boat, stormy sea’. These scenarios highlight the capacity and motivation of national governments to protect species subject to harvesting, and the possible role of the international communities to promote conservation, for example through the Red List assessments. The scenario planning and Red List assessments are complimentary. The model is used for Red List assessments to inform conservation in cases where good data is available, but is used for scenario planning to inform institutional planning for improve conservation in cases where good data is not available.

2.5. Scope and limitations of the evaluation framework

The objective of this framework is to provide a simplified means of assessing the extinction risk of different species. The framework assumes a logistic function with no non-linear response to density (Fowler term) for all the species modelled. Although this function is unlikely to be realistic for all species, there are a number of reasons why this assumption is adopted. First is to ensure comparability between the different species, second is to reduce dependence upon unavailable data,

Box 1

Description of scenarios used to classify species in terms of IUCN listing/scenario planning.

Plain sailing: In this scenario, species risk of extinction is not a cause for concern. The population is above B_{MSY} , the catchability coefficient is low, harvests are below MSY and profitability is low. (Sus score = 4; IUCN listing = LC).

Ready for the storm: There is a minor risk of species extinction under this scenario. Only one of the sustainability indices indicates unsustainability. In the case of weak institutional capacity it may be desirable to impose a protection status on these resources (the precautionary principle). (Sus score = 3; IUCN listing = NT).

Even keel but going south: In this scenario, future species extinction is a very real risk but there may be some mitigating factors to reduce the risk. Two of the four sustainability measures are adequate. However, at the same time, two of the four measures are inadequate. The development agenda is survivalist, focused on trying to cope with the consequences of unsustainable development and poor economic growth. Weak institutional capacity may further threaten the survival of the species. (Sus score = 2; IUCN listing = VU).

Dangerous waters: The survival of the species is of serious concern in this scenario. Only one of the four sustainability indices indicates a positive outcome. The development agenda is survivalist and support from the international community is needed to ensure survival of species. (Sus score = 1; IUCN listing = EN).

Leaky boat, stormy sea: A grave scenario in which species extinction is virtually guaranteed unless there is dramatic and sustained intervention from the international community. The development agenda is survivalist, but high profitability and low stock densities make survival extremely difficult. Decision-makers generally adopt a short-term perspective and there is little capacity within government to reduce risk. (Sus score = 0; IUCN listing = CR).

(Adapted from Cartwright et al., 2013)

and third is that it is the least data demanding. It may also be shown that the use of 0.5k as the benchmark for the sustainability assessment provides a more conservative assessment of extinction risk for long-lived species. For example, McCullough (1999) argues that the B_{MSY} of long-lived k selected species is approximately 75–80% of k . Rhinos would fit in this category. This implies that harvests should occur when the species is closer to carrying capacity than under our methodology. Therefore, comparing our population measure with 0.5k favours long-lived species and prejudices short-lived species, the latter being more resilient to hunting pressure (e.g. Robinson & Redford, 1994). Our methodology is therefore more precautionary with regard to species which are more threatened due to their long lifespans and commensurate lower reproductive rates (Fowler, 1981). Clark, Brook, Delean, Akçakaya, and Bradshaw (2010) demonstrate that where both the intrinsic growth rate r and the density dependent term (θ) are unknown, it is better to assume $\theta = 1$ since r and θ are not independent of each other, which is also the final reason for adopting the standard logistic function. In order to ensure better comparability between r -values we therefore assume the density dependent term is equal to unity.

The data for the primary resources evaluated (i.e. rhino, abalone) emerge either from the literature, or from a dynamic model, where it is possible to estimate unknown parameters based on the known population trajectories of the species. This approach provides a means of assessing extinction risk where detailed information on the spatial distribution of species or habitat requirements is not available, for example as required by population viability analysis (Akçakaya & Sjögren-Gulve, 2000).

Another question arises as to the applicability of these models for assessing harvested systems. The original Gordon-Schaefer fisheries model used to develop the sustainability measures assumes that harvesting occurs under communal tenure. Gordon (1954) himself states this in his seminal paper, believing that his model had quite limited scope of application. However, the ensuing 60 years have brought quite sharp debate around this into two disparate groups. The first group challenged the definition of communal, arguing that not all communal resources are overexploited and that a more narrow definition tenure should be applied, namely ‘open access’ to describe overexploited stocks (e.g. Berkes, Feeny, McCay, & Acheson, 1989). The conclusion from this is that communal tenure may be beneficial for conservation, and it is worth noting this. However, a second disparate group has demonstrated that these models are applicable even where strict open access did not apply (e.g. Pearce & Turner, 1990). When open access was not applicable, the catch per unit effort c would be higher to not only take into consideration the opportunity cost of harvesting but also include the expected cost of getting caught poaching due to

enforcement¹. Although different resources could exist in different states of tenure, the global c would then be calculated by taking into consideration the factors just mentioned, or alternatively by using optimisation to estimate the missing value of c from a system dynamics model. There is growing support in the literature to confirm this second assessment of the Gordon-Schaefer fisheries model. For example, Erwin Bulte, in his 2003 paper, argues that poaching and open access harvesting are in fact interchangeable (Bulte, 2003). This conclusion is further put forward by Hall, Milner-Gulland, and Courchamp (2008). On the basis of this we conclude that our assessment framework is applicable to all species subject to harvesting.

It is important to emphasise that these are extremely simple system dynamics models used to fit the model with the historical data. For example, the rhino model uses only ten parameters, with only two of them unsupported. The dangers of over-fitting (Ginzburg & Jensen, 2001), therefore, is low. However, even if over-fitting was a concern, the system dynamics model is subjected to a range of validation tests, including sensitivity analysis, extreme conditions testing, structure validation and dimensional consistency testing (see Crookes, 2016, 2017). This exceeds the requirements of Ginzburg and Jensen (2001), who only propose sensitivity analysis as a means of eliminating over-fitted theories. In the system dynamics model, a Monte Carlo simulation is used as the basis for assessing parameter uncertainty as well as variability in the models (see Crookes et al., 2013; Jeon & Shin, 2014). Although no model can be fully validated, it does strengthen the robustness of the model.

The IUCN criteria are designed to be broadly applicable to a wide range of taxa (Collen et al., 2016), and our approach [based on dynamic models] can, at best, only inform about species that are harvested. Therefore, we do not propose our tool as a replacement of the existing tools of assessment, but rather as supplementary to them. However, it is worth noting the potentially substantial number of species that could fall into this category. A recent article published in the journal *Nature* (Maxwell, Fuller, Brooks, & Watson, 2016) analysed the threat information for 8688 ‘threatened’ and ‘near-threatened’ species contained in the IUCN Red List of Threatened Species. Although they found other threats to species, the single biggest threat was overexploitation. It affected 6241 (over 70%) of the species considered.

Most IUCN criteria only assess one component (e.g. population or habitat). Our framework, although simplistic, proposes four binary measures to assess the extinction risk for exploited species. If data are only available for population (Criteria A) or habitat (Criteria B), or any other existing criteria (C–E) then these criteria should be used.

¹ We thank an anonymous reviewer for highlighting this point

Furthermore, our framework presupposes that data are available in order to conduct such an assessment. This may seem quite restrictive, but data from the forest zone of the Afrotropics alone suggests that this is not the case. Taylor et al. (2015) collated data for 177 species across 11 countries in West and Central Africa that would fall within this assessment classification. This excludes data from other sources such as IUCN's own databases.

Threat status is based on the criteria that give the most threatened status. The current approach may therefore supplement current assessment methods if it potentially results in a more conservative assessment of extinction risk compared to the existing methods of assessment. Furthermore, like the IUCN tools which assess symptoms of threat, our tool also assesses symptoms. For example, the catchability coefficient (q) indicates how easily a resource may be harvested, which in turn is dependent on threats such as accessibility of the resource, logging pressure and habitat intactness. Similarly, profitability also potentially indicates symptoms of multiple threats, such as the "banking on extinction" (Mason, Bulte, & Horan, 2012) and "trading on extinction" (Crookes, 2016) hypotheses. We therefore believe that the tool proposed here adds value to the IUCN suite of tools.

The tool is useful for modelling exploited populations across a range of land tenure structures (e.g. communal, private, government). Different tenure structures could also be accommodated through adjustments to the cost price ratio or catchability coefficient. For example, under communal tenure a community has exclusive access to a resource, which may lower the price at which a resource is sold. Catchability may also be reduced if harvesting rules are in place. If tenure structures differ across countries or regions it may be necessary to disaggregate the model across tenure structures or countries to take these factors into consideration. This would add complexity to the model. An alternative is to simply model the total population and attempt to estimate aggregate indicators using Monte Carlo simulation. For species subject to complex land tenure structures or heterogeneous population dynamics across different countries, a more complex model may be required.

In this case we use a scoring method to assess extinction risk. However, it is possible to use the system dynamics model in order to calculate a probability of extinction (see Crookes, 2018). This may align better with the IUCN Red List Criteria E, but is also a topic for future research.

In conclusion, Box (1976) states that "all models are wrong. Some are useful". We believe that, in spite of some limitations in this approach, that it is nonetheless a useful framework for assessing extinction risk in exploited populations.

3. Results

This section provides the results from the classification scheme used for either Red listing (where indicated) or scenario assessment (where data are more uncertain, for example because it may be dated). A Microsoft Excel spreadsheet is provided as supplementary information (S1 file) to provide further clarity and data on the assessment methodology.

3.1. Comparing classification from this study with IUCN classification

First we report on the classification of two species that were evaluated using the methodology described in the study (see Table 1), namely through the construction of a system dynamics model to estimate the values of the unknown parameter values and then comparing these with the IUCN classification (if available).

The *a priori* classification that White Rhinos are near threatened does not take into consideration current exploitation. Our classification that incorporates exploitation assesses White rhinos as endangered (see Table 1). For although White Rhinos numbers have been increasing for years, a 2016 model predicted that populations would decline from

Table 1

An IUCN classification of selected species versus the classification from this study.

Resource	IUCN Listing	This study (S. African populations only)
White Rhino	Near threatened	Endangered
South African abalone	Not assessed	Endangered

The classification for the present study is based on the sustainability scores calculated with parameters from the system dynamics model: Sus score = 4 – Extinction risk: Least concern; Sus score = 3 – Extinction risk: Near threatened; Sus score = 2 – Extinction risk: Vulnerable; Sus score = 1 – Extinction risk: Endangered; Sus score = 0 – Extinction risk: Critically endangered. The extinction risks follow the IUCN Red List definitions of these terms.

18,489 at the end of 2015 to 14,775 at the end 2020 based on last 5 years' poaching (Emslie & Adcock, 2016). Our assessment supports this conclusion. The long-term steady state population levels are very low. The present analysis is based on 2015 data. The population has changed since 2015, but unfortunately no estimates of global White Rhino numbers were available to the authors (at the time of writing) subsequent to 2015. This issue does underscore the importance of repeated and regular reassessments of extinction risk based on latest available data, because the situation may change over time. It is however relatively easy to re-run these models with the latest available data, and obtain new parameter values with which to conduct the assessment.

Our results also show that South African abalone in the wild is subject to a high risk of extinction, given both the low cost-price ratio and harvests exceeding the MSY. The *a priori* hypothesis that abalone is sustainably managed is not supported by our assessment of extinction risk that takes into consideration poaching in the wild. A more accurate assessment would be that South African abalone is endangered. The loss of abalone in the wild may seem insignificant given the extensive commercial farming of abalone. However, its loss potentially has two implications: first, natural breeding stock is lost, and second, there may be impacts on the ecosystem due to the loss of abalone in the wild. Urgent attention is required to conserve this valuable marine resource.

3.2. Extended sustainability assessment: tabular analysis

Next we present the results from the extended sustainability assessment using scenario planning. Table 2 summarises the results of the scoring of the four measures of sustainability employed in the study. None of the resources pass all four sustainability tests. Mona monkeys and African civets pass three of the four tests, and the scenario analysis indicates that a higher level of threat status may be appropriate. Mona monkeys and African civets are both currently both assessed as Least

Table 2

Scenario analysis.

	Population $x^* > 0.5K$	Harvest $h < MSY$	Profitability $c/p > 1?$	Catchability $qk < 1?$	Sus score ($\Sigma y = 1$)
Mona monkey	Y	Y	N	Y	3
African civet	Y	Y	N	Y	3
Common squid	N	Y	Y	N	2
Abalone	N	N	N	Y	1
Black Rhino (LV)	N	Y	N	N	1
Elephant (LV)	N	N	N	Y	1
Minke whale	N	Y	N	N	1
Babirusa	N	N	N	Y	1
White Rhino (SA)	N	Y	N	N	1

Notes: N = Not sustainable; Y = Sustainable. Sus score: 4 = Plain sailing; 3 = Ready for the storm; 2 = Even keel but going south; 1 = Dangerous waters; 0 = Leaky boat, stormy seas. SA = South Africa; LV = Luangwa Valley (Zambia).

Concern (LC). This assessment suggests an assessment of Near Threatened (NT) may be more appropriate, but again we highlight the need to obtain more recent data with which make a more accurate assessment. The need for a more recent assessment is also highlighted by the conflicting findings in the literature. For example, Cowlishaw et al. (2005) conclude that there may be post-depletion sustainability but their study did not detect any Mona Monkeys or African civets in the Takoradi Market where they conducted their assessment. At the same time there is also evidence of changes in spatial harvesting patterns in the Atwemonon market over time, which may point to unsustainability (Crookes, Ankudey, & Milner-Gulland, 2006) but these authors also caution on the limitations of using market studies to assess sustainability. Further work is therefore required to investigate the sustainability of these species further.

The squid species (*T. Pacifus*) was assessed as 'even keel but going south' under our scenario analysis, with two of the four sustainability tests passed. Luangwa Valley Rhino (Rhino (LV)), abalone, Luangwa Valley Elephant (Elephant (LV)), Minke whales and Baribusa are endangered, with only one of the three sustainability tests passed. Under our scenario analysis, these are classified in the 'dangerous waters' category. It should be noted that the Luangwa Valley Elephant assessment uses data from 1985 (see Milner-Gulland & Leader-Williams, 1992). Based on this data, Black Rhino were assessed as endangered. The Luangwa Valley Zambian Black Rhino population subsequently became locally extinct (although Black Rhinos were subsequently reintroduced into Northern Luangwa and the population has recovered somewhat). Although Milner-Gulland and Leader-Williams (1992) only generated data for Luangwa Valley, the assessment of Black Rhinos as endangered would probably have been accurate had our assessment framework been used at the time when they obtained their data. Between 1970 and 1992, the global population of this species decreased 96%, from 65,000 Black Rhinos in 1970 only 2475 surviving in the wild in 1992 (Emslie & Brooks, 1999). This was due to poaching pressure caused by demand for rhino horn in Asia and the Middle East (Emslie & Brooks, 1999). It was only subsequent to this that numbers began recovering (Emslie & Brooks, 1999).

The more recent assessment of White Rhino in South Africa uses data from 2015 (Rhino (SA) in Table 2). This data indicate that White Rhino are also endangered. Only one of the sustainability measures is passed for this species. Lessons learnt from Luangwa Valley show that although populations are currently high this species could also be at risk of extinction due to overexploitation. Again, the data for White Rhino and South African abalone are the most recent of the assessments in this study. In the next section we conclude with an evaluation of these two resources.

3.3. Extended sustainability assessment: graphical analysis

Next we conduct a graphical analysis of the sustainability data for the extended analysis. Fig. 3 makes it possible to unpack the sustainability assessment further by plotting the different sustainability measures on graphs. The horizontal and vertical axes represent the boundaries of sustainability. Sustainability is measured in terms of x/k , which refers to population proportion to carrying capacity, and qk , which refers to the catchability coefficient (see Fig. 3a), or c/p , which refers to the cost-price ratio and qk (see Fig. 3b). In both instances, the further away a population is from the origin, the more that measure contributes to the sustainability (high) or unsustainability (low) of the resource. For example, the catchability coefficient (qk) for squid is extremely high and this, coupled with it being a short-lived species, makes sustainability a great threat (as measured by x/k , see Fig. 3, top graph). White Rhino, on the other hand, are threatened with extinction because of a low x/k ratio (Fig. 3a) and low c/p ratio (Fig. 3b). The catchability measure (x axis, both graphs), is also high for White Rhino populations, further highlighting a vulnerability to overexploitation.

The roman numerals in the different quadrants indicate the number

of sustainability measures passed. In terms of the sustainability measures proposed, the bottom right quadrant is the most undesirable quadrant for a species to be in. By contrast, the top left quadrant is the most desirable. Mona monkeys and African civets, for example, appear to be safe from a stock density perspective; however, low c/p ratios may threaten these species.

4. Discussion

We employ two means of assessing extinction risk in exploited species. Where there is reasonable certainty associated with the data, but not all parameters are known, a predator-prey model may be constructed and calibrated with historical data in order to estimate the unknown parameter values. These values may then be used in a sustainability assessment using IUCN Red List classification. Our analysis here shows that the current assessments of exploited species may not be sufficiently precautionary. Our framework does not seek to replace the current IUCN Red List assessment. Rather, it highlights a number of tools which may be used to improve the assessment of exploited species.

If there is too great a degree of uncertainty associated with the data, then it is not preferable for the tool to be used in a Red List assessment. In this case, a scenario planning approach may be more preferable. To demonstrate this, we employ an extended sustainability assessment. Our framework highlights the importance of taking into consideration profitability parameters in an extinction risk assessment. If the c/p ratio was used as the sole extinction risk measure, then only squid (*T. Pacifus*) of the nine species studied would be sustainable. This is largely consistent with *a priori* expectations. It is only if the profit incentive is removed that population trajectories improve. However, weighting of parameters in the assessment is a normative question and a topic for future research.

Our extended sustainability assessment using scenario analysis also highlights the institutional considerations to be taken into account when populations are overexploited. In particular, our results show that these populations are more at risk of extinction than currently reflected in IUCN Red List assessments. Therefore, institutional factors need to be taken into consideration, including the capacity of national governments to manage the resources in question. Appropriate listings on Red List databases and other interventions by the international community are crucial to ensuring the long-term survival of these species.

Institutional capacity is extremely important when it comes to overexploitation (e.g. Barrett, Brandon, Gibson, & Gjertsen, 2001; Basurto & Coleman, 2010), hence the focus of our extended sustainability on institutional capacity. The weaker the institutions, the more vulnerable to overexploitation and the worse the extinction risk in terms of our classification. Do property rights matter in such an assessment of extinction risk? The answer is yes and no. Yes, property rights are important as they relate to institutional capacity at a local level. However, in term of the requirements of the model, we have demonstrated that a particular property rights regime does not limit the use of the model. It is applicable across all property rights regimes where overexploitation is occurring.

Our sustainability assessment results in a more conservative assessment of extinction risk compared to the IUCN classification. Is it possible to have a too conservative assessment of extinction risk? There are concerns that the IUCN criteria already result in an overly cautious assessment of extinction risk in certain fish populations (e.g. Davies & Baum, 2012). Would a too precautionary assessment not place undue pressure on industries supported by the harvesting of exploited species? These are very legitimate concerns. However, at the same time, the natural environment is under great threat due to human exploitation, to the extent that many believe that a sixth mass extinction of species is underway (Barnosky et al., 2011; Estes et al., 2011). Our tool is consistent with the precautionary principle that states that, under conditions of uncertainty, conservationists should act to ensure the survival of the species in question (Cooney, 2004; IUCN, 2007). However, under

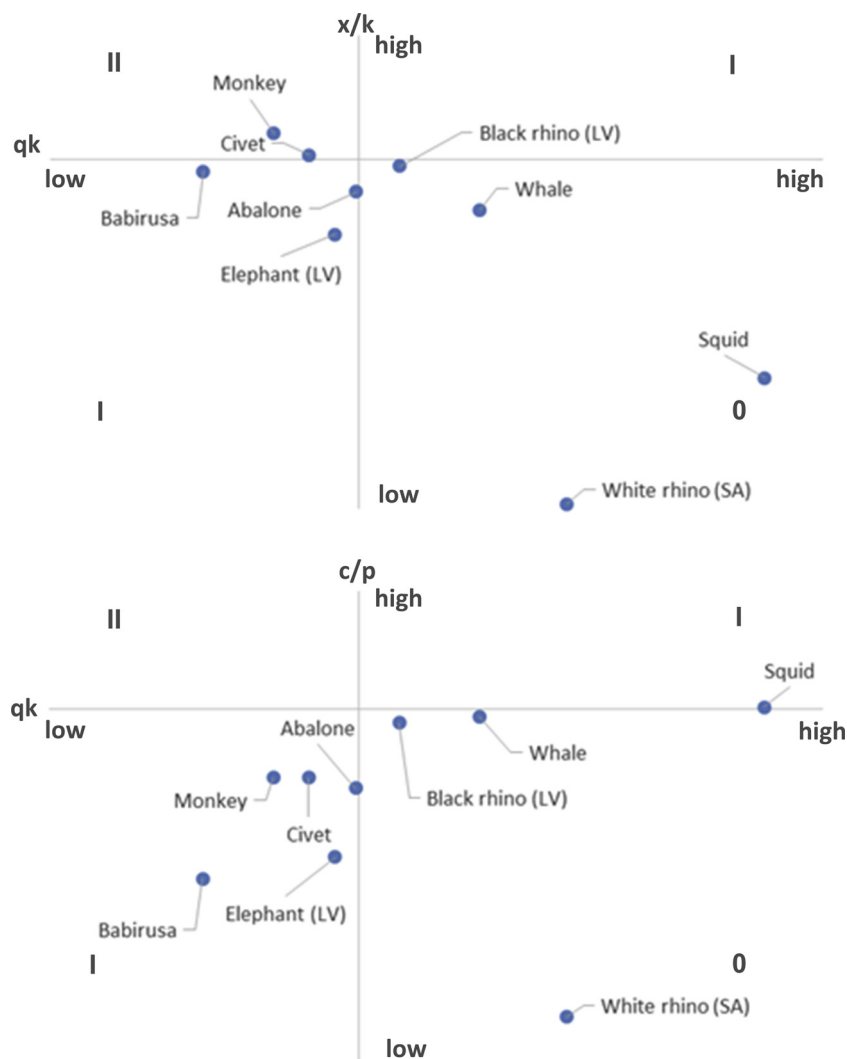


Fig. 3. Illustration of three of the measures of sustainability.

conditions of excessive uncertainty, scenario planning (see Table 2) may be preferable to an actual quantification of extinction risk.

A second possible concern relates to the scope of the assessment. The present analysis of extinction risk (see Table 1) is only for South African populations of the species in question. The South African population would need to be sufficiently representative in order to be used as a global classification for these species. The abalone (*H. Midae*) only occurs off the coast of South Africa, so the South African sub-population encompasses 100% of the global population. South Africa has approximately 93% of the White Rhinos in the world (Emslie et al., 2016). This, it is argued, is a reasonably comprehensive boundary for a global assessment of these species.

However, notwithstanding this concern, our analysis also highlights the possibility that overexploitation of populations in a particular country or region may in fact be indicative of overexploitation of entire populations of species. For example, we noted that the population assessment of Black rhinos in Luangwa valley in 1985 using our methodology probably accurately reflected the situation for the species as a whole at that time. This observation would certainly hold for many fish stocks harvested for consumption. This observation would also most probably hold for many other species harvested for bushmeat as well, since socioeconomic conditions are often comparable across many countries that harvest bushmeat, and if a species is palatable for consumption in one country it is likely to be palatable in other areas where the species occurs (see e.g. Rosser & Mainka, 2002). Even for non-

consumptive harvesting, such as collecting of wildlife for domestication purposes, the same species may be harvested across a variety of local, regional and global populations (such as psittacines). As another example, poaching of rhino horn is widespread for Black and White rhino species. However, it is substantially less for the Greater one horned (Indian) species (*Rhinoceros unicornis*). Emslie, Milliken, and Talukdar (2013) argue that “one can speculate that the dramatic increase in prices paid for African horn and the greater amount of horn/rhino in Africa might be reducing pressure on Asian rhino.” (p.28). Many species therefore share similar characteristics that make them favourable for harvesting, whether this is for consumptive or non-consumptive purposes, and modelling a population in a specific region may be sufficient in order to obtain a global understanding of the extinction risk. Research further investigating this possibility would certainly be informative. If this hypothesis proved incorrect, multi-country assessments may be conducted and the results aggregated.

Nourani, Kaboli, Farhoodinia, and Collen (2017) propose a classification scheme where long-term monitoring data on species are not available. They use scenario analysis to estimate population trajectories and compare their methodology with existing IUCN classifications. Their work addresses IUCN criteria A–D but does not provide an alternative for criterion E (quantitative analysis). The extinction risk framework proposed in this study may have an impact on a number of IUCN criteria, including A (population) or C (small populations). It provides a means to use criterion E (extinction risk) of the IUCN risk

assessment framework, in cases where some monitoring data of population trends are available, but where detailed spatially explicit and habitat specific data are not needed. The framework is useful for exploited species where harvesting and profitability data are available. Although this framework would not be required for all species, our results show that the framework is useful for assessing the extinction risk of exploited species harvested under a range of conditions.

Acknowledgements

This project forms part of a three-year project on new methods for endangered species modelling. Funding from the National Research Foundation (NRF) is gratefully acknowledged. The authors would also like to acknowledge SAEON for hosting the project, and L. van der Elst and E. Belcher for the editing of the manuscript. We also thank E.J. Milner-Gulland, H. Resit Akçakaya and P. Rule for comments on an earlier draft.

Appendix A. deriving the sustainability conditions

Following Clark (1990), the Gordon-Schaefer model is:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{k}\right) - qEx \quad (A1)$$

$$\frac{dE}{dt} = n'E(qx - c/p) \quad (A2)$$

where n' is an adjustment parameter, r is the intrinsic growth rate, x are the stocks (or population), k is the carrying capacity, q is the catchability coefficient, E is the harvesting effort and p is the price of the resource and c is the cost per unit effort. To calculate B_{MSY} , take derivatives of dx/dt with respect to x and set equal to 0. This gives $x = k/2$ or $x/k = 0.5$. This is the first sustainability measure (population measure).

To derive the profitability measure and catchability measure, set $TR-TC = 0$ to obtain stocks at equilibrium. Re-writing gives $x = \frac{c}{pq}$ or $\frac{x}{k} = \frac{c}{pqk}$

The equilibrium is stable if $c/(pq) < k$ (see Holden et al., 2018), and if $c/pq > k$ the population converges on k .

The left hand term (x/k) gives dimensionless stocks and the right hand term ($c/(pqk)$) is the cost price ratio divided by qk^* . If $c/p^* > 1$ the equilibrium stocks (x/k) will increase the term on the left compared with if $c/p^* = 1$. If $c/p^* < 1$ the term on the left will increase. This is the profitability measure. The other term qk^* also generates a unitless estimate. It is basically

$$qk^* = \frac{c/p^*}{x/k} \quad (A3)$$

So it is the amount by which the cost price ratio exceeds the stock ratio. If harvesting costs are low (or prices high) relative to stock densities (in other words if qk is less than 1) then again the term on the left hand side will increase (catchability measure).

Another way of looking at this is to consider the harvest function, $H = qEx$. If units for harvest (H) is the same as the units for the number of individuals in the population (x), the units cancel each other out. Therefore, the catchability coefficient's units are 1/effort units. Effort could be number of hours, number of expeditions and so on and vary from study to study. Therefore, the catchability coefficient's units are not comparable across studies. Also, the c 's units are costs per unit effort and p 's units are price per unit harvest. Often these units are also different. In order to derive dimensionless units for qk and c/p , the solution is to multiply the top and bottom by catch per unit effort (H/E). Dimensionlessly, this means that qk^* is actually:

$$\frac{qk}{H/E} \quad (A4)$$

and c/p^* is actually

$$\frac{c}{pH/E} \quad (A5)$$

For the catchability coefficient measure this means that if $qk > H/E$ (in other words catchability is high relative to unit harvests), sustainability will decrease ($qk^* > 1$), and for the profitability measure it means that if $c/p > H/E$ (in other words costs are high relative to unit harvests) the sustainability will increase ($c/p^* > 1$). It is these unit free measures that are used in the assessment. The supplementary material (S1) contains more details on this calculation.

Appendix B. Comparison between Microsoft Excel Solver and Vensim® optimisation to estimate a missing parameter value in a predator-prey model

Here we compare the optimisation functions of Vensim® and Microsoft Excel Solver in the case where one parameter value in the model is unknown. We use the predator-prey model of Opsomer and Conrad (1994) in order to evaluate this. The model differential equations are:

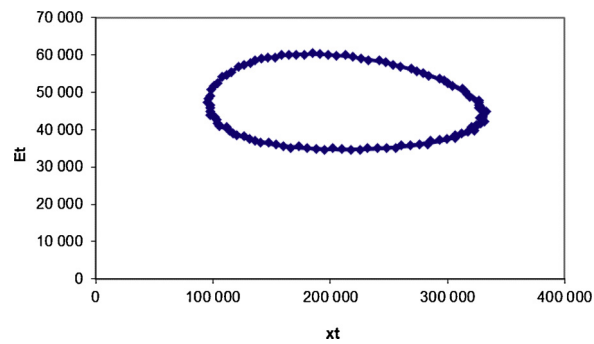
$$\frac{dx}{dt} = (ax^b - wx) - dqEx^v \quad (B1)$$

$$\frac{dE}{dt} = n'E \left(qx^v - \frac{c}{p} \right) \quad (B2)$$

Where E is fishing effort in time t , x is stocks of Northern anchovy in time t , n' is the adjustment coefficient c/p is the cost price ratio and the other parameters are constants. This is a slightly more general form of the model equations given in Appendix A (Equation (B1) reduces to Equation (A1), by setting $b = 2$, $r = -w$, $v = 1$ and $k = (w/a)$, and $d = 1$, and Equation (B2) reduces to Equation (A2) by setting $v = 1$). We use this more general form of the model, since the authors have already derived the conditions under which a limit cycle (where effort and stocks fluctuate and never converge on an equilibrium) would be achieved. In their paper, this is attained for a value for $c/p = 3$ and $n' = 0.1$. The true value of the parameters in this case would be (Table B1):

Table B1
'true' values of parameters in case of limit cycle.

b =	0.7365
c = 1/d =	1.333333
d =	0.75
a =	38.5132
q =	0.03147
v =	0.3739
n' =	0.1
c/p =	3
w =	1

**Fig. B1.** plot of x_t against E_t .**Table B2**
Summary table for different optimisation routines.

	n'	RMSE
Constraint: $0 < n' < 1$		
Starting	0.05	9,601
Microsoft Excel Solver GRG2 optimisation	0.044961	9,481
Vensim® Powell optimisation (v.5.10e)	0.004223	9,236
Vensim® Powell optimisation (v.6.4b)	0.004221	9,236
True	0.1	0
Constraint: $0 < n' < 0.19$		
Vensim® MCMC (v 6.4b)	0.1*	0

Notes: RMSE = Root Mean Square Error.

* Convergence in all chains after 1671 iterations.

The graphical plot of x_t and E_t is shown in Fig. B1.

If we assume that n' is unknown, we wish to establish which optimisation routine will converge on the 'true' solution. The optimisation routines employed include:

- 1 Microsoft Excel Solver GRG2 optimisation
- 2 Vensim® Powell optimisation (two software versions, v.5.10e and v.6.4b)
- 3 Vensim® Markov Chain Monte Carlo (MCMC) simulation

We estimate the true E_t and then compare E_t under the different estimates for n' by comparing the sum of differences (the lower the sum of differences the closer n' is to its 'true' value. We start with a 'best guess' of $n' = 0.05$). Table B2 summarises the results.

The results show that although Powell optimisation resulted in an improvement on Microsoft Excel Solver for this type of problem (limit cycle), only Vensim® MCMC was able to arrive at the 'true' value of the parameter. It is therefore preferable to use Vensim® MCMC over Excel solver to obtain the value of the missing parameters in the case of predator-prey models characterised by complex cyclical fluctuations.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jnc.2019.125750>.

References

- Abernethy, K. A., Coad, L., Taylor, G., Lee, M. E., & Maisels, F. (2013). Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. *Philosophical Transactions of the Royal Society B*, 368, 20120303. <https://doi.org/10.1098/rstb.2012.0303>.
- Akçakaya, H. R., & Ferson, S. (2001). *Ramas red list: Threatened species classifications under uncertainty: User manual for version 2.0*. New York: Applied Biomathematics.
- Akçakaya, H. R., & Sjögren-Gulve, P. (2000). Population viability analysis in conservation planning: An overview. *Ecological Bulletins*, 48, 9–21.
- Akçakaya, H. R., Ferson, S., Burgman, M. A., Keith, D. A., Mace, G. M., & Todd, C. A. (2000). Making consistent IUCN classifications under uncertainty. *Conservation Biology*, 14, 1001–1013. <https://doi.org/10.1046/j.1523-1739.2000.99125.x>.

- Allebone-Webb, S. M., Kumpel, N. F., Rist, J., Cowlisshaw, G., Rowcliffe, J. M., & Milner-Gulland, E. J. (2011). Use of market data to assess bushmeat hunting sustainability in Equatorial Guinea. *Conservation Biology*, 25, 597–606. <https://doi.org/10.1111/j.1523-1739.2011.01681.x>.
- Amundsen, E. S., Bjørndal, T., & Conrad, J. M. (1995). Open access harvesting of the Northeast Atlantic minke whale. *Environmental Resource Economics*, 6, 167–185. <https://doi.org/10.1007/BF00691682>.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57. <https://doi.org/10.1038/nature09678>.
- Barrett, C. B., Brandon, K., Gibson, C., & Gjertsen, H. (2001). Conserving tropical biodiversity amid weak institutions. *BioScience*, 51(6), 497–502. [https://doi.org/10.1641/0006-3568\(2001\)051\[0497:CTBAWI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0497:CTBAWI]2.0.CO;2).
- Basurto, X., & Coleman, E. (2010). Institutional and ecological interplay for successful self-governance of community-based fisheries. *Ecological Economics*, 69(5), 1094–1103. <https://doi.org/10.1016/j.ecolecon.2009.12.001>.
- Berkes, F., Feeny, D., McCay, B. J., & Acheson, J. M. (1989). The benefits of the commons. *Nature*, 340(6229), 91.
- Bestler, R., Bliognaut, J. N., & Crookes, D. J. (2019). The impact of human behaviour and restoration on the economic lifespan of the proposed Ntabelanga and Laleni dams, South Africa: A system dynamics approach. *Water Resources and Economics*, 26, 100126. <https://doi.org/10.1016/j.wre.2018.08.002>.
- Bjørndal, T., & Conrad, J. M. (1987). The dynamics of an open access fishery. *Canadian Journal of Economics*, 20, 74–85. <https://doi.org/10.2307/135232>.
- Bliognaut, J. N., & Aronson, J. (2008). Getting serious about maintaining biodiversity. *Conservation Letters*, 1, 12–17. <https://doi.org/10.1111/j.1755-263X.2008.00006.x>.
- Bliognaut, J. N., De Wit, M. P., & Barnes, J. (2008). The economic value of elephants. In R. J. Scholes, & K. G. Mennell (Eds.). *Elephant management – A scientific assessment for South Africa*. Johannesburg: Wits University Press.
- Box, G. E. P. (1976). Science and statistics. *Journal of the American Statistical Association*, 71, 791–799. <https://doi.org/10.1080/01621459.1976.10480949>.
- Bulte, E. (2003). Open access harvesting of wildlife: The poaching pit and conservation of endangered species. *Agricultural Economics*, 28(1), 27–37.
- Butterworth, D. S., Plagányi, É. E., Robinson, W. M. L., Moosa, N., & De Moor, C. L. (2015). Penguin modelling approach queried. *Ecological Modelling*, 316, 78–80.
- Cartwright, A., Roberts, D., Bliognaut, J. N., De Wit, M. P., Goldberg, K., Mander, M., et al. (2013). Economics of climate change adaptation at the local scale under conditions of uncertainty and resource constraints: The case of Durban. *Environment and Urbanization*, 25, 139–156. <https://doi.org/10.1177/0956247813477814>.
- Clark, F., Brook, B. W., Delean, A., Akçakaya, H. R., & Bradshaw, C. J. (2010). The theta-logistic is unreliable for modelling most census data. *Methods in Ecology and Evolution*, 1, 253–262. <https://doi.org/10.1111/j.2041-210X.2010.00029.x>.
- Clark, C. W. (1990). *Mathematical bioeconomics. The optimal management of renewable resources* (2nd ed.). New York: Wiley.
- Collen, B., Dulvy, N. K., Gaston, K. J., Gärdenfors, U., Keith, D. A., Punt, A. E., et al. (2016). Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biology Letters*, 12, 20150843.
- Cooney, R. (2004). *The precautionary principle in biodiversity conservation and natural resource management: An issues paper for policy-makers, researchers and practitioners*. Switzerland and Cambridge: IUCN.
- Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signorel, L., Bull, L., et al. (2006). Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biology*, 4(12), e415. <https://doi.org/10.1371/journal.pbio.0040415>.
- Cowlisshaw, G., Mendelson, S., & Rowcliffe, J. M. (2005). Evidence for post-depletion sustainability in a mature bushmeat market. *The Journal of Applied Ecology*, 42, 460–468. <https://doi.org/10.1111/j.1365-2664.2005.01046.x>.
- Crookes, D. J. (2016). Trading on extinction: An open access deterrence model for the South African abalone fishery. *South African Journal of Science*, 112, 105–113. <https://doi.org/10.17159/sajs.2016/20150237>.
- Crookes, D. J. (2017). Does a reduction in the price of rhino horn prevent poaching? *Journal for Nature Conservation*, 39, 73–82. <https://doi.org/10.1016/j.jnc.2017.07.008>.
- Crookes, D. J. (2018). Does the construction of a desalination plant necessarily imply that water supply costs will increase? A system dynamics analysis. *Water Resources and Economics*, 21, 29–39. <https://doi.org/10.1016/j.wre.2017.11.002>.
- Crookes, D. J., & Bliognaut, J. N. (2015). Debunking the myth that a legal trade will solve the rhino horn crisis: A system dynamics model for market demand. *Journal for Nature Conservation*, 28, 11–18. <https://doi.org/10.1016/j.jnc.2015.08.001>.
- Crookes, D. J., & Bliognaut, J. N. (2016b). Predator-prey analysis using system dynamics: An application to the steel industry. *South African Journal of Economic and Management Sciences*, 19, 733–746. <https://doi.org/10.4102/sajems.v19i5.1587>.
- Crookes, D. J., & Bliognaut, J. N. (2016a). A categorisation and evaluation of rhino management policies. *Development Southern Africa*, 33, 459–469. <https://doi.org/10.1080/0376835X.2016.1179100>.
- Crookes, D. J., Ankudey, N., & Milner-Gulland, E. J. (2006). The usefulness of a long-term bushmeat market dataset as an indicator of system dynamics. *Environmental Conservation*, 32, 333–339. <https://doi.org/10.1017/S037689290500250X>.
- Crookes, D. J., & Bliognaut, J. N. (2019). Investing in natural capital and national security: A comparative review of restoration projects in South Africa. *Heliyon*, 5(5), e01765. <https://doi.org/10.1016/j.heliyon.2019.e01765>.
- Crookes, D. J., Bliognaut, J. N., De Wit, M. P., Esler, K. J., Le Maitre, D. C., Milton, S. J., et al. (2013). System dynamic modelling to assess economic viability and risk trade-offs for ecological restoration in South Africa. *Journal of Environmental Management*, 120, 138–147. <https://doi.org/10.1016/j.jenvman.2013.02.001>.
- Damania, R., Milner-Gulland, E. J., & Crookes, D. J. (2005). A bioeconomic model of bushmeat hunting. *Proceedings of the Royal Society B*, 272, 259–266.
- Davies, T. D., & Baum, J. K. (2012). Extinction risk and overfishing: Reconciling conservation and fisheries perspectives on the status of marine fishes. *Scientific Reports*, 2. <https://doi.org/10.1038/srep00561> Article number: 561.
- Dulvy, N. K., Ellis, J. R., Goodwin, N. B., Grant, A., Reynolds, J. D., & Jennings, S. (2004). Methods of assessing extinction risk in marine fishes. *Fish and Fisheries*, 5, 255–276. <https://doi.org/10.1111/j.1467-2679.2004.00158.x>.
- Emslie, R. H., Milliken, T., & Talukdar, B. (2013). African and Asian rhinoceroses – Status, conservation and trade. *CITES Report of the Secretariat "Species Trade and Conservation- Rhinoceroses". Sixteenth Meeting of the Conference of the Parties Bangkok (Thailand), 3-14 March 2013* CoP16 Doc. 54.2 (Rev. 1).
- Emslie, R. H., Milliken, T., Talukdar, B., Ellis, S., Adcock, K., & Knight, M. H. (2016). African and Asian rhinoceroses – Status, conservation and trade. *A Report from the IUCN Species Survival Commission (IUCN SSC) African and Asian Rhino Specialist Groups and TRAFFIC to the CITES Secretariat Pursuant to Resolution Conf. 9.14 (Rev. CoP15) CoP17 Doc 68*.
- Emslie, R., & Adcock, K. (2016). A conservation assessment of ceratotherium simum simum. In M. F. Child, L. Roxburgh, E. Do Linh San, D. Raimondo, & H. T. Davies-Mostert (Eds.). *The Red list of mammals of South Africa, Swaziland and Lesotho*. South Africa: South African National Biodiversity Institute and Endangered Wildlife Trust.
- Emslie, R., & Brooks, M. (1999). *African rhino. Status survey and conservation action plan*. Gland, Switzerland and Cambridge, UK: IUCN/SSC African Rhino Specialist Group IUCN, ix + 92 pp.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., et al. (2011). Trophic downgrading of planet Earth. *Science*, 333, 301–306. <https://doi.org/10.1126/science.1205106>.
- Fa, J. E., & Brown, D. (2009). Impacts of hunting on mammals in African tropical moist forests: A review and synthesis. *Mammal Review*, 39, 231–264. <https://doi.org/10.1111/j.1365-2907.2009.00149.x>.
- Fowler, C. W. (1981). Density dependence as related to life history strategy. *Ecology*, 62, 602–610. <https://doi.org/10.2307/1937727>.
- Gordon, H. S. (1954). The economic theory of a common-property resource: The fishery. *The Journal of Political Economy*, 62(2), 124–142.
- Ginzburg, L. R., & Jensen, C. X. J. (2001). Rules of thumb for judging ecological theories. *Trends in Ecology & Evolution*, 19, 121–126. <https://doi.org/10.1016/j.tree.2003.11.004>.
- Hall, R. J., Milner-Gulland, E. J., & Courchamp, F. (2008). Endangering the endangered: The effects of perceived rarity on species exploitation. *Conservation Letters*, 1, 75–81. <https://doi.org/10.1111/j.1755-263X.2008.00013.x>.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H., et al. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, 330, 1503–1509.
- Holden, M. H., Biggs, D., Brink, H., Bal, P., Rhodes, J., & McDonald-Madden, E. (2018). Increase anti-poaching law-enforcement or reduce demand for wildlife products? A framework to guide strategic conservation investments. *Conservation Letters*, 1–9. <https://doi.org/10.1111/conl.12618>.
- Holden, M. H., & McDonald-Madden, E. (2017). High prices for rare species can drive large populations extinct: The anthropogenic Allee effect revisited. *Journal of Theoretical Biology*, 429, 170–180. <https://doi.org/10.1016/j.jtbi.2017.06.019>.
- Hoshino, E., Milner-Gulland, E. J., & Hillary, R. M. (2012). Bioeconomic adaptive management procedures for short-lived species: A case study of Pacific saury (*Cololabis saira*) and Japanese common squid (*Todarodes pacificus*). *Fisheries Research*, 121, 17–30. <https://doi.org/10.1016/j.fishres.2012.01.007>.
- IUCN (2007). Guidelines for applying the precautionary principle to biodiversity conservation and natural resource management. *As Approved by the 67th Meeting of the IUCN Council, 14-16 May*.
- IUCN (2012). *IUCN red list categories and criteria: Version 3.1* (2nd edition). Gland and Cambridge: IUCN.
- Jeon, C., & Shin, J. (2014). Long-term renewable energy technology valuation using system dynamics and Monte Carlo simulation: Photovoltaic technology case. *Energy*, 66, 447–457. <https://doi.org/10.1016/j.energy.2014.01.050>.
- Larrosa, C., Carrasco, L. R., & Milner-Gulland, E. J. (2016). Unintended feedbacks: Challenges and opportunities for improving conservation effectiveness. *Conservation Letters*, 9, 316–326. <https://doi.org/10.1111/conl.12240>.
- Lindsey, P. A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., et al. (2013). The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation*, 160, 80–96. <https://doi.org/10.1016/j.biocon.2012.12.020>.
- Ling, S., & Milner-Gulland, E. J. (2006). Assessment of the sustainability of bushmeat hunting based on dynamic bioeconomic models. *Conservation Biology*, 20, 1294–1299. <https://doi.org/10.1111/j.1523-1739.2006.00414.x>.
- Lopes, A. A. (2014). Civil unrest and the poaching of rhinos in the Kaziranga National Park, India. *Ecological Economics*, 103, 20–28. <https://doi.org/10.1016/j.ecolecon.2014.04.006>.
- Mace, G. M., Collar, N. J., Gaston, K. J., Hilton-Taylor, C., Akçakaya, H. R., Leader-Williams, N., et al. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, 22, 1424–1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>.
- Mason, C. F., Bulte, E. H., & Horan, R. D. (2012). Banking on extinction: Endangered species and speculation. *Oxford Review of Economic Policy*, 28, 180–192. <https://doi.org/10.1093/oxrep/grs006>.
- Maxwell, S., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). The ravages of guns, nets and bulldozers. *Nature*, 536, 143–145. <https://doi.org/10.1038/536143a>.
- McCullough, D. R. (1999). Density dependence and life-history strategies of ungulates. *Journal of Mammalogy*, 80, 1130–1146. <https://doi.org/10.2307/1383164>.
- Milner-Gulland, E. J., & Akçakaya, H. R. (2001). Sustainability indices for exploited populations. *Trends in Ecology and Evolution*, 16, 586–592. [https://doi.org/10.1016/S0169-5347\(01\)02278-9](https://doi.org/10.1016/S0169-5347(01)02278-9).

- Milner-Gulland, E. J., & Bennett, E. L. (2003). Wild meat: The bigger picture. *Trends in Ecology & Evolution*, 18, 351–357. [https://doi.org/10.1016/S0169-5347\(03\)00123-X](https://doi.org/10.1016/S0169-5347(03)00123-X).
- Milner-Gulland, E. J., & Clayton, L. (2002). The trade in babirusas and wild pigs in North Sulawesi, Indonesia. *Ecological Economics*, 42, 165–183. [https://doi.org/10.1016/S0921-8009\(02\)00047-2](https://doi.org/10.1016/S0921-8009(02)00047-2).
- 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. *The Journal of Applied Ecology*, 29, 388–401. <https://doi.org/10.2307/2404508>.
- Milner-Gulland, E. J., & Rowcliffe, M. J. (2007). *Wildlife conservation and sustainable use: A handbook of techniques*. Oxford: Oxford University Press.
- Mudavanhu, S., Blignaut, J. N., Vink, N., Crookes, D., & Nkambule, N. (2017). An economic analysis of different land-use options to assist in the control of the invasive Prosopis (Mesquite) tree. *African Journal of Agriculture and Resource Economics*, 12(4), 366–411.
- Nasi, R., Taber, A., & Van Vliet, N. (2011). Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *The International Forestry Review*, 13, 355–368. <https://doi.org/10.1505/146554811798293872>.
- Nourani, E., Kaboli, M., Farhoodinia, M., & Collen, B. (2017). National assessment of threatened species using sparse data: IUCN Red List classification of Anatidae in Iran. *Animal Conservation*, 20, 42–50. <https://doi.org/10.1111/acv.12282>.
- Opsomer, J.-D., & Conrad, J. M. (1994). An open-access analysis of northern anchovy fishery. *Journal of Environmental Economics and Management*, 27, 21–37. <https://doi.org/10.1006/jeem.1994.1023>.
- Pauly, D., Watson, R., & Alder, J. (2005). Global trends in world fisheries: Impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 360, 5–12. <https://doi.org/10.1098/rstb.2004.1574>.
- Pearce, D. W., & Turner, R. K. (1990). *Economics of natural resources and the environment*. Baltimore: The John Hopkins University Press Third impression.
- Peterson, G. D., Cumming, G. S., & Carpenter, S. R. (2003). Scenario planning: A tool for conservation in an uncertain world. *Conservation Biology*, 17, 358–366. <https://doi.org/10.1046/j.1523-1739.2003.01491.x>.
- Purvis, A., Gittleman, J. L., Cowlishaw, G., & Mace, G. M. (2000). Predicting extinction risk in declining species. *Proceedings of the Royal Society of London Series B*, 267, 1947–1952. <https://doi.org/10.1098/rspb.2000.1234>.
- Robinson, J. G., & Bennett, E. L. (2004). Having your wildlife and eating it too: An analysis of hunting sustainability across tropical ecosystems. *Animal Conservation*, 7, 397–408. <https://doi.org/10.1017/S1367943004001532>.
- Robinson, J. G., & Redford, K. H. (1994). Measuring the sustainability of hunting in tropical forests. *Oryx*, 28, 249–256. <https://doi.org/10.1017/S0030605300028647>.
- Rosser, A. M., & Mainka, S. A. (2002). Overexploitation and species extinctions. *Conservation Biology*, 16(3), 584–586. <https://doi.org/10.1046/j.1523-1739.2002.01635.x>.
- Saayman, M., & Saayman, A. (2017). Is the rhino worth saving? A sustainable tourism perspective. *Journal of Sustainable Tourism*, 25, 251–264. <https://doi.org/10.1080/09669582.2016.1197229>.
- Sterman, J. D. (2000). *Business dynamics: Systems thinking and modeling for a complex world*. Boston: Irwin/McGraw-Hill.
- Swart, J. (1990). A system dynamics approach to predator–prey modelling. *System Dynamics Review*, 6, 94–99.
- Taylor, G., Scharlemann, J. P., Rowcliffe, M., Kumpel, N., Harfoot, M. B., Fa, J. E., et al. (2015). Synthesising bushmeat research effort in West and Central Africa: A new regional database. *Biological Conservation*, 1, 199–205. <https://doi.org/10.1016/j.biocon.2014.11.001>.
- Vundla, T., Blignaut, J. N., & Crookes, D. (2017). Aquatic weeds: to control or not to control. The case of the Midmar Dam, KwaZulu-Natal, South Africa. *African Journal of Agricultural and Resource Economics*, 12(4), 412–429.
- Wilén, J. E. (1976). *Common property resources and the dynamics of overexploitation: The case of the North Pacific Fur Seal*. University of British Columbia, Department of Economics Working 18 Paper No. 3, Vancouver.
- Wilkie, D. S., Starkey, M., Abernethy, K., Effa Nsame, E., Telfer, P., & Godoy, R. (2005). Role of prices and wealth in consumer demand for bushmeat in Gabon, Central Africa. *Conservation Biology*, 19, 1–7. <https://doi.org/10.1111/j.1523-1739.2005.00372.x>.