THE USE OF A

DELPHI TECHNIQUE WITH GIS FOR ESTIMATING

THE GLOBAL ABUNDANCE OF TOP PREDATORS:

THE LION IN AFRICA

P. Ferreras* and S H Cousins, Ecosystems Group, IERC, Cranfield University, Cranfield, Beds, MK43 0AL

*Present address, Zoology Department, Oxford University, South Parks Road, Oxford OX1 3PS, UK

revised 25th Oct 1996 ms dated 14 August 1996 Key words

New Methods, Ecosystem theory, biodiversity, human impact measure, environmental assessment, uncertainty, Delphi, Top Predators, Lion.

•

Summary

1. A new method is presented for estimating the abundance of a species where a Delphi technique for consulting experts is combined with the GIS manipulation of biological data (Leaf Area Index) and databases describing human activities. Spice by a Gis

2. Fourteen experts on lion populations *Panthera leo* were identified and asked to prioritise factors which affect the abundance of lions inside and outside national parks or protected areas. They were also asked to comment on the factors identified from the literature and adjust a map predicting lion abundances based on those factors.

3. A consensus was reached after two iterations of consulting the experts and a third and final map estimating the abundance of lions outside protected areas was produced. A total population of 75,800 representing 57,200 outside protected areas and 18,600 inside was estimated to be representative of 1980.

4. A population of 784,700 was estimated over the present range of the lion if contemporary human activities were absent. The comparison of the existing and potential populations represents one summary measure of human impact on ecosystems. In this framework, top predators define ecosystems as objects rather than as concepts.

5. Sensitivity tests were used to prioritise observation effort and a list of methods for fieldwork, supplied by the experts, were proposed as techniques to test the above estimates.

INTRODUCTION

The measurement of human impact on the global system requires the definition of a reference state representing pre-human impact and comparison to a known present state. At the global level changes in temperature and atmospheric consistuents have been of particular interest. Recent monitoring has allowed trends to be established which then in turn require comparison to a baseline as for example in the PAGES program of IGBP objectives to put recent trends in global temperature in a 600077 year context. In ecology species extinctions is one measure which has been aggregated to the global level and compared to a baseline estimate of global species number. Another method of measuring the human impact on ecosystems is to compare the existing abundance of large top predators to a reference state of their abundance where modern humans are assumed absent. Human expansion has long reduced the abundance of large top predators; patoralism has led to hunting to prevent predators killing livestock; agriculture removes foraging areas of the predators herbivorous prey; habitat loss or disturbance also have negative effects on the predators.

rebr

oţ

There are also theoretical reasons why a count of top predators compliments biodiversity measures in ecology. Top predators can be used to define ecosystems as bounded objects (Cousins 1990) in which energy flows from the green plant to the top predator. Quantifying the removal of these ecosystem objects where they recently existed is a direct measure of global human impact on ecosystems (Cousins 1994). The count of top predators is thus a quantitative measure of the state of global ecosystems to compliment the qualitative measure ie the number tot types of life on earth. Both measures have uncertainties. In this

15

paper we use a technique, Delphi analysis, which is designed to structure uncertain knowledge, to determine a first estimate of the top predator measure of Human impact at a continental scale.

It is increasingly true that large top predators are confined to national parks or protected areas, or are found in regions remote from human activity (Nowell & Jackson 1996). Globally the abundance of large top predators is a measure of the number of full scale ecosystem objects present on earth (Cousins 1994). Estimating and monitoring the abundance of top predators is important for the conservation of the predators, their prey and their habitat, as well as providing a measure of human impact.

Global assessments of top predator abundance pose several problems, derived mainly from the predator's biology. Being widely distributed large animals, the areas to prospect are usually also large and heterogeneous. Due to the generally elusive behaviour of predators they are difficult to count, and so studies of their distribution are not common. These studies usually involve indirect measures of their abundance and refer to geographically restricted areas. Pugmarks are successfully used to count tigers (Panthera tigris) in India, (Jackson 1994); hunting numbers serve as estimates of wolves (Canis lupus), bears (Ursus arctos), lynx (Lynx lynx) (...refs.., Scandinavia, USA); scent stations were used to estimate bobcat (Lynx rufus) populations (Conner, Labisky and Progulske 1983). But global estimations of top predators are dificult to obtain, even with indirect methods (an exception, perhaps the tiger: Jackson 1994).

Even being one of the more observable felids, estimates of the lion's (Panthera leo) world population are still guite imprecise. According to the Cat Action Plan (Nowell & Jackson, 1996), between 30,000 and 100,000 African lions live in the wild at present (outside Africa, only a small population c. 300 of India. Detailed Asiatic lion survives in information on population size is only available for a handful of lion populations in well studied and controlled protected areas (Stander, 1991 1992a, 1992b; Eloff, 1973; Smuts, 1976; Ruggiero, 1991; Bertram, 1973; Rudnai 1973a, 1973b, 1974; Packer et al., 1991; Van Ordsol et al., 1985; Packer et al., 1988). However, little is known about the situation of lion populations outside protected areas, where lion numbers are strongly affected by (Nowell & Jackson 1996). human activities

Revis

1993

A Johnsi

Geographical Information Systems (GIS) have been proved useful for conservation assessment of endangered species, e.g. the Florida panther (Maehr and Cox, 1995) and the African elephant (Michelmore, 1994). We have used GIS as a tool to model lion distribution and abundance in Africa taking into account natural and human-related variables. We used a Delphi technique (Brown and Helmer 1964), as an interactive method to check and improve our model results. The effect of the technique is to formalize current expert opinion on lion abundance and to seek a consensus on the estimating technique used.

Our objectives were: 1) to develop a technique to estimate global lion distribution using a GIS containing a plant productivity database and human activities databases; 2) to calibrate and improve this estimate through specific structured questionnaires sent to lion experts

most

METHODS

As а base map we have used lion geographical the distribution map for Africa (Nowell and Jackson 1996), and we assume that the lion does not occur outside this area. Following these authors, confirmed lion presence occurs in a number (49) of protected areas (mainly National Parks) inside this maximum current range, but no information is available outside such areas. We built a lion density geo-referenced database from the information contained in 37 studies on 19 African lion populations inside parks (see Table 1).

TABLE 1 HERE

As a measure of potential vegetation we used Woodward et al. (1995) Leaf Area Index (LAI), which takes into account climate (temperature and rainfall) and soil characteristics. We identified the potential LAI value for each geo-referenced data point to obtain the relationship between potential primary productivity and reported lion density (Fig. 1).

FIGURE 1 HERE

This empirical relationship characterises the energy input to an ecosystem and its resultant output as lion density but in doing so treats the contents of ecosystem (or ecosystem object) as a black box. The relationship between primary productivity and top predators is consistent with Colinvaux and Barnett (1979) who suggested that the density of top predators is a synoptic measure of the energy efficiency of an ecosystem and that this would vary with primary productivity. Assuming the absence of human activity, the potential lion densities in the distribution area (Fig. 2) can be estimated from the relationship with LAI. Under present conditions these densities are only commonly found in protected areas. The potential lion population where individuals are defined as adults of sub-adults (- define-) is the sum of these densities over the area of the present range and this totals 784,700 individuals.

X

(soults: 4+ years; mb-soults: 2-4 years; Statespher Scholler 1972) FIGURE 2 HERE

Outside protected areas, where human activity has the greatest impact, there is little information available to us and to derive an estimate we have adopted a Delphi technique in combination with geographical databases in a GIS (IDRISI Extense 1995)

Within the species current range we have combined the lion density - vegetation (LAI) relationship, which we call the "positive factor", with a series of "negative factors" arising from human activities. We used a series of decision rules which we derived from the literature about how human impact reduces the potential natural lion density through human settlement (UNEP GRID), agriculture or cattle density. We made these rules explicit as the Delphi progressed. We assume that lions are not present where the land is used for agriculture, and that the lion density reduction is related to the extent of agriculture in any one grid square. We used Wilson & Henderson-Sellers (1985) database as the source for agricultural land use. This and the rest of the global databases we have used have a resolution of 1 degree latitude x 1 degree longitude, which represents 110 x 110 km at the equator. We assumed that lions, unless in a protected area, would be also absent in squares with high human populations and that lion density would be reduced in areas with intermediate human densities. Cattle farming has highly significant negative effects on lion abundance. This can be indirect by the replacement of lion prey by livestock, or through a direct effect by the extermination of lions which are considered a potential risk to cattle. We used Aldeajayai & Crowder (1985) as source for cattle densities in Africa. (Figure 3)

Fibure 3 Hore

The IDRISI package has been used to manipulate the different geographical databases and to produce our model of lion abundance distribution. We supposed that lion density outside parks decreases with distance from parks, all other factors being equal. In order to model this effect we have estimated for each square an effective distance to the nearest protected area which is a function not only of the real distance but also a function of the habitat between them. To do this we used the inverse of the habitat suitability values to define a Frictionfunction as an input to the IDRISRI Cost module. The latter is normally used to determine economic catchments which decline in effectiveness with distance and are used here in an analogous A Delphi approach was taken to calibrate and refine way. our results.

DELPHI METHOD

This methodology was originally developed (Brown and Helmer 1964) to cope with uncertainty in making business forecasts and has been widely used in the social sciences although less so today (Sackman 1975). The Delphi approach works by gathering a set of 'experts' in the topic area, canvassing their opinions and special knowledge relevant to a problem that normally contains considerable uncertainty in its true outcome. These experts give their views unconstrained by peer pressure and are given the opportunity to change their opinions in a second, or subsequent rounds of questioning when they see the results of the expert group as a whole. In this study we have applied the technique to uncertainty in space, the distribution of the lion, rather than uncertainty in time. We identified lion experts as those who published major primary research papers on lion ecology or those who have synthesised lion distribution or abundance data. Fourteen experts were identified at round 1.

Round 1

The experts received a package from us containing three numbered and sealed envelopes. These were opened and completed in sequence by the recipients, as follows:

Envelope 1 contained two empty tables with the same headings as shown in Table 2. The experts were asked to complete one table for Lions outside parks and one for inside parks by answering the question " What do you consider are the main important factors (state at least 4) that influence the abundance of Lions inside/outside protected areas in Africa? Range them in order of importance by ticking the appropriate cell". Experts were asked for any additional comments.

Envelope 2 contained a list of factors (Agriculture, Human Settlements, Cattle, Distance to protected areas, plant productivity) and asked to rank them in order of importance to the reduction in lion density outside parks. They could also make additional comments.

Envelope 3

TABLE 2 HERE

This envelope contained Table 2 showing our own choice of factors which affect lion densities and the scaling we gave to them. We included a map, Fig. 4, produced by these scalings but we did not disclose to the experts the values of the scalings used. In fact we linearly transformed the categories as no effect = 100% lion density derived from LAI relationship (Figure 1) and 25%, 50%, 75% and 100% reductions respectively to 'no lions'.

The following set of questions asked:

1 Do you think the lion density map is in agreement with your previous choices?

2 Now you have seen the map made from our choices. Would you change any of your previous choices?

3 Do you know any lion populations not shown on our map? Please, mark them and their approximate size in the map. **4** Do you think we have predicted populations where they do no exist? Do you think we have overestimated? Please, mark them in the map (your size estimation where possible).

Round 1 results

7 of the 14 experts replied. Responses included the experts grading of effect of the factor on lion populations. Our unconstrained request (envelope 1) for information about factors influencing lion abundance produced the following list of factors ranked from the experts gradings:

Inside protected areas

1 Prey availability (including habitat,

rainfall/productivity)

- 2 level of protection (including poaching, fencing, trophy hunting)
- 3 Size of protected area
- 4 Others : disease, intra- and inter specific competion, hunting on boarders, human disturbance, water points in arid areas)

Outside protected areas

- 1 Agriculture (habitat transformation)
- 2 Human settlement
- 3 Pastoralism (poisoning)
- 4 Hunting, trapping, snaring
- 5 Prey availability (rainfall/productivity)

6 Diseases

Using the data gathered from envelope 2 for factors that reduce lion densities outside parks, the rankings in Table 2 were assessed to be broadly correct. The mean of rankings 1-5 for all experts for the categories were as follows:

1	Agriculture	1.7

Human Settlement 1.5
Cattle 2.4
Distance to protected area 3.7-4.1
Plant productivity 3.7

In the above low values indicate the greatest effect. Comments also indicated that we should increase the effect of low human population densities. The range of values on distance to protected areas was based on one expert's assessment that distance to protected areas was important only in moderately populated areas but was less important a factor in very sparsely populated regions. At this stage none of the experts wanted to change their opinions in response to our list of priority factors or the map, Figure 4.

Round 2

We modified the prediction procedure in response to the comments and rankings received from the experts. We added any population mentioned by an expert as missing on our map, and similarly removed populations where these were considered in error. Both these changes were few and concerned only 5 populations. From the comments received we were advised to split the lower category of human settlement density in two to provide a more graduated effect of human impact, see Table 3 where two changes in scaling are also shown. These changed scalings allowed a new density estimate and map to be produced (Figure 5). This was sent to the 7 experts who had responded to round 1 plus one newly identified expert. They received a summary of the comments that were made in Round 1 and the changes we incorporated using these. The numerical values used in the prediction were included explicitly in Round 2 by sending Table 4. The experts were then asked regarding inside and then outside parks:

Do you agree with the present ranking?

If not what would you change ?

We then sought agreement on the overall approach by making our scaling factors explicit in numerical terms and asking:

Do you think we make any wrong assumptions in our calculations?

Would you change any of the numerical values in Table 4? and finally,

Do you think our map is closer to reality than map one?

Round 2 results

Agreement among the experts who had responded to round 2 indicated that we had reached the consensus view that terminates the Delphi exercise. 6 out of the 8 polled replied to the round 2 questionnaire. Of the 6, all agreed on the ranking used outside parks and 5 out of 6 agreed with the rankings we used 6th being concerned that level of inside parks with the protection should be the least important factor because protection should be available in the parks by definition. However our purpose was to develop a method for population estimates outside parks.

Comments on the comparison of maps between the first and second rounds yielded 5 out of 6 views that it was an improvement, with the one identified error that we had too greatly reduced the distribution of lion in Southern Africa and suggestions for change were made by the expert. A further comment from a different expert agreed with the distribution as a whole but was concerned about the density values presented, these being in broad bands where it was felt that actual densities lay at the lower end of these bands rather than at the mid points for example. In practice the data on lion densities in the model is held at а high resolution as derived from the model calculations and so when summing the populations no additional The broad bands of lion densities were only errors are made. used to display the data.

In comments on the parameter values in table 4 there was again consensus this time on а residual error that we had underestimated the effect of low human population numbers on the lion population. We were advised to increase the effect of 10,000-25,000 population in a grid square to a 50% reduction in lion number (from 25%); another expert suggested this level be applied to human populations below 10,000 per grid square, however that was below the resolution of our population database and so we were able not to plot the human population distribution at this density. A further two experts pointed to a 'slight effect' of human populations below 10,000. Our conclusion here was that we should adopt the suggestion of increasing the impact of 10K-25K population to the 25% suitability level.

There was also a view expressed by two of the experts that where agriculture took up 50% of the grid square only 25%-30% of the

remaining area should be considered as a component of lion suitability. This appears logical and would apply some effect of low human populations since rural population and agriculture are spatially related. We therefore adopted the 25% suitability suggestion.

In round 2 we also asked the experts what methods would they use to count lion numbers outside parks. The following set of techniques were presented:

Playback recordings of roaring lions and/or hyenas feeding at kills.

Interview process, although time consuming, should be part of the estimating method; hunting organisations, game departments, livestock organisations. Experts from West Africa and Zimbabwe should be added.

Presence/absence surveys can be done by questioning local authorities and people, with checks on ground truth where necessary. Density surveys will have to be confined to selected representative areas and will be a big challenge.

Tracks, listening for sounds, baiting and calling.

Visual count, mark/recapture, bait, photo-trap, track count, interview, sighting records - see also Nowell and Jackson 1996.

This concluded the Delphi consultation of experts.

FINAL RESULTS

The information received from Round 2 was used to modify table 4 specifically as indicated above with regard to agriculture and population effects. This was used to produce a final map and calculate a total lion abundance estimate.

The lion density function obtained from the lion densities reported in the literature and the Leaf Area Index (LAI) model (Woodward et al 1995) has a maximum for LAI values between 3 and 5 and lion density decreases at lower and higher LAI values (Fig. 1). The maximum density mainly correspond to savannah and dry forests. We have supposed that density of lions outside parks decreases from squares closest to the parks and it is zero at an effective distance of 5 or more degrees. Decreases are larger where they take into account other negative factors such as farming or livestock. According to our model, lions could reach a distance of about 500 km from protected areas but at a very low densities.

FIGURE 6 HERE

In the final lion distribution map, Figure 6, we have added those lion populations reported outside parks but not predicted by the model, such as Southern Somalia and Southern Sudan, as suggested by some experts. According to our final model, about 75,800 lions exist in Africa for our composite datum year. Of these 18,600 of them are allocated inside protected areas (25%) and the proportion decreases away from protected areas, only a 1% being found at distances above 300 km. Sensitivity Testing and Field Observations

As a preparation for field testing the predictions made from this GIS model we have undertaken a sensitivity analysis. This analysis identifies the most important variables predicted by the model as affecting the lion abundances. The analysis was made by varying the % natural density values of the factors identified in Table 4 by a multiple of +/- 10%. The values in brackets in Table 4 were the values used for the final map, Fig. 5.

TABLE 5 HERE

The sensitivity analysis, Table 5, was designed to show the relative effect of each of these factors on the overall population estimate. This information can be used to preate a stratify the data collection design and prioritise field data collection in order to validate and improve current lion abundance estimates.

DISCUSSION

The scale of the species range that large top predators occupy make direct field work estimates of their global abundance extremely difficult. Similarly the factors which determine their abundance vary greatly across the range. GIS rule based models are capable of adapting the local estimates of species abundance according to the geographical variation in the factors used to model the abundance. More generally the Delphi technique can be seen accessing distributed knowledge and intelligence which may be consistent with newly developing communication media such as the Internet. The use of a Delphi the rules applied exercise to assess in the GIS. their relationships and the results in the form of the distribution maps, has been shown to be a viable process and consensus among the experts responding was reached. Expert knowledge about, for example, the densities of settlement that have an effect on the lion population in a grid square was something that we had initially underestimated. Conversely the need to alter the rate at which lion numbers declined with distance from protected areas lead to changes in the spatial extent and abundance estimates. Overall from our first map estimates fell from 89000 to 75000 in the third and final one. While these estimates come within that of Nowell and Jackson (1996) validation of densities outside parks will be needed. The present distribution estimates and sensitivity analysis can provide a framework for prioritising data collection. If the field observations are accompanied by an assessment of the human impact factors and LAI values at the observation areas then such observations can be used to parameterize GIS models to make improved estimates.

One difficulty with the present estimate is the variation in the dates the data were collected. This is particularly so for agriculture and pastoralism. The data sources in Wilson and Henderson-Sellers (1985) for Africa were published between 1954 and 1982 with a mean publication year of 1972. Data for these publications relate to source data gathered about a decade earlier. We assume that the agricultural data are overall representative of 1960. Settlement location is stable over periods of decades although some settlements will have changed their size category in the past 30 years. The base population data is for 1985. The experts were not asked about the 'dateline' of their expertise although the basis of selecting them were from publications which for the 7 respondents had a mean latest date of 1992.

Thus our estimate will not adequately take into account agricultural expansion since 1960 although from the sensitivity analysis this may not be a serious shortcoming. Thus we should conclude that 76,000 from our method will overestimate the current population and should be considered representative of the period 1960-1980. As humans have expanded in number we have 'appropriated the products of photosynthesis' (Vitousek et al 1986) which historically would have fed herbiovores and ultimately sustained large top predators. For this reason and for other causes of top predator decline, such as, pollution and hunting, it has been proposed that estimating top predator abundance, in comparison to the potential abundance of those predators, provides a synoptic measure of human impact at a global level (Cousins 1994).

In the near future much more detailed contempory land use and vegetation data derived from remote sensing will become available for Africa and future work will allow improved contempory estimates of lion populations. It is the future capability of regular updates of land use and vegetation data that offers the prospect of charting the size of the African lion population as one of the limited global set of large top predators. In this case it will provide one measure of the overall human impact on ecosystems at a continental scale.

REFERENCES

- Aldeajayai, J.F. & Crowder, M. (1985) Historical Atlas of Africa. Longman.
- Berry, H.H. (1987). Ecological background and management application of contraception in free-living African lions. Proceedings of the Conference on contraception in Wildlife, Philadelphia.
- Bertram, B.C.R. (1975). The social system of lions. Scientific American 232: 54-65.
- Bertram, B.C.R. (1979). Serengeti predators and their social systems. In Serengeti: Dynamics of an ecosystem: 221-248. Sinclair, A.R.E. and Norton-Griffith, M. (Ed.). Chicago: University Chicago Press.
- Bourlière, F. (1965). Densities and biomasses of some ungulate populations in Eastern Congo and Rwanda, with notes of population structure and lion/ugulate ratios. Zoologica Africana 1(1): 199-207.
- Brown, B. & Helmer, O. (1964) "Improving the Reliability of Estimates Obtained from a Consensus of Experts," P-2986, RAND Corporation; Santa Monica, Calif.
- Conner, M.C., Labisky, R.F. & Progulske, D.R. (1983) Scentstation indices as measures of population abundance for bobcats, raccoons, gray foxes and oppossums. Wildlife Society Bulletin 11: 146-152
- Cousins SH (1990) Countable ecosystems deriving from a new food web entity. Oikos 57(2):270-275
- Cousins SH (1994) Taxonomy and functional biotic measurement, or, will the Ark work? In: P.L.Forey CJH, and R.I.Vanc-Wright (ed) Systematics and Conservation Evaluation, vol 50. Clarendon Press, Oxford, pp 397-419
- Dunham, K.M. (1992). Response of a lion (Panthera leo)
 population to changing prey availability.
 J.Zool.,Lond. 227: 330-333.

- East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. Afr.J.Ecol. 22: 245-270.
- Elliott, J.P. and Cowan, McT. (1978). Territoriality, density, and prey of the lion in Ngorongoro Crater, Tanzania. Can.J.Zool. 56: 1726-1734.
- Eloff, F.C. (1973). Lion predation in the Kalahari Gembsbok National Park. J.Sth.Afr.Wildl.Mgmt.Ass. 3(2): 59-63.
- Eloff, F.C. (1973). Ecology and behavior of the Kalahari lion. In The World's Cats. Vol. I: Ecology and Conservation: 90-126. Eaton, R.L. (Ed.). Winston, Oregon: World Wildlife Safari.
- Fisher, J., Simon, N. and Vincent, J. (1969). Asiatic lion. In Wildlife in Danger: 81-84. Fisher, J., Simon, N. and Vincent, J. (Ed.). New York: The Viking Press.
- Foster, J.B. and Coe, M.J. (1968). The biomass of game animals in Nairobi National Park, 1960-1966. J.Zool., London 155: 413-425.
- Hanby, J.P. and Bygott, J.D. (1979). Population changes in lions and other predators. In Serengeti: Dynamics of an ecosystem: 249-262. Sinclair, A.R.E. and Norton-Griffiths, M. (Ed.). Chicago: University Chicago Press.
- Jackson, P. (1994) India's 1993 Census 3.750 tigers. Cat news 21 : 9-10
- Lamprey, H.F. (1964). Estimation of the large mammal densities, biomass and energy exchange in the Tarangire Game Reserve and the Masai Steppe in Tanganyika. E.Afr.Wildl.J. 2: 1-46.
- Makacha, S. (1969). Observations on lions in the Lake Manyara National Park, Tanzania. E.Afr.Wildl.J. 7: 99-103.
- Michelmore F. (1994) Keeping elephants on the map: Case studies of the application of GIS for conservation. In: Mapping the Diversity of Nature: 107-125. Miller R.I. (Ed.). London: Chapman & Hall.
- Mills, M.G.L. and Shenk, T.M. (1992). Predator-prey relationships: the impact of lion predation on

wildebeest and zebra populations. J.Anim.Ecol. 61: 693-702.

- Mills, M.G.L., Wolff, P., Le, , Riche, E.A.N. and Meyer, I.J. (1978). Some population characteristics of the lion Panthera leo in the Kalahari Gembsbok National Park. Koedoe 21: 163-171.
- Mitchell, B.L., Shenton, J.B. and Uys, J.C.M. (1965).
 Predation on large mammals in the Kafue National
 Park, Zambia. Zoologica Africana 1(1): 297-318.
- Nowell, K. and Jackson, P. (1996). Wild Cats: Status Survey and Conservation Action Plan. Gland, Switzerland: IUCN.
- Packer, C., Herbst, L., Pusey, A.E., Bygott, D., Hanby, J.P., Cairns, S.J., Borgerhoff, and
- Mulder, M. (1988). Reproductive success of lions. In Reproductive success: Studies of individual variation in cotrasting breeding systems: 363-383. Clutton-Brock, T.H. and Ed, (Ed.). Chicago: University of Chicago Press.
- Packer, C., Pusey, A.E., Rowley, H., Gilbert, D.A., Martenson, J.O. and Brien, S.J. (1991). Case study of a population bottleneck: Lions fo the Ngorongoro Crater. Cons. Biol. 5(2): 219-230.
- Packer, C., Scheel, D. and Pusey, A.E. (1990). Why lions form groups: food is not enough. Am.Nat. 136: 1-19.
- Pusey, A.E. and Packer, C. (1987). The evolution of sex-biased dispersal in lions. Behaviour 101: 275-310.
- Ravi-Chellam & Johnsingh, A.J.T. (1993) Management of the Asiatic lions in the Gir Forest, India. In n. Dunstone and M.L. Gorman, eds. Mammals as predators. Proc. Symp. Zool. Soc. Lond. 65. Clarendon, Oxford.
- Rodgers, W.A. (1974). The lion (Panthera leo, Linn.) population of the eastern Selous Game Reserve. E.Afr.Wildl.J. 12: 313-317.
- Rudnai, J. (1974). The pattern of lion predation in Nairobi Park. E.Afr.Wildl.J. 12: 213-225.

- Rudnai, J.A. (1973). The social life of the lion: A study of the behaviour of wild lions (Panthera leo massaica [Neumann]) in the Nairobi National Park, Kenya. Lancaster: Medical and Technical Publishing Co. Ltd..
- Ruggiero, R.G. (1991). Prey selection of the lion (Panthera leo L.) in the Manovo-Gouda-St.Floris National Park, Central African Republic. Mammalia 55(1): 23-33.
- Schaller, G.B. (1972). The Serengeti Lion. Chicago: University of Chicago Press.
- Smuts, G.L. (1976). Population characteristics and recent history of lions in two parts of the Kruger National Park. Koedoe 19: 153-164.
- Smuts, G.L. (1978). Effects if population reduction on the travels and reproduction of lions in Kruger National Park. Carnivore 1: 62-72.
- Smuts, G.L., Hanks, J. and Whyte, I.J. (1978). Reproduction and social organization of lions from the Kruger National Park. Carnivore 1(1): 17-28.
- Stander, P.E. (1991). Demography of lions in the Etosha National Park, Namibia. Madoqua 18(1): 1-9.
- Stander, P.E. (1992). Foraging dunamics of lions in a semi-arid environment. Can.J.Zool. 70: 8-21.
- Stander, P.E. (1992). Cooperative hunting in lions: the role of the individual. Behav. Ecol. Sociobiol. 29: 445-454.
- Stander, P.E. and Albon, S.D. (1993). Hunting success of lions in a semi-arid environment. Symp.zool.Soc.Lond. 65: 127-143.
- Starfield, A.M. and Bleloch, A.L. (1983). An initial assessment of possible lion population indicators. S.Afr.J.Wildl.Res. 13: 9-11.
- Van Lavieren, L.P. and Bosch, M.L. (1977). Evaluation des densities de grands mammiferes dans le Parc National de Bouba Ndjida, Cameroun. La Terre et la Vie 31: 3-32.
- Van Ordsol, K.G. (1982). Ranges and food habits of lion in Rwenzori National Park, Uganda. Symp.zool.Soc.Lond. 49: 325-340.

- Van Ordsol, K.G. (1984). Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. Afr.J.Ecol. 22: 79-99.
- Van Ordsol, K.G., Hanby, J.P. and Bygott, J.D. (1985). Ecological correlates of lion social organization (Panthera leo). J.Zool.,Lond. 206: 97-112.
- Viljoen, P.C. (1993). The effects of chages in prey availability on lion predation in a large natural ecosystem in northern Botswana. Symp.zool.Soc.Lond. 65: 193-213.
- Vitousek PM, Ehrlick PR, Ehrlich AH, Matson PA (1986) Human appropriation of the products of photosynthesis. BioScience. 36:368-373.
- Wilson, M.F., Henderson-Sellers, A. (1985) A global archive of land cover and soils data for use in general circulation climate models. J. Climatology 5:119-143
- Woodward, F.I. (1987) Climate and plant distribution. Cambridge University Press, London, England.
- Yamazaki, K. (1996). Social variation of lions in a maledepopulated area in Zambia. J.Wildl.Manage. 60(3): 490-497

TABLE 1: Lion populations for which information on population size and density are available in the literature and references used for each population.

POPULATION	COUNTRY	DATE**	SOURCE*
Kalahari-Gembsbok	Botswana-S.Africa	1970-77	7,8,14
Etosha	Namibia	1980-89	1,29,30,31,32
Kaudom	Namibia	1995	16
Chobe	Botswana	1983-85	37
Kruger	S.Africa	1974-90	13,26,27,28
Selous	Tanzania	1967-72	21
Serengeti	Tanzania	1966-87	2,3,10,17,18,1 9,20,25,36
Ngorongoro	Tanzania	1964-89	6,12,18,36
Nairobi	Kenya	1960-72	9,22,23
Queen Elyzabeth (Rwenzori)	Uganda	1974-75	34,35,36
Taranguire	Tanzania	1958-61	11
Virunga (Albert N.P.)	Zaire-Rwanda	1959-60	4,5
Kafue	Zambia	1965	15
Kagera	Rwanda	1959-60	4,5
Arli + Pendjari	Upper Volta + Benin	1973-74	4,5
Manovo-Gouda-St.Floris	Central R.Africa	1982-84	24
Mkomazi	Tanzania	1970	5
Bouba Ndjida	Cameroon	1974-76	5,33
Wankie (Hwange)	Zimbabwe	1975	5

* References: 1: BERRY (1987); 2: BERTRAM (1975); 3: BERTRAM (1979); 4: BOURLIÈRE (1965); 5: EAST (1984); 6: ELLIOTT and COWAN (1978); 7: ELOFF (1973); 8: ELOFF (1973); 9: FOSTER and COE (1968); 10: HANBY and BYGOTT (1979); 11: LAMPREY (1964); 12: MAKACHA (1969); 13: MILLS and SHENK (1992); 14: MILLS, WOLFF, LE RICHE and MEYER (1978); 15: MITCHELL, SHENTON and UYS (1965); 16: NOWELL and JACKSON (1996); 17: PACKER, HERBST, PUSEY, BYGOTT, HANBY, CAIRNS, BORGERHOFF and MULDER (1988); 18: PACKER, PUSEY, ROWLEY, GILBERT, MARTENSON and O'BRIEN (1991); 19: PACKER, SCHEEL and PUSEY (1990); 20: PUSEY and PACKER (1987); 21: RODGERS (1974); 22: RUDNAI (1974); 23: RUDNAI (1973); 24: RUGGIERO (1991); 25: SCHALLER (1972); 26: SMUTS (1976); 27: SMUTS (1978); 28: SMUTS, HANKS and WHYTE (1978); 29: STANDER (1991); 30: STANDER (1992); 31: STANDER (1992); 32: STANDER and ALBON (1993); 33: VAN LAVIEREN and BOSCH (1977); 34: VAN ORDSOL (1982); 35: VAN ORDSOL (1984); 36: VAN ORDSOL, HANBY and BYGOTT (1985); 37: VILJOEN (1993)

** When references from studies carried out during different periods were consulted, the earliest and latest dates are shown.

TABLE 2: Initial set of factors and levels of effect on lion distribution proposed by the authors to the lion-experts in the first Delphi questionnaire.

FACTOR	No effect on lions	Slight effect on lions	Some effect on lions	Large effect on lions	Total effect (no lions)
AGRICULTURE					Х
HUMAN >25.000 /100x100 Km					Х
HUMAN <25.000 /100x100 Km	Х				
MAIN CATTLE AREAS					Х
SECONDARY CATTLE AREAS			Х		
DISTANCE TO PARKS > 100 Km					Х
DISTANCE TO PARKS < 100 Km			Х		
PLANT PRODUCTIVITY				Х	

TABLE 3: Changes of effects of human factors on lion density after considerations of experts' comments to Questionnaire 1. This table was submitted to experts as part of Questionnaire 2.

FACTOR	No effect on lions	Slight effect on lions	Some effect on lions	Large effect on lions	Total effect (no lions)
AGRICULTURE					Х
HUMAN >25.000 /100x100 Km					Х
HUMAN <25.000 and >10.000 /100x100 Km	(X)		>X		
HUMAN <10.000 /100x100 Km	Х				
MAIN CATTLE AREAS					Х
SECONDARY CATTLE AREAS			Х		
DISTANCE TO PARKS > 100 Km				X<	(X)
DISTANCE TO PARKS < 100 Km			Х		
PLANT PRODUCTIVITY				X	

(X)---->**X**

Old position

New position

TABLE 4: Numerical values of human factors in reducing lion densities, reviewed after Delphi Questionnaire 1 and submitted to experts in Round 2. A linear scale between 0 and 100 % shows this effects as percentage of the expected 'natural' density according to plant productivity.

FACTOR	LEVEL	EFFECT (% Natural Density)		
		0100		
Human population in > $25,000$ 100 x 100 km		0		
	10,000-25,000	50		
	< 10,000			
Cattle	Main areas	.10		
	Secondary areas	50		
Distance from 0° long/lat protected area		100		
	1° long/lat	25		
	2° long/lat	12		
	3° long/lat	.6		
	4° long/lat	.3		
	$>4^{\circ}$ long/lat	0		
Agriculture: Effect proportional to area, e.g.:	100% Area	0		
	50% Area	50		
	0% Area	100		

TABLE 5: Results of the sensitivity análisis of the model for lion abundante in Africa.

Factor	-10% factor		+10% fa	Average Sensitivity	
	Effect	Effect	Effect	Effect	
	(lions)	(%)	(lions)	(%)	(%)
Agriculture	75320	-0,16	75567	0,16	0,16
Human population	72446	-3,97	76180	0,98	2,47
Cattle	67718	-10,24	79074	4,81	7,53
Distance to park	71099	-5,76	90091	19,4	12,59

FIGURE LEGENDS

FIGURE 1: Relationship between lion density (adults and subadults / 100 km²) and potential primary productivity expresed as Leaf Index (L.A.I.) according to the information on lion density contained in 34 studies on 19 African lion populations Woodward et al. (19..) L.A.I. database.

FIGURE 2: Potential lion density in the current maximum range (Nowell & Jackson, 1996) as expected according to potential primary productivity - lion density relationship.

FIGURE 3: Percentage of reductions in maximum habitat suitability resulting from human activities such as human population, cattle density, distance from protected areas and agriculture in 1°x1° latitude-longitude squares within potential lion range. The scale indicates a reduction of maximum potential lion density (0% no reduction, 100% complete reduction). Crosses indicate the position of protected areas containing lions.

FIGURE 4: First lion distribution map obtained from the L.A.I. - density relationship and our first set of factors on lion density reduction by human factors. This map was submitted to experts in Delphi Round 1 to comments.

FIGURE 4: Second lion distribution map obtained from comments from the experts to Delphi Questionnaire Round 1. This map was submitted to experts in Delphi Round 2 to comments.

FIGURE 5: Final map of expected current lion densities after considerations of experts' comments to Questionnaire 2.



12190152 13/08/1/P

Lion potential density in maximum current range



121





SUTTAGUTY URP 13/03/96

HG. 3



FIRST LION DISTRIBUTION MAP



Figure 1 6/10/96

sim s Lefter & comin

96/01/9.

Second lion distribution map





