

Science and Management in a Conservation Crisis: a Case Study with Rhinoceros

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Abstract: *I suggest that a conservation crisis is a predictable sequence of five stages: population decline, crisis management, stabilization, precarious recovery, and sustained recovery. Each stage has different research priorities, constraints, and opportunities that cause a mismatch between conservation needs and research practice. The conservation crisis over the rhinoceros was characterized by rapid decline due to illegal hunting and trade in rhinoceros horn. I conducted a literature review (1980–2000) on rhinoceros during this crisis to illustrate the five stages. I also examined the bibliographies of the African and Asian conservation action plans to illustrate literature availability and use. I sought to determine whether a retrospective understanding of trends in the scientific literature during conservation crises could help us better target research efforts and meet the challenge of conserving rare species. The scientific literature on rhinoceros increased during the crisis but became dominated by ex situ laboratory-based studies, whereas the number of in situ ecological studies remained low, although the conservation action plans identified in situ and ecological studies as conservation priorities. Moreover, the bibliographies of the conservation action plans were dominated by unpublished material (56%), and only 25% of citations came from scientific journals, although peer review and critique contributes to maintaining and improving the quality of conservation science. Thus, I suggest that research matched conservation needs poorly. However, the predictability of the crisis sequence means that it should be possible to preempt conservation research needs. The effect of a conservation crisis on research may be ameliorated by abandoning the dualism of applied and basic research and better targeting research effort by identifying when research is relatively unimportant, exploiting opportunities for science by management, establishing collaborative publishing relationships between managers and researchers, and prioritizing in situ ecological research.*

Ciencia y Manejo en una Crisis de Conservación: Un Estudio de Caso con Rinocerontes

Resumen: *Se sugiere que una crisis de conservación es una secuencia predecible de cinco etapas: declinación de la población, manejo de crisis, estabilización, recuperación precaria y recuperación sostenible. Cada etapa tiene distintas prioridades de investigación, limitaciones y oportunidades que exigen un ajuste entre las necesidades de conservación y la práctica de la investigación. La crisis de conservación con el rinoceronte se caracterizó por una rápida declinación debido a la cacería y comercio ilegal de cuerno de rinoceronte. Se realizó una revisión de la bibliografía (1980–2000) sobre rinocerontes durante esta crisis de conservación para ejemplificar estas cinco etapas. Se revisaron también las bibliografías de los planes de conservación africanos y asiáticos para ejemplificar la disponibilidad y el uso de la bibliografía. Se intentó determinar si el entendimiento retrospectivo de tendencias en la literatura científica durante la crisis de conservación nos ayudaría a enfocar los esfuerzos de investigación de mejor manera y enfrentar el reto de conservar especies raras. La bibliografía sobre rinocerontes aumentó durante la crisis pero fue dominada por estudios de laboratorio ex situ, a pesar de que los planes de conservación identificaron como prioridades de conservación los estudios in situ y ecológicos. Más aun, las bibliografías de los planes de conservación estuvieron dominadas por material no publicado (56%), y solo 25% de las citas provenían de revistas científicas, aún cuando la revisión y crítica por pares contribuye a mantener y mejorar la calidad de la ciencia en conservación. Por lo tanto, sugiero que*

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la investigación no cumplió con las necesidades de conservación adecuadamente. Sin embargo, la secuencia predecible de la crisis significa que es posible anticiparse a las necesidades de investigación. El efecto de la crisis de conservación sobre la investigación puede aprovecharse mejor si se abandona la dualidad entre la investigación básica y aplicada y se enfoca más en los esfuerzos de investigación identificando aquella investigación de poca importancia, explotando las oportunidades para el manejo científico, publicando trabajos que surgen de la colaboración de manejadores e investigadores y priorizando la investigación ecológica in situ.

Introduction

Conservation biology is a crisis science (Soulé 1985) and conservation crises motivate impassioned calls for science to contribute to species and habitat rescue (Western & Pearl 1989; Dobson 1995; Balmford et al. 1998). However, research is necessarily a lower priority than management in a crisis. Moreover, conservation crises limit research because species and habitat become small and scattered remnants that are logistically and politically difficult to examine. When research occurs it is undertaken opportunistically alongside management programs that, because they intervene in ways seldom complementary with research schedules and questions, necessarily limit the questions that can be answered. Furthermore, a large proportion of the species is often transferred to captivity, particularly in developed nations with larger resources, so ex situ and laboratory-based studies flourish. A conservation crisis may have considerable influence on the amounts and types of research conducted and may limit the contribution of science.

The case of the rhinoceros—Indian (*Rhinoceros unicornis*), Javan (*Rhinoceros sondaicus*), Sumatran (*Dicerorhinus sumatrensis*), white (*Ceratotherium simum*), and black (*Diceros bicornis*)—is an instructive example of how science responds to and is shaped by a conservation crisis. Rhinoceros are suffering or recovering from dramatic declines and population fragmentation (Fig. 1a; Foose & van Strien 1997; Emslie & Brooks 1999). Rhinoceros were moved between parks or transferred to captivity for safety and breeding with a view to reintroduction (Foose & Miller 1994; Hall-Martin & Knight 1994). Paramilitary security and metapopulation management on a continental scale have had slow but convincing success at population stabilization and recovery. I illustrate how a conservation crisis causes a predictable sequence of changes in the research done that is poorly synchronized with conservation research priorities. I evaluated the role of research in the conservation of rare species and asked how a retrospective understanding of trends in the scientific literature during conservation crises can help us better target research efforts.

Literature Survey

I generated a sample of the published scientific literature on rhinoceros species and categorized articles into fields

of investigation. I used OVID Biological Abstracts Database (<http://gateway2.ovid.com/fldguide/biosis.htm>) of 7000 serials (<http://www.ovid.com>) to identify the scientific literature on rhinoceros. Records from 1980 to 2000 were searched for articles containing rhinoceros genera and species names as keywords. There were 261 articles that contained at least one of these keywords. I imported the article titles, abstracts, and keywords into Endnote (Institute for Scientific Information 2000) (available from the author upon request). I placed articles in one of the following categories: paleobiology, anatomy, disease, genetics, physiology, management

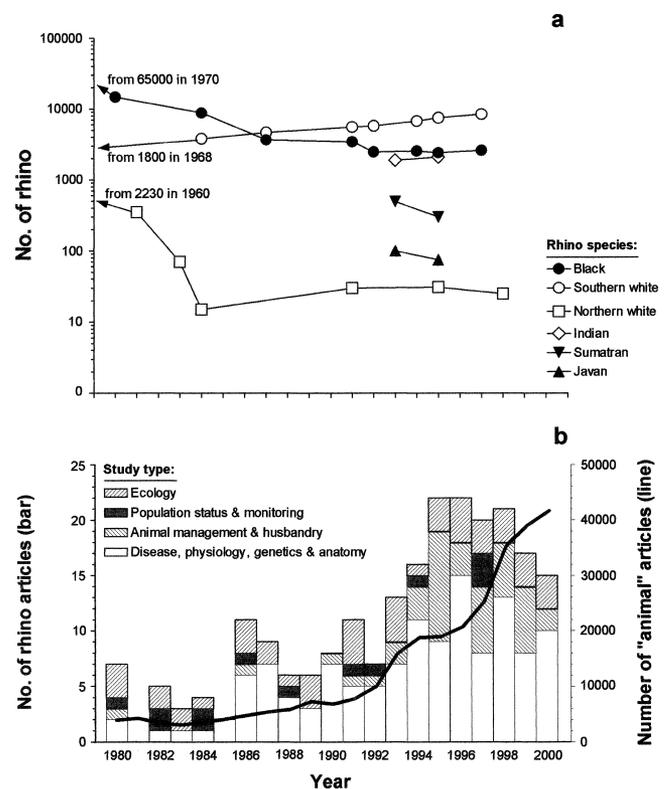


Figure 1. The scientific literature on rhinoceros during the conservation crisis as rhinoceros numbers declined and stabilized: (a) trends in rhinoceros numbers for the five species (Foose & van Strien 1997; Emslie & Brooks 1999) and (b) the change in the number and composition of rhinoceros publications from 1980 to 2000, and the size of the "animal" literature during the same period.

and husbandry, population status and monitoring, or ecology topics. Nineteen articles that were not about rhinoceros were excluded from further analyses. To quantify the size of the literature during the same period, I also searched for the keyword *animal*.

Articles about rhinoceros ecology were further described by one or more research topics and whether they described experimental or multipopulation comparative work. Topics included demography, habitat use, social behavior, feeding behavior, activity behavior, nutrition, population monitoring methods, community relationships (e.g., mutualism with oxpeckers, seed dispersal, and their effect on vegetation), parental behavior, antipredator behavior, mating systems, population viability, reproductive behavior, interspecific behaviors, and learning behavior.

The published scientific literature on rhinoceros increased as numbers declined, and corresponded, in part, to growth in the animal literature (Fig. 1). The increase in the number of scientific articles was mainly due to an increase in anatomical, genetics, disease, and physiological studies of rhinoceros (5 articles from 1981 to 1985, 27 from 1986 to 1990, 37 from 1991 to 1995, and 44 from 1996 to 2000) and in animal management and husbandry research that was a prominent feature of the 1990s (2 articles from 1981 to 1990 and 38 from 1991 to 2000). The amount of in situ research on rhinoceros ecology and population status and monitoring changed less during the crisis (9 articles from 1981 to 1985, 11

from 1986 to 1990, 15 from 1991 to 1995, and 19 from 1996 to 2000; Fig. 1b). Thus, the rhinoceros literature was dominated by research that largely originated from ex situ (captive animal) studies (Fig. 2). Only 45 articles (19%) were devoted to in situ rhinoceros ecology, and most of these were descriptions of rhinoceros diet, habitat use, and demography (71%; Fig. 3). For most research topics there were fewer than four articles, and many topics were absent altogether, such as investigations of dispersal, intraspecific communication, intrinsic influences on effective population size, behavioral development, maternal investment and juvenile growth, and epidemiology. Furthermore, experimental or comparative ecological studies of multiple populations were rare. All except four articles (e.g., Berger & Cunningham 1994b) reported on observational and descriptive studies on single populations.

Emslie and Brooks (1999) listed 16 research areas of immediate need in rhinoceros conservation. Meeting those research needs would require the application of research to disease, genetics, physiology, management and husbandry, population status and monitoring, and ecology topics, and some needs require research in more than one field. For example, using DNA genotyping of fecal samples to monitor population size and composition requires the application of research in genetics, and population status and monitoring. Current needs entail more research on ecology topics, population status and monitoring, in situ management, and genetics, and less ex situ research, particularly on rhinoceros physiology and disease, compared with what has already been done (Fig. 2). Anatomy and paleobiology were not identified as research needs but represented 16% of published research on rhinoceros (Fig. 2).

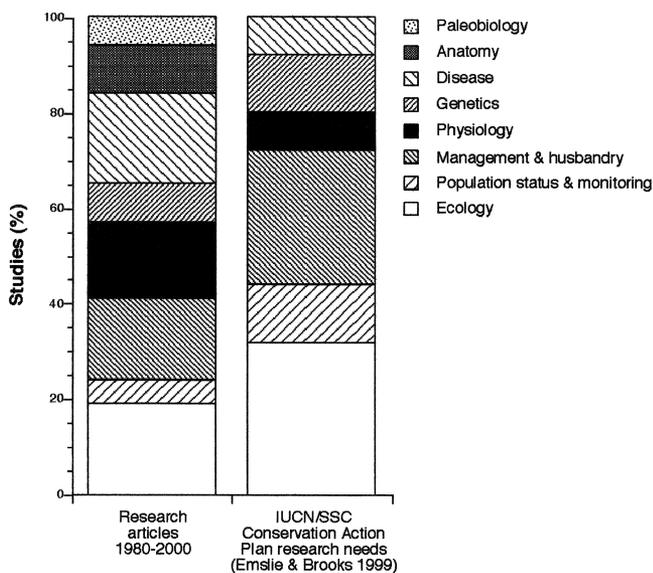


Figure 2. Difference in emphasis of the scientific literature (1980–2000) and conservation research needs described in the World Conservation Union/Species Survival Commission Status and Conservation Action Plan for the African Rhinoceros (Emslie & Brooks 1999).

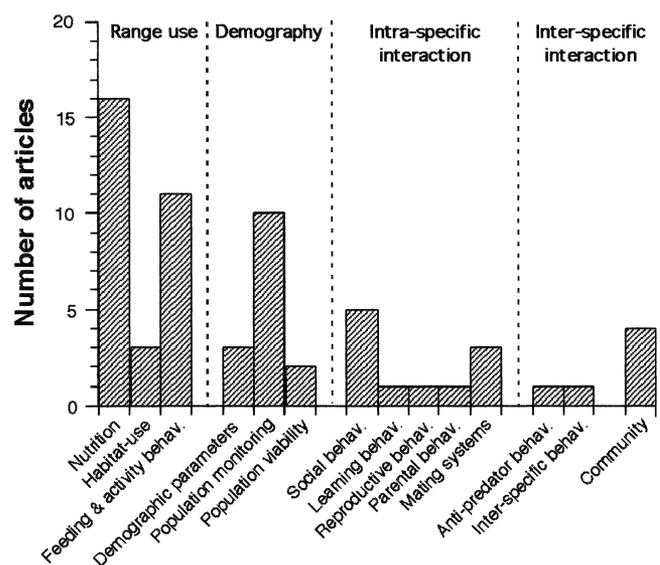


Figure 3. Topics covered by the 45 articles on rhinoceros ecology from a sample of 261.

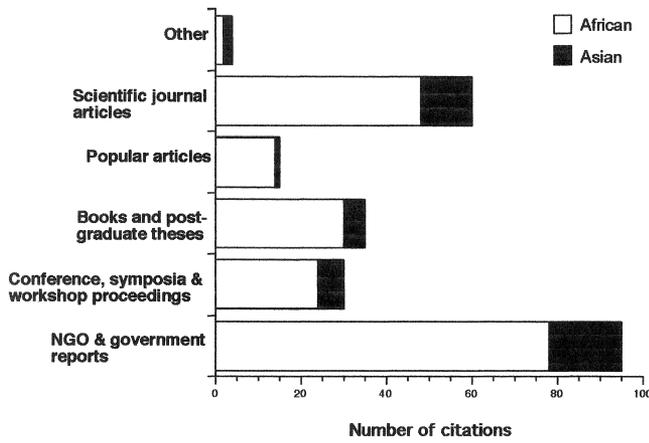


Figure 4. The origins of the literature cited in the World Conservation Union/Species Survival Commission Status and Conservation Action Plans for the African and Asian rhinoceros (Foose & van Strien 1997; Emslie & Brooks 1999).

I used the bibliographies of Foose and van Strien (1997) and Emslie and Brooks (1999) to assess the composition and utility of the rhinoceros conservation literature because these are the current authoritative summaries of

rhinoceros conservation. I classified their citations as either reports (government and nongovernment); conference, symposia, or workshop proceedings; books and postgraduate theses; popular articles (not subject to scientific peer review); and articles in scientific journals (peer reviewed). Their bibliographies reflected an underdeveloped scientific literature dominated by unpublished reports, theses, and conference, symposia, or workshop proceedings (56%). Only 25% of citations were from the peer-reviewed literature (Fig. 4).

Stages of the Rhinoceros Crisis and Its Literature

I suggest that a conservation crisis has five sequential stages: population decline, crisis management, stabilization at a low number, precarious recovery, and sustained recovery (Table 1). During decline, research on the causes of decline (e.g., trade in rhinoceros horn; Hall-Martin et al. 1993) and how to best monitor populations (Galli & Flammand 1995) are most needed. During crisis management the most urgent needs are for research into animal management and husbandry techniques because management necessarily involves animal immobilization, translocation, and captivity (Schaffer et al. 1998; Radcliffe et al. 2000), investigations of popula-

Table 1. Changes in the research opportunities and conservation research needs characteristic of each phase of conservation crises, and the research on rhinoceros that occurred (see also Fig. 1b).

Phase	Research opportunity	Conservation research needs	Rhinoceros research that occurred
Decline population loss	politically unfettered but may be limited by threats to personnel and focal animals	identify and quantify agents of decline: population and illegal trade status and monitoring	small amounts in all fields
Crisis management problem identified and animals protected and/or animals transferred to safe parks and captivity	in situ, limited by threats to safety of personnel, sample size, and management interventions ex situ, limited by sample size and regulatory restrictions	population genetics, reproduction and disease captive and wild animal management and husbandry techniques	small amounts in all fields
Stabilization population decline halted captive breeding	in situ, limited by regulatory restrictions and sample size ex situ, opportunities increase and diversify	population ecology: nutrition, range use, demography, social organization, and breeding biology for application in population viability analysis	increase in genetics, anatomy, physiology and disease research from captive and immobilized wild animals
Precarious recovery net in situ population recruitment captive animal reintroduction	in situ, opportunities exist to take advantage of existing management programs ex situ, infrastructure well established and productive	community ecology: population regulation, community relationships, and habitat capacity for application in ecological management	burgeoning of ex situ research in genetics, anatomy, physiology, and disease increase in research on management and husbandry techniques
Sustained recovery self-sustaining wild populations	in situ, opportunities increase and diversify	ecology: all aspects	

tion genetics to describe and prioritize conservation units (Ashley et al. 1990), and study of reproduction and disease to monitor and assist breeding and health (Patton et al. 1999; Fischer-Tenhagen et al. 2000). Few publications appeared during rhinoceros decline and crisis management, and they did not target these topics (Fig. 1b) because research was severely limited by threats to personnel and study animals, conservation regulation, management interventions, and the sample sizes possible (Table 1).

During population stabilization, the greatest need is for ecological studies, particularly on nutrition, range use, demography, social organization, and breeding biology. Data from these studies need to be used in population viability analyses so that resources and management effort among the remnant populations can be apportioned properly (Table 1). During rhinoceros stabilization, however, there was instead an increase in ex situ research on genetics, anatomy, physiology, and disease (Fig. 1b) because captive animals became more readily available, particularly to researchers in western nations with larger research budgets and infrastructure. At the same time that opportunities for ex situ research were burgeoning, restrictions on in situ research remained severe (Table 1).

Recent conservation successes, particularly in South Africa, suggest that black rhinoceros may be in recovery and that southern white rhinoceros have been in recovery for some time (Fig. 1a). Consequently, opportunities for field research are likely to improve, but they will be limited largely to taking advantage of management programs (e.g., Berger et al. 1993). Thus, further increases in the amount of management and husbandry research published are likely, although the period of critical translocations between parks and into captivity occurred during the late 1970s and 1980s (Foose & Miller 1994; Hall-Martin & Knight 1994). The greatest requirement now is for more ecological knowledge of the rhinoceros, particularly its population regulation, habitat capacity, competition with other species, and effects on the vegetation community, and for this knowledge to be applied to the ecological management of the relatively small reserves that constitute the metapopulation (Emslie & Brooks 1999) (Table 1; Fig. 3). However, ex situ research continues to burgeon. It remains to be seen whether science will catch up with conservation needs in the recovery phase of the crisis.

The rhinoceros crisis motivated calls for greater participation by scientists but also imposed a predictable sequence of changing conditions characterized by (1) changes in the relative importance of research, (2) changing conservation research needs, (3) greater in situ research constraints, and (4) improved ex situ research opportunities. These conditions dictated the research actually done at each stage in the crisis. Research did not coincide with conservation needs, pri-

marily because conservation crises dictate the most severe constraints on the research most needed at each stage. As well as limiting the research most needed, crises also divert attention toward laboratory-based ex situ research, although in situ research in ecology has the broadest and most immediate utility in conservation (Western & Pearl 1989; Mace et al. 1998). Researchers understandably took advantage of easier and more available ex situ research opportunities in the greatest number. The domination of the literature by laboratory science is expected given its greater technological, financial, and publishing returns (Clinchy & Krebs 1997). Thus, it should come as no surprise when calls for greater scientific participation in a conservation crisis, particularly for in situ ecological research, are poorly met. The scientific literature on the rhinoceros has always been one or two stages, or over a decade, behind its conservation needs, a much longer period than can be blamed on publishing time. In an unfortunate twist, the development of the scientific literature is hindered by the very conservation crisis it might assist.

Unfortunately, a deficient literature in turn limits the development of ecological knowledge, concepts, and management tools. Improving management depends on new information being subject to independent quality control and readily available to a diverse audience of potential contributors. The process of peer review and critique is a fundamental tool in advancing the quality of conservation science (Calver & King 1999). Unfortunately, the literature on rhinoceros displays the features of a literature in its infancy because a large portion of it is in less accessible forms not always subject to independent scrutiny. Moreover, experimental and comparative studies on multiple populations, which would normally provide more robust information (Armstrong et al. 1994), are rare.

The conservation history of the rhinoceros—rapid decline to small, scattered populations and massive captivity and translocation programs—is similar to that of other taxa, particularly other megafauna, and their literature follows a similar pattern (New Zealand Kakapo [*Strigops habroptilus*], Poulton 1982; Arabian Oryx [*Oryx leucoryx*], Stanley-Price 1989; Eurasian and African Equidae, Duncan 1992; North American bison [*Bison bison*], Berger & Cunningham 1994a). Addressing these shortcomings in the literature is an important part of conservation research if we are to avoid repeating mistakes, consolidate conservation successes, and build a more complete foundation of knowledge.

Counterproductive Dualism of Applied and Basic Research

Authors have responded to these shortcomings in the literature by calling for a greater emphasis on applied research (e.g., Emslie & Brooks 1999). Conservation managers are understandably critical of basic (“pure”); Gavin

1986) research with less obvious utility and of claims about the importance of such research, particularly when it attracts resources that could achieve greater conservation returns if invested in species and habitat protection. My review indicates, however, that even if the motivation and funds for applied research were larger, a conservation crisis would still constrain the amount and type of research done in the way described here for the rhinoceros (Table 1).

Thus, I suggest that an emphasis by researchers on basic research is not the problem. Indeed, experience in the management of wildlife populations the world over suggests that it is the balance of applied and basic research that most benefits the conservation and management of species (Caughley 1994), and volumes of examples show how (e.g., Mills et al. 1993; Berger 1996; Caro 1998; Mace et al. 1998; Sutherland 1998). Basic research provides a theoretical foundation and serendipitous advances, whereas applied research finds solutions to current problems. In conservation the two types of study are mutually supporting and complementary. A combination of applied and basic research is also more likely to attract researchers and funding that are traditionally discouraged from participating by apparently low academic profitability and scorn for rare-animal research (Diamond 1986). Thus, in a necessarily cooperative community of conservation managers and researchers, the dichotomy of applied and basic research is divisive. Caughley (1994) refused to recognize it and called it an "awkward distinction." I think we need to be less kind: this dichotomy is a counterproductive dualism in conservation biology. A more useful distinction should be made between targeted and nontargeted research. Nontargeted research is rarely designed within a theoretical framework, lacks a hypothesis structure or clearly stated goals, and is not synchronized with the conservation crisis for greatest utility. The science of conservation would be best served by targeted research that answers conceptual questions in field programs carefully timed with crises stage to also satisfy immediate information needs.

Targeting Research and Coping with a Conservation Crisis

By being aware that a conservation crisis occurs in a series of predictable stages with determinate implications for research priorities, constraints, and opportunities, we might make better decisions about where and when to expend research efforts. I make three suggestions about targeting research efforts.

First, it is necessary to determine when research is a low priority. The success of rhinoceros populations in South Africa is primarily characterized not by scientific research but by managers gambling on bold attempts to establish new populations in like habitat with armed security (e.g., Player 1972). The success or failure of rhi-

noceros conservation is determined not by science but by sociopolitical relationships and the cost-benefit ratio of poaching versus protection (Leader-Williams et al. 1990; Leader-Williams & Milner-Gulland 1993). Thus, claims by researchers about the relevance of their work in a conservation crisis are understandably met with chagrin by conservation managers. Conservation biologists must begin by acknowledging that most research, particularly during the desperate stages of decline and crisis management, is relatively unimportant and that resources are better invested in political and economic solutions. Nevertheless, management provides a few largely unappreciated and fortuitous opportunities for important conservation science (e.g., Berger et al. 1993; Cunningham & Berger 1997; Alibhai et al. 2001). Management that is not tailored as a scientific experiment is a lost opportunity to document and improve management techniques and ecological understanding (MacNab 1983; Armstrong et al. 1994; Lancia et al. 1996).

Moreover, the literature is undeveloped because conservation crises inevitably dictate priorities other than research for managers. Managers necessarily relegate detailed analyses and publishing in crises, although they are responsible for most of the gathering and storage of rhinoceros information and often maintain large and valuable historical data sets. Researchers, on the other hand, necessarily prioritize publishing to generate research support and funding. This difference in how conservation managers and researchers prioritize publishing is the origin of conflict between the two that occasionally boils over into the scientific literature (e.g., Lindeque and Erb 1995; Berger & Cunningham 1996; Alibhai & Jewell 2001; du Toit 2001). When acrimonious debate occurs even the most respectable study tends to be largely ignored by managers, although it may have important implications for conservation practice. Thus, researchers need to consider that getting their findings accepted by the management community can be as important as having them published. Fortunately, such conflict is not inevitable. When researchers and managers regard each other's priorities as complementary, their collaborative relationships provide opportunities to use management programs as scientific experiments and shift significant amounts of important, but presently inaccessible, information into the peer-reviewed literature. In this way the impacts of conservation crises on the development and application of knowledge, particularly in situ ecology, might be somewhat ameliorated.

The success of southern white rhinoceros conservation provides an instructive example of this collaborative process. During the rhinoceros crisis in Umfolozi Game Reserve the collaborative relationship between Player and Co and Harthoorn developed innovative rhinoceros capture and transport techniques (Player 1972) that enabled radical but successful in situ management. Harthoorn published his findings (Harthoorn 1962a;

Harthoorn 1962b), thus laying the foundation for immediate application and refinement of these techniques to other places and species (e.g., King & Carter 1965). The consequence of this collaboration between researcher and management is a long, progressive and innovative history of rhinoceros management (McKenzie 2001). The opportunities today for management on a continental scale of the rhinoceros metapopulation can be traced back to this formative collaboration between crisis managers and scientists and the dissemination by publication of the influential science that resulted.

Second, it is necessary to determine what kinds of research mitigate the limitations imposed by conservation crises. A broader multispecies approach (Forsyth et al. 2000), a thematic approach that ignores taxonomic boundaries (du Toit & Broomhall 2000), or a focus on studies of ecological processes rather than species (Balmford et al. 1998) are likely to reduce the impact of a conservation crisis on research but still enable researchers to contribute to species-centered conservation. For example, a study of the communicative processes used by rhinoceros in organizing themselves on the landscape could be applied to other sites and taxa and could have broader utility in conservation management than another study describing one more population's social and spatial structure. Rhinoceros communication might be manipulated to reduce intraspecific conflict and manage dispersal after translocations for metapopulation security and management. Such manipulations are opportunities to conduct robust experimental and theoretical research and to develop conservation management tools. Understanding and manipulating ecological processes provide opportunities to meet both research and conservation goals that descriptive and autecological studies do not.

Third, agencies should be prepared to go to greater lengths to augment opportunities for the most-needed research, particularly in situ ecological studies. After all, in situ conservation is the long-term goal and has been more successful and cost-effective than captive recovery (Leader-Williams & Albon 1988; Leader-Williams 1990; Balmford et al. 1995). Moreover, the new genetics, physiological, and veterinary literature from ex situ research has provided valuable new conservation tools and knowledge, and companion studies in genetics and physiology contribute to ecological programs. Without field trials, however, these new tools cannot be applied to conservation problems. Field studies also bridge the gap between laboratory-based ex situ studies and in situ conservation management and in turn define new priorities for future ex situ study.

Unless conservation managers and researchers are cooperatively proactive in these ways, conservation crises will inevitably continue to dictate extreme disparities between research practice and conservation needs, thus limiting the contribution science can make to conserva-

tion. Understanding the structure of conservation crises and their influence on scientific practice is a first step to better targeting research. Research priorities, effort, and funding should be allocated with the foresight that conservation needs follow a predictable series of stages during a crisis, a process that imposes nonresearch priorities and shifting constraints on the scientific opportunities most needed.

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Literature Cited

- Alibhai, S. K., and Z. Jewell. 2001. Hot under the collar: the failure of radio-collars on black rhinoceros *Diceros bicornis*. *Oryx* 35:284-288.
- Alibhai, S. K., Z. C. Jewell, and S. S. Towindo. 2001. Effects of immobilization on fertility in female black rhino (*Diceros bicornis*). *Journal of Zoology (London)* 253:333-345.
- Armstrong, D. P., T. Soderquist, and R. Southgate. 1994. Designing experimental reintroductions as experiments. Pages 27-29 in M. Serena, editor. *Reintroduction biology of Australian and New Zealand fauna*. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.
- Ashley, M. V., D. J. Melnick, and D. Western. 1990. Conservation genetics of the black rhinoceros (*Diceros bicornis*). I. Evidence from the mitochondrial DNA of three populations. *Conservation Biology* 4:71-77.
- Balmford, A., N. Leader-Williams, and M. J. B. Green. 1995. Parks or arks: where to conserve threatened mammals? *Biodiversity and Conservation* 4:595-607.
- Balmford, A., G. M. Mace, and J. R. Ginsberg. 1998. The challenges to conservation in a changing world: putting processes on the map. Pages 1-28 in G. M. Mace, A. Balmford, and J. R. Ginsberg, editors. *Conservation in a changing world*. Cambridge University Press, Cambridge, United Kingdom.
- Berger, J. 1996. Animal behaviour and plundered mammals: Is the study of mating systems a scientific luxury or a conservation necessity? *Oikos* 77:207-216.
- Berger, J., and C. Cunningham. 1994a. Bison: mating and conservation in small populations. Columbia University Press, New York.
- Berger, J., and C. Cunningham. 1994b. Phenotypic alterations, evolutionarily significant structures, and rhino conservation. *Conservation Biology* 8:833-840.
- Berger, J., and C. Cunningham. 1996. Is rhinoceros dehorning scientifically prudent? *Pachyderm* 21:60-68.
- Berger, J., C. Cunningham, A. A. Gwuseb, and M. Lindeque. 1993. "Costs" and short-term survivorship of hornless black rhinos. *Conservation Biology* 7:920-924.

- Calver, M. C., and D. R. King. 1999. Why publication matters in conservation biology. *Pacific Conservation Biology* 6:2-8.
- Caro, T., editor. 1998. Behavioral ecology and conservation biology. Oxford University Press, New York.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Clinchy, M., and C. J. Krebs. 1997. Viva Caughley! *Conservation Biology* 11:831-833.
- Cunningham, C., and J. Berger. 1997. Horn of darkness: rhinoceros on the edge. Oxford University Press, New York.
- Diamond, J. 1986. The design of a nature reserve system for Indonesian New Guinea. Pages 485-503 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Dobson, A. P. 1995. Conservation and biodiversity. Scientific American Library, New York.
- du Toit, R. 2001. Rationale for ongoing radio-collaring of black rhinos: a response to Alibhai and Jewell. *Oryx* 35:289-290.
- du Toit, J. T., and L. S. Broomhall. 2000. Mammal research in southern Africa: present patterns and future priorities. *South African Journal of Science* 96:225-230.
- Duncan, P., editor. 1992. Zebra, asses, and horses: an action plan for the conservation of wild equids. World Conservation Union, Gland, Switzerland.
- Emslie, R., and M. Brooks. 1999. African rhino. Status survey and conservation action plan. World Conservation Union/Species Survival Commission, African Rhinoceros Specialist Group, Gland, Switzerland and Cambridge, U.K.
- Fischer-Tenhagen, C., C. Hamblin, S. Quandt, and K. Frolich. 2000. Serosurvey for selected infectious disease agents in free-ranging black and white rhinoceros in Africa. *Journal of Wildlife Diseases* 36:316-323.
- Foose, T. J., and R. E. Miller. 1994. African rhinoceros populations in North America. Pages 31-34 in Proceedings of a South African Veterinary Association symposium on rhinos as game ranch animals. Onderstepoort, South Africa.
- Foose, T. J., and N. van Strien. 1997. Asian rhinos: status survey and conservation action plan. World Conservation Union, Gland, Switzerland.
- Forsyth, D. M., J. P. Parkes, and G. J. Hickling. 2000. A case for multi-species management of sympatric herbivore pest impacts in the Southern Alps, New Zealand. *New Zealand Journal of Ecology* 24:97-103.
- Galli, N. S., and J. R. B. Flammand. 1995. Darting and marking black rhinoceros on foot: part of a monitoring and population estimation technique in Hluhluwe-Umfolozi Park, South Africa. *Pachyderm* 20:33-38.
- Gavin, T. A. 1986. Population biology and the potential loss of a participant allele. *Bulletin of the Ecological Society of America* 66:171-175.
- Hall-Martin, A. J., and M. H. Knight. 1994. Conservation and management of black rhinoceros in South African National Parks. Pages 11-19 Proceedings of a South African Veterinary Association symposium on rhinos as game ranch animals. Onderstepoort, South Africa.
- Hall-Martin, A. J., N. J. van der Merwe, J. A. Lee-Thorp, R. A. Armstrong, C. H. Mehl, S. Struben, and R. Tykot. 1993. Determination of species and geographic origin of rhinoceros horn by isotopic analysis and its possible application to trade control. Pages 123-130 in O. A. Ryder, editor. Proceedings of an international conference on rhinoceros biology and conservation. Zoological Society of San Diego, San Diego.
- Harthorn, A. 1962a. Capture of white (square-lipped) rhinoceros, *Ceratotherium simum simum* (Burchell), with the use of the drug immobilization technique. *Canadian Journal of Comparative Medicine* 26:203-208.
- Harthorn, A. M. 1962b. The capture and relocation of the white (square-lipped) rhinoceros, *Ceratotherium simum simum*, using drug-immobilising techniques, at the Umfolozi Game Reserve. *Natal. Lammergeyer* 2:1-9.
- Institute for Scientific Information (ISI). 2000. Endnote. ISI, Research Soft, Berkeley, California.
- King, J., and B. Carter. 1965. The use of the oripavine derivative M-99 for the immobilization of the black rhinoceros (*Diceros bicornis*) and its antagonism with the related compound M-285. *East African Wildlife Journal* 3:19-27.
- Lancia, R. A., C. E. Braun, M. W. Collopy, R. D. Dueser, J. G. Kie, C. J. Martinka, J. D. Nichols, T. D. Nudds, W. R. Porath, and N. G. Tilghman. 1996. ARM! for the future: adaptive resource management in the wildlife profession. *Wildlife Society Bulletin* 24:436-442.
- Leader-Williams, N. 1990. Black rhinos and African elephants: lessons for conservation funding. *Oryx* 24:23-29.
- Leader-Williams, N., and S. D. Albon. 1988. Allocation of resources for conservation. *Nature* 336:533-535.
- Leader-Williams, N., and E. J. Milner-Gulland. 1993. Policies for the enforcement of wildlife laws: the balance between detection and penalties in Luangwa Valley, Zambia. *Conservation Biology* 7:611-617.
- Leader-Williams, N., S. D. Albon, and P. S. M. Berry. 1990. Illegal exploitation of black rhinoceros and elephant populations: patterns of decline, law enforcement and patrol effort in Luangwa Valley Zambia. *Journal of Applied Ecology* 27:1055-1087.
- Lindeque, M., and K. Erb. 1995. Research on the effects of temporary horn removal on black rhinos in Namibia. *Pachyderm* 20:27-30.
- Mace, G. M., A. Balmford, and J. R. Ginsberg, editors. 1998. Conservation in a changing world. Cambridge University Press, Cambridge, United Kingdom.
- MacNab, J. 1983. Wildlife management as scientific experimentation. *Wildlife Society Bulletin* 11:397-401.
- McKenzie, A. 2001. The capture and care manual. Wildlife Decision Support Services, Lynnwood Ridge, South Africa Available from <http://www.wildlifedecisionsupport.com/captureandcare/index.html> (accessed July 2002).
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* 43:219-224.
- Patton, M. L., R. R. Swaisgood, N. M. Czekala, A. M. White, G. A. Fetter, J. P. Montagne, R. G. Rieches, and V. A. Lance. 1999. Reproductive cycle length and pregnancy in the southern white rhinoceros (*Ceratotherium simum simum*) as determined by fecal pregnane analysis and observations of mating behavior. *Zoo Biology* 18:111-127.
- Player, I. 1972. The white rhinoceros saga. William Collins, London.
- Poulton, S. 1982. Kakapo: a bibliography. Page 88. New Zealand Wildlife Service, Department of Internal Affairs, Wellington.
- Radcliffe, R. W., S. T. Ferrell, and S. E. Childs. 2000. Butorphanol and azaperone as a safe alternative for repeated chemical restraint in captive white rhinoceros (*Ceratotherium simum*). *Journal of Zoo and Wildlife Medicine* 31:196-200.
- Schaffer, N. E., J. G. Walasek, D. C. Hall, W. M. Bryant, and M. C. Reed. 1998. Cage restraints for rhinoceroses. *Zoo Biology* 17:343-359.
- Soulé, M. E. 1985. What is conservation biology? *BioScience* 35:727-734.
- Stanley-Price, M. R. 1989. Animal re-introductions: the Arabian Oryx in Oman. Cambridge studies in applied ecology and resource management. Cambridge University Press, Cambridge, United Kingdom.
- Sutherland, W. J., editor. 1998. Conservation science and action. Blackwell Science, Oxford, United Kingdom.
- Western, D., and M. C. Pearl, editors. 1989. Conservation for the twenty-first century. Oxford University Press, New York.