

Modeling the viability of the free-ranging cheetah population in Namibia: an object-oriented Bayesian network approach

SANDRA JOHNSON,^{1,†} LAURIE MARKER,² KERRIE MENGENSEN,¹ CHRIS H. GORDON,^{2,5} JÖRG MELZHEIMER,³
ANNE SCHMIDT-KÜNTZEL,² MATTI NGHIKEMBUA,² EZEQUIEL FABIANO,² JOSEPHINE HENGHALI,^{4,6}
AND BETTINA WACHTER³

¹Queensland University of Technology, GPO Box 2434, Brisbane, Queensland 4001 Australia

²Cheetah Conservation Fund, P.O. Box 1755, Otjiwarongo, Namibia

³Leibniz Institute for Zoo and Wildlife Research, Berlin, Alfred-Kowalke-Str. 17, 10315 Germany

⁴Ministry of Environment and Tourism, P.O. Box 13306, Windhoek, Namibia

Citation: Johnson, S., L. Marker, K. Mengersen, C. H. Gordon, J. Melzheimer, A. Schmidt-Küntzel, M. Nghikembua, E. Fabiano, J. Henghali, and B. Wachter. 2013. Modeling the viability of the free-ranging cheetah population in Namibia: an object-oriented Bayesian network approach. *Ecosphere* 4(7):90. <http://dx.doi.org/10.1890/ES12-00357.1>

Abstract. Conservation of free-ranging cheetah (*Acinonyx jubatus*) populations is multi faceted and needs to be addressed from an ecological, biological and management perspective. There is a wealth of published research, each focusing on a particular aspect of cheetah conservation. Identifying the most important factors, making sense of various (and sometimes contrasting) findings, and taking decisions when little or no empirical data is available, are everyday challenges facing conservationists. Bayesian networks (BN) provide a statistical modeling framework that enables analysis and integration of information addressing different aspects of conservation. There has been an increased interest in the use of BNs to model conservation issues, however the development of more sophisticated BNs, utilizing object-oriented (OO) features, is still at the frontier of ecological research. We describe an integrated, parallel modeling process followed during a BN modeling workshop held in Namibia to combine expert knowledge and data about free-ranging cheetahs. The aim of the workshop was to obtain a more comprehensive view of the current viability of the free-ranging cheetah population in Namibia, and to predict the effect different scenarios may have on the future viability of this free-ranging cheetah population. Furthermore, a complementary aim was to identify influential parameters of the model to more effectively target those parameters having the greatest impact on population viability. The BN was developed by aggregating diverse perspectives from local and independent scientists, agents from the national ministry, conservation agency members and local fieldworkers. This integrated BN approach facilitates OO modeling in a multi-expert context which lends itself to a series of integrated, yet independent, subnetworks describing different scientific and management components. We created three subnetworks in parallel: a biological, ecological and human factors network, which were then combined to create a complete representation of free-ranging cheetah population viability. Such OOBNs have widespread relevance to the effective and targeted conservation management of vulnerable and endangered species.

Key words: *Acinonyx jubatus*; carnivore conservation; IBNDC; integrated modeling; Namibia; object-oriented Bayesian network (OOBN); parallel modeling; population viability; predator conservation; wildlife management.

Received 14 November 2012; revised 7 May 2013; accepted 28 May 2013; final version received 29 June 2013; **published** 30 July 2013. Corresponding Editor: G. Chapron.

Copyright: © 2013 Johnson et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

⁵ Present address: Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford, UK.

⁶ Deceased.

† **E-mail:** sandra.johnson@qut.edu.au

INTRODUCTION

Species conservation and biodiversity management are complex environmental issues. When addressed from the different ecological, economic and management perspectives, they are likely to have quite diverse objectives. However, ignoring a particular perspective may lead to an incorrect and over-simplified view of the issues of concern. Instead, all perspectives need to be considered and integrated to form a cohesive model for use in planning strategic conservation actions. Bayesian networks (BNs) are ideally suited for interactive, integrated modeling (Johnson et al. 2010a). A BN is a mathematical model (Pearl 1988, Neapolitan 1990, Jensen and Nielsen 2007) providing a graphical representation of key factors and interactions for an outcome of interest (Jensen and Nielsen 2007, Uusitalo 2007, Johnson et al. 2010a, b) such as the viability of a free-ranging cheetah (*Acinonyx jubatus*) population. Key factors are represented as nodes in the diagram and their dependencies on other key factors and the outcome of interest (target node) are depicted as directed links to form a directed acyclic graph (Lauritzen and Sheehan 2003, Johnson et al. 2010b). Underlying each node is a conditional probability table (CPT) that is determined by the states of the node and its parent nodes (Table 1). The information used to populate the CPTs in the network may originate from diverse sources such as empirical data, expert opinion and simulation outputs (Pearl 2000, Jensen and Nielsen 2007).

Bayesian networks are growing in popularity in environmental disciplines (Uusitalo 2007) but the development of more sophisticated BNs, utilizing dynamic and object-oriented (OO) features is still at the frontier of ecological research, where the available data may be sparse and the underlying biological and physical models very complex (Johnson and Mengersen 2012). Object-oriented Bayesian networks (OOBN) are BNs which have interface nodes (input nodes and output nodes) and instance nodes (representing another network or network fragment). Interface nodes enable connectivity with other OOBNs by providing the flow of information into (input node) and out of (output node) the BN from, or to, other OOBNs (Hugin 2007, Jensen and Nielsen 2007, Johnson et al. 2010a). This enables

the construction of complex and dynamic models (Koller and Pfeffer 1997, Johnson et al. 2010a) when traditional BNs are often inadequate (Uusitalo 2007, Johnson and Mengersen 2012). Moreover, environmental or conservation issues may be modeled by a series of integrated subnetworks describing different scientific components, combining scientific and management perspectives, or pooling similar contributions developed in different locations by different research groups (Johnson and Mengersen 2012).

There is a range of alternatives to BN models for describing complex systems and making decisions about alternative strategies. Some of these, such as agent based models, are explicitly based on a systems approach and focus on system modeling, behavior and description (Tang et al. 2009). They provide a more mechanistic description of a system and the model components are linked by a set of rules rather than probabilities. Other alternatives, such as multi-attribute and multi-criteria models, decision trees and cost-benefit methods, are mainly focused on decision analysis, which embrace a range of methods for evaluating alternative strategies in complex decision making (Chankong and Haimes 1983).

Species conservation presents an appropriate exposition of an integrated approach to modeling, because it requires distinct, yet inter-related, aspects of ecological, biological and human factors to be taken into account. BNs are generally easier to use and understand than many of the alternative models, and incorporates uncertainty in the model and decision making within different contexts (Jensen and Nielsen 2007, Barton et al. 2012). Moreover their visual nature allows stakeholders with different backgrounds to engage with the model, aiding and directing communication (Henriksen et al. 2012). Here we apply an OOBN to a vulnerable species of high relevance, the free-ranging cheetah population in Namibia, to exemplify the power of this modeling approach for conservation management.

Over the past century, free-ranging cheetahs have undergone a drastic reduction in both global geographic range and population size, leaving Namibia as one of the remaining strongholds for the species (Marker et al. 2007). The current global free-ranging cheetah popula-

Table 1. Example of a conditional probability table (CPT) showing the *Female mate choice* node with states *increase* and *decrease* (left below) and parent nodes *Cheetah removal* with states *decrease* and *increase*, *Intraspecific density* with states *higher*, *medium* and *lower* and *Immigration/emigration* with states *gain* and *loss*.

Female mate choice	Cheetah removal											
	Decrease						Increase					
	Intraspecific density											
	Higher		Medium		Lower		Higher		Medium		Lower	
	Immigration/emigration											
	Gain	Loss	Gain	Loss	Gain	Loss	Gain	Loss	Gain	Loss	Gain	Loss
Increase	0.8	0.75	0.7	0.65	0.6	0.55	0.55	0.5	0.45	0.4	0.35	0.3
Decrease	0.2	0.25	0.3	0.35	0.4	0.45	0.45	0.5	0.55	0.6	0.65	0.7

tion is estimated at less than 12,000 individuals, with the majority of cheetahs being found outside protected areas (Purchase et al. 2007). Based on these estimates, the free-ranging cheetah population in Namibia consists of more than a third of the world population (Hanssen and Stander 2004, Marker et al. 2007, Purchase et al. 2007). However, the steady increase in human population size is resulting in an increase in livestock numbers and valuable game species, which intensifies the conflict between humans and cheetahs. Effective management and maintenance of a healthy cheetah population in Namibia is considered critical for cheetah conservation worldwide (Woodroffe et al. 2007). Furthermore, knowledge gained from this population could prove invaluable for cheetah conservation and management in other range countries (Marker et al. 2007). The viability of the free-ranging cheetah population in Namibia was the focus of a Bayesian network modeling workshop at Cheetah Conservation Fund (CCF) in Namibia in June 2008, bringing together conservationists, researchers and government representatives.

This paper models the factors influencing the viability of the Namibian cheetahs using the reservoir of data and expert opinion available for the north-central free-ranging cheetah population and discusses five possible scenarios and strategies for reducing identified threats to ensure the long-term conservation of this valuable population. The application of OOBN modeling techniques with its parallel concurrent development of inter-related, yet self-contained networks by specialist expert teams (Johnson et al. 2010a) is eminently transferrable to modeling the issues

facing conservation and management of other species of interest or concern.

MATERIALS AND METHODS

Study area

Free-ranging cheetahs are distributed throughout most of Namibia, with the highest densities in northern and central Namibia (Fig. 1). This study uses data and information from this core population.

OOBN modeling

We used the iterative Bayesian network development cycle (IBNDC) approach, which had been trialed at a cheetah relocation BN modeling workshop in South Africa (Johnson et al. 2010b). The IBNDC is divided into two parts, a *Core Process* and an *Iterative Process*. During the *Core Process* the target node was carefully defined by the expert teams. Thereafter the key factors believed to affect the target node were identified, defined and grouped into logical, coherent groups which were allocated to subnetworks (Johnson et al. 2010b). Fig. 2 captures the key steps and activities comprising the IBNDC approach. The workshop participants split into groups in accordance with the subnetwork which best suited their expert knowledge.

For the *Iterative Process*, we used BN modeling software conducive to OO modeling (Hugin), which is required for the IBNDC heuristic, as described in Johnson et al. (2010b). To start the *Iterative Process*, each team reviewed the nodes (key factors) and represented dependencies as arrows (directed links) between the nodes (key factors) in the network to illustrate the direction

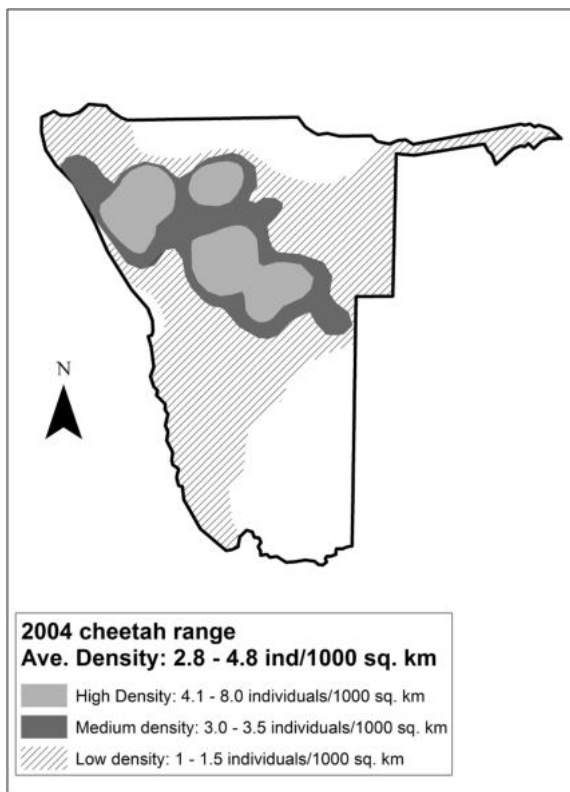


Fig. 1. Map of Namibia showing the distribution and density of the cheetah population in Namibia in 2004 (adapted from Marker et al. 2007).

of the relationship between them. Then the teams specified the interfaces for the subnetworks, which dictate the flow of information between different subnetworks. An interface for a subnetwork consists of input and output nodes. The expert teams identified nodes that were of interest to more than one subnetwork. Each of these nodes would be ‘owned’ by a particular OOBN subnetwork that would create it as an output node to make it visible to the other subnetworks that needed to include it in their model (Johnson and Mengersen 2012). Thereafter the OOBN subnetworks that needed to model the effects of this node on other factors in their subnetwork, created a corresponding input node (a ‘placeholder’ node). The states of the node were decided by the team creating the output node and the other team ensured that their input node exactly matched those states (Fig. 3) (Jensen and Nielsen 2007, Johnson and Mengersen 2012). The interfaces therefore enable the creation of

integrated, yet separate, networks, by allowing the flow of information through the input and output nodes (Johnson et al. 2010a). Essentially the set of interface nodes can be viewed as the model’s ‘information gateway’, setting up ‘bridges’ (connection points) and paths to guide the flow of information between the model’s OOBN subnetworks.

The teams were consequently able to work on the structure and content of their subnetworks without impacting on the other subnetworks, since the interfaces dictate the means of communication with the other OOBN subnetworks. This is an important concept in OO modeling known as encapsulation, or information hiding (Pastor et al. 2001, Booch et al. 2007).

The IBNDC *Iterative Process* consists of four repeating (R) phases, Phase 1R (define), Phase 2R (quantify), Phase 3R (validate) and Phase 4R (evaluate) (Fig. 2; Johnson et al. 2010b). For each team, Phase 1R involved the careful definition and documentation of the nodes and their interactions (see above). During Phase 2R the nodes were quantified. This encompassed agreeing on how the node could be measured and what information was available to determine the probability distribution of the node, the definition of the possible states of the nodes and their thresholds, and populating the CPT for the node given the different combinations of states of the parent nodes (Table 1).

In Phase 3R the OOBN subnetworks were validated by compiling and running the BN, and then checking to see whether the predictions were consistent with known behavior and whether the BN respected known causal relationships. The testing was primarily done using expert knowledge to interpret the observed behavior of the OOBN. If there were inconsistencies, this could be due to either an error in the entered data (evidence), an error in one of the CPTs or in the directed links between the nodes. Inconsistent behavior necessitated the reassessment of nodes, states and probabilities which were addressed in the next iteration (Johnson et al. 2010b). At the end of Phase 3R the subnetworks were reviewed by the other teams as a ‘sanity check’ and evaluation of the OOBN subnetwork, which are typical Phase 4R activities. To process the changes resulting from the Phase 4R evaluation, another iteration of the

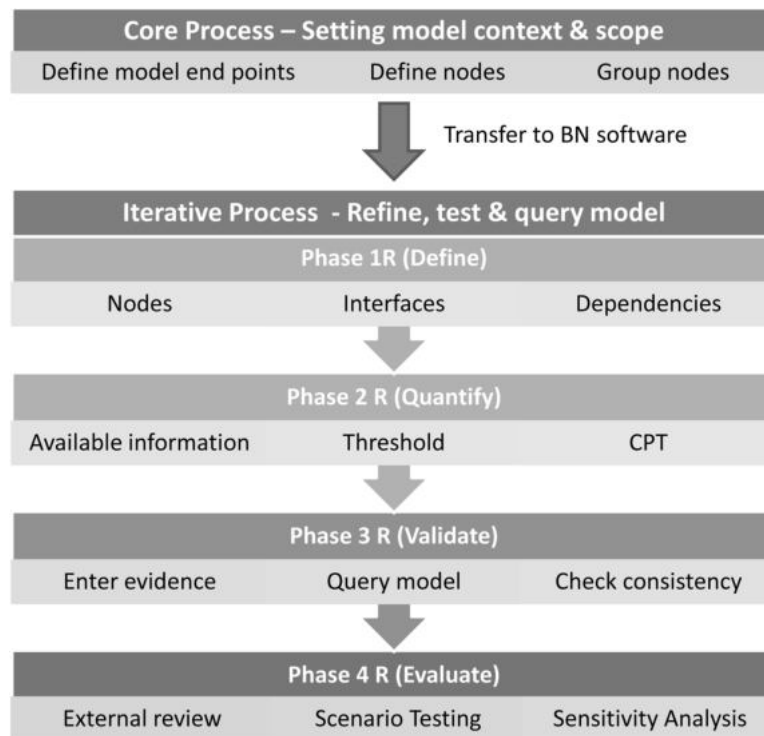


Fig. 2. A conceptual diagram of the Iterative Bayesian Network Development Cycle (IBNDC), showing the key modeling activities for building an OOBN.

IBNDC is then invoked. Once the subnetworks were in a stable condition, they were merged into the overall network and the final set of iterations was performed on the entire OOBN (Johnson et al. 2010b). This involved scenario testing and sensitivity analysis for both evidence (observed values of nodes) and parameters (probability values of CPTs) of the combined network.

Scenario testing

A key feature of BN modeling is inference, which enables us to draw conclusions about the outcome of interest (Bednarski et al. 2004). For this case study the outcome of interest (or target variable) is the viability of the free-ranging cheetah population in north-central Namibia. The OOBN model is a joint probability distribution across all the nodes identified by the expert teams.

A BN is often used to answer questions about the conditional distribution of the target variable based on values of specific variables in the BN (Laskey 1995). Evidence is entered into the

network to represent various scenarios of interest and this evidence is propagated through the BN resulting in changed probabilities for the states of the target variable. The evidence will also result in probability changes in other nodes (variables) in the model because of information flows along the various pathways in the model (Taroni et al. 2006, Jensen and Nielsen 2007). Some open pathways may become blocked and some blocked pathways may be opened up when evidence is entered in the BN, depending on the nature of the associations between nodes (Jensen and Nielsen 2007). The arcs in the BN reflect the nature of the associations and the conditional probability tables describe the strengths of these relationships (Korb and Nicholson 2004, Taroni et al. 2006). For example, we may want to run queries such as ‘what happens if we are certain that cheetah removal is decreasing?’ From a probabilistic perspective, being certain that cheetah removal is decreasing, is equivalent to setting the ‘decrease’ state of cheetah removal to 100%.

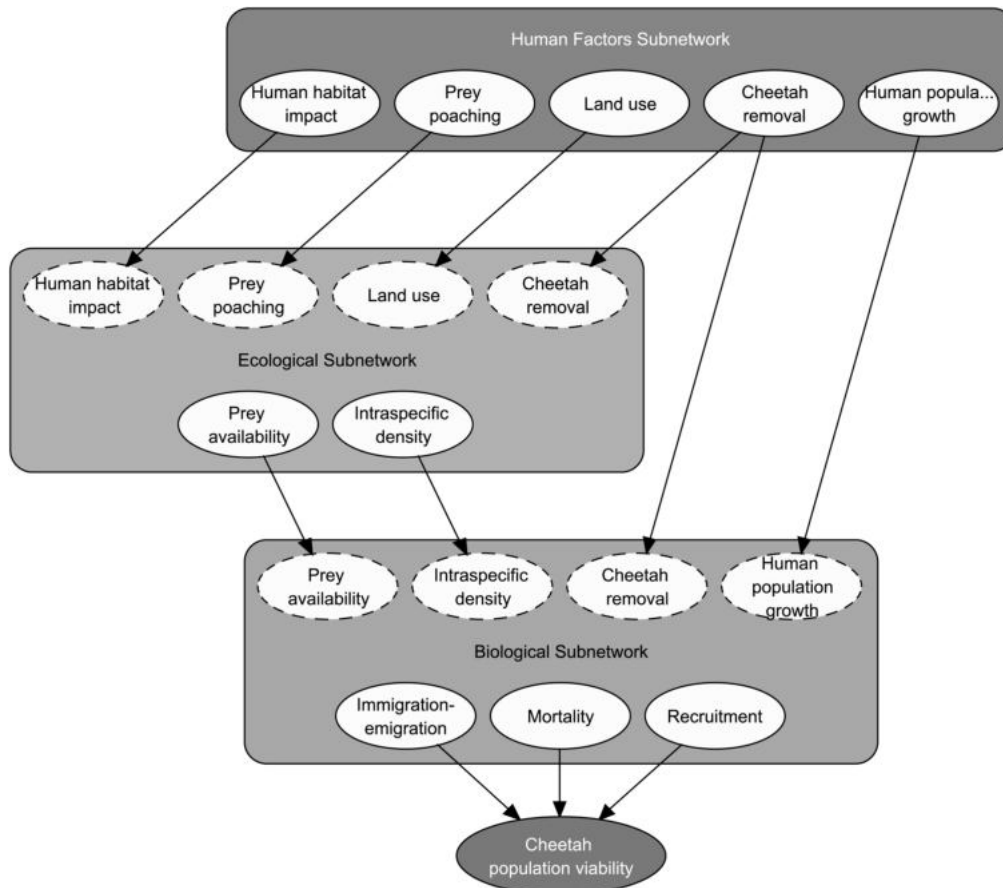


Fig. 3. Interface nodes for the three OOBN subnetworks. The human factors OOBN subnetwork has five output nodes (eclipse with solid line): *Human population growth*, *Cheetah removal*, *Human habitat impact*, *Prey poaching* and *Land use*. The ecological factors OOBN subnetwork has four input nodes (eclipse with broken line): *Cheetah removal*, *Human habitat impact*, *Prey poaching*, *Land use* and two output nodes: *Prey availability*, *Intraspecific competition*. The biological factors OOBN subnetwork has four input nodes: *Human population growth*, *Cheetah removal*, *Prey availability* and *Intraspecific density* and three output nodes: *Recruitment*, *Immigration-emigration* and *Mortality* which all feed into the target node of the combined network, *Cheetah population viability*.

It is important to ensure that we understand the sensitivity of the BN to variations in the evidence (observed values of nodes) and parameters (probability values of CPTs) in the network (Johnson et al. 2010b). Due to the lack of available data or the nature of the information, some parameters may have to be elicited from experts (Bednarski et al. 2004). This information may be biased and based on intuition rather than real data. However, many parameters do not require great precision (Onisko and Druzdzel 2011) and expert opinions are ideally suited to estimate them. Nonetheless, it is critical for the authenticity and predictive accuracy of the BN inference to

refine those parameters that are shown to have a more profound effect on the target node (Onisko and Druzdzel 2011). If the probabilities of these parameters are inaccurate or incorrect, they can result in false or misleading conclusions and predictions being made.

Sensitivity analysis

Sensitivity analysis of a BN is therefore a vital part of the evaluation process. It involves the assessment of the sensitivity of the target node to variations in the evidence entered into the network (evidence sensitivity) and to variations in the values of the parameters (parameter

sensitivity) (Varis and Kuikka 1999, Bednarski et al. 2004). Evidence sensitivity measures the degree of variation in the BN's posterior distribution resulting from changes in the evidence and assists the expert team in targeting future data collection and identifying any errors in the BN structure or CPTs (Jensen and Nielsen 2007, Johnson et al. 2010b). Two popular ways in which to measure evidence sensitivity are entropy and mutual information (Pollino et al. 2007a). Entropy measures the randomness of a variable (key factor) (Pearl 1988, Korb and Nicholson 2004, Kjaerulff and Madsen 2007) and the higher the value the more random the variable. Mutual information gives an indication of the extent to which the joint probability of two variables differs from what it would have been if they were independent (Korb and Nicholson 2004, Pollino et al. 2007b). Therefore a value of 0 for mutual information between two factors means that they are independent (Pearl 1988, Kjaerulff and Madsen 2007).

Using parameter sensitivity we can identify those parameters which cause the biggest changes in the posterior probabilities of the outcome of interest. Efforts are then directed to improve the level of accuracy for those parameters (Pollino et al. 2007b) and to channel expert elicitation efforts (van der Gaag et al. 2007). One way in which sensitivity analysis can be performed is by varying one of the parameters while keeping all the others fixed and then measuring the variation in the output parameter (Bednarski et al. 2004).

RESULTS

Core process

The objective of the expert teams was to model the viability of the free-ranging cheetah population in north-central Namibia. Viability was defined as the cheetah population having a positive annual growth rate. The experts nominated the factors believed to affect the viability of this cheetah population, which readily separated into three coherent groups: human, ecological and biological factors. The experts aligned themselves with the group which best suited their skill set and entered the factors into the chosen BN software package (Hugin). Each of the three groups created nodes that became part of separate, self-contained BN submodels.

Iterative process

Reviewing the nodes in each of the subnetworks identified nodes common to more than one subnetwork. These nodes formed the sub-model interfaces and are shown in the high level view of the integrated OOBN model in Fig. 3. The input nodes have a broken line and the output nodes a solid line.

The integrated OOBN model consists of the three OOBN submodels (human, ecological and biological) and the target node, which is the viability of the free-ranging cheetah population (Fig. 3). The OOBN subnetworks are discussed in more detail below to clarify the selection of the key factors (written in italic font) for each subnetwork and those shared between subnetworks.

For the overall integrated OOBN, the biological factors were determined to have a direct effect on the viability of the cheetah population (*Recruitment, Immigration-emigration and Mortality*) (Fig. 3). The conditional probability table describing the influence of these three factors on the population viability is shown in Table 2. These probabilities were elicited by consensus from the three teams of experts. Expert opinion regarding the Namibian cheetah population was substantiated by demographic estimates including age structure, sex ratio, and cheetah removals drawn from the literature (Marker et al. 2003a, b, 2007, 2008). Two human factors (*Human population growth, Cheetah removal*) and two ecological factors (*Prey availability, Intraspecific density*) were identified as directly affecting biological factors. The ecological factors are in turn deemed to be affected by the human factors *Cheetah removal, Human habitat impact, Prey poaching* and *Land use* (Fig. 3).

Human factors OOBN

The thirteen nodes of the human factors OOBN are shown in Fig. 4. The expert teams believed the human factors identified in the workshop to influence both the ecology and biology of the free-ranging cheetah population. They nominated *Human population growth, Cheetah removal, Human habitat impact, Prey poaching* and *Land use* as output nodes for access by the biological and ecological factors OOBNs (Fig. 3). These five nodes formed the human factors interface.

Human-carnivore conflict is a major issue for

Table 2. The expert elicited conditional probability table (CPT) for *Cheetah population viability*, which is determined by parent nodes *Recruitment*, *Mortality* and *Immigration/emigration*.

Cheetah population viability	Recruitment							
	Increased				Decreased			
	Mortality							
	Increased		Decreased		Increased		Decreased	
Cheetah population viability	Immigration/emigration							
	Gain	Loss	Gain	Loss	Gain	Loss	Gain	Loss
Gain	0.55	0.45	0.90	0.80	0.20	0.10	0.55	0.45
Loss	0.45	0.55	0.10	0.20	0.80	0.90	0.45	0.55

carnivore conservation (Woodroffe et al. 2007). Considerable research has been conducted on Namibian cheetahs and has shown that this population has been reduced in numbers due to perceived and actual livestock and game losses leading to *Human cheetah conflict* (Marker et al. 2002, 2003a, b). The biggest threats to cheetahs are the loss of suitable habitat and prey availability, and indiscriminate removals and killing (*Cheetah removal*).

Commercial farmlands in Namibia have higher game and carnivore densities and species richness, as well as lower human population pressures than communal lands (Kauffman et al. 2007). They are managed for livestock and wildlife, whereas communal lands are managed only for livestock (Kauffman et al. 2007). High

livestock densities compounded by ineffective livestock and veld management practices result in productive wildlife habitat becoming overgrazed and bush encroached (de Klerk 2004) (*Livestock & wildlife management*).

To mitigate the *Human cheetah conflict*, *Farmer education* was considered crucial to long term conservation strategies by the expert team. Developing education and training programs that promote an integrated approach to livestock, wildlife and predator management are vital to improving basic understanding of farm production principles including animal health, breeding, financial management, rangeland management, and predator conflict prevention. More generally, *Environmental education* (educating all levels of society) has been identified as a priority for

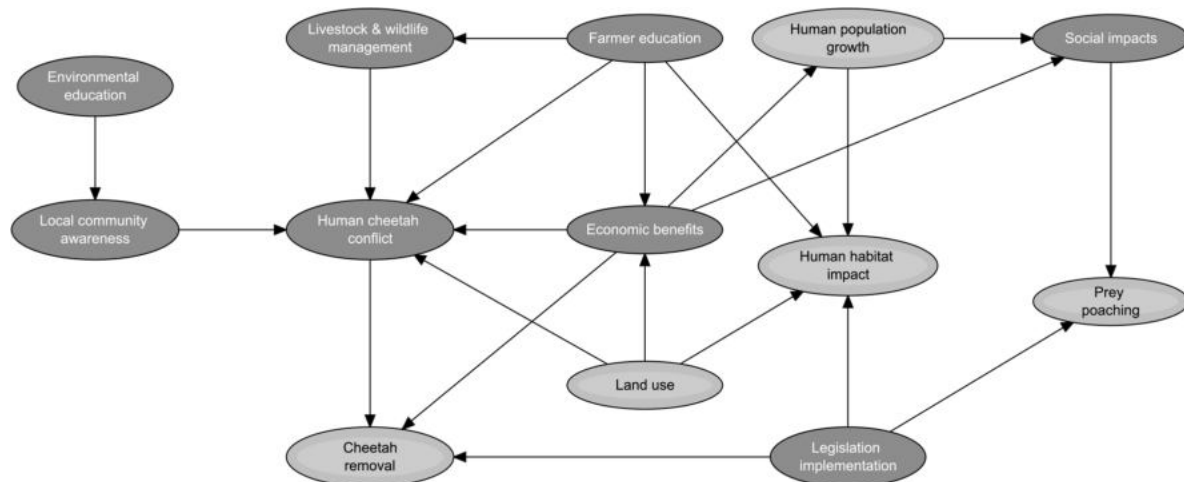


Fig. 4. Human factors OOBN subnetwork showing output nodes (double line eclipse with solid outer line): *Cheetah removal*, *Land use*, *Human population growth*, *Human habitat impact* and *Prey poaching*. These five nodes form the interface of this OOBN.

cheetah conservation throughout cheetah-range countries (Purchase et al. 2007). Given that human-carnivore conflict is multi-faceted, there is a need to create a knowledge based society.

Changes in *Land use* from commercial to communal systems, e.g., where large tracks of land are subdivided for resettlement, are likely to have significant effects on wildlife population density and species diversity. Ownership of resources and the land tenure systems, especially on communal lands, also influence the manner in which people perceive natural resources. As such, it is believed that communal resources would continue to be exploited, unless people are empowered with the responsibility to manage the resources on a sustainable basis. Identified *Land use* categories were commercial farmlands, communal land and protected land. Land tenure systems play a key role in determining the outcomes and implementation of management decisions (Muntifering et al. 2006, Nghikembua 2008) (*Local community awareness*).

Commercial and communal farmlands support an integrated livestock and wildlife based economy. Productive rangelands provide a direct economic incentive to farmers, therefore stocking rates and livestock densities are raised, especially in good rainfall seasons. *Economic benefits* may be derived from both agriculture and conservation enterprises such as bee-keeping and ecotourism. Financial benefits raise positive tolerance, attitudes and perception towards predators (Marker 2002), whereas poor economic benefits may compel the removal of carnivores, perceived as threats. This is especially the case in areas with no conservancies where benefits from wildlife resources are limited due to user rights. The human factors subnetwork team believed that increased economic benefit may also have a negative effect because farmers stand to lose more from game or livestock loss to cheetahs.

Namibia is sparsely populated (National Planning Commission 2004), its climate and unreliable rainfall creating a fragile environment with limited productivity. An increase in human population puts further pressure on limited natural resources to satisfy basic human needs such as food security, shelter, health, and employment (*Human population growth*).

Legislation implementation encompasses both the existence and implementation of acts, poli-

cies, and approved protocols to prevent the decline of an endangered species, protect suitable habitat and promote coexistence with farmers, including those administered by the Ministry of Agriculture, Ministry of Environment and Tourism, and Ministry of Land and Resettlement. Land resettlement policies could have a direct impact on habitat suitability for the free-ranging cheetah population, especially where individual farms are reduced to smaller units, thereby increasing the risk of rangeland degradation and low productivity. *Human habitat impact* on cheetah population viability may be incidental, purposeful or unintentional and is dependent on the effects of four key factors: *Land use*, *Human population growth*, *Farmer education* and *Legislation implementation*.

Ecological factors OOBN

Fig. 5 depicts the ecological factors subnetwork containing eleven nodes, of which six form the interface with other OOBN subnetworks. There are four input nodes from the human factors OOBN and two output nodes which are accessed by the biological OOBN.

The ecological OOBN was designed around the two core ecological factors: prey availability and competition (intraspecific and intraguild). While ecological factors can have a significant effect on species within ecosystems, it is the pressures from other factors that most affect the ecological balance. The expert team determined that human factors (*Cheetah removal*, *Human habitat impact*, *Prey poaching* and *Land use*) would have the greatest impact on the ecology of the cheetah. The ecological factors *Prey availability* and *Intraspecific density* would in turn affect the biology of the cheetah.

Namibian cheetahs are known to show prey preference for native game species (Marker et al. 2002). However, *Prey availability* is dependent on numerous factors such as habitat parameters and climatic factors. Besides these intrinsic factors, the legal and illegal removal of potential prey (*Prey poaching*) due to human activities such as poaching and game harvesting (e.g., biltong, meat and trophy hunting) plays an important role in prey availability for cheetahs. Consequently, *Prey poaching* (output node from the human factors OOBN) is included in this subnetwork as an input node. Additionally,

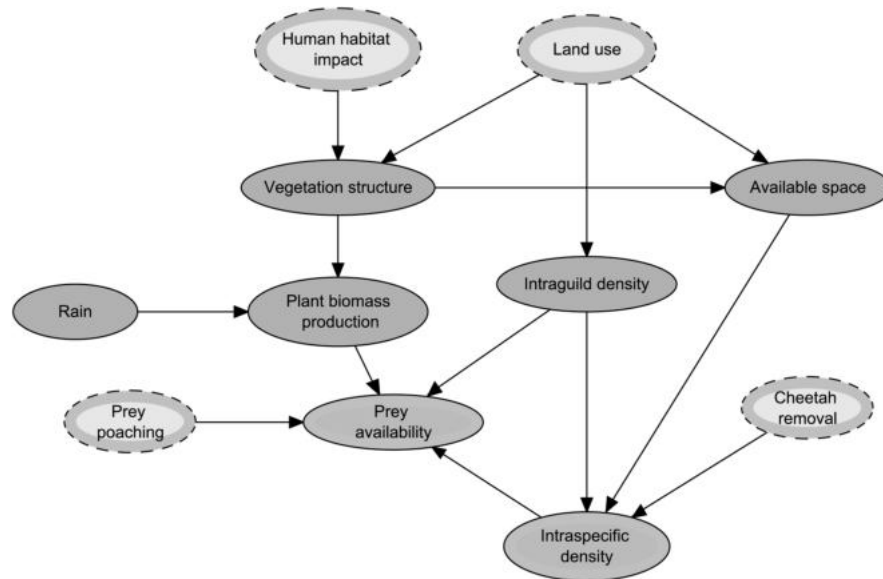


Fig. 5. Ecological factors OOBN subnetwork showing four input nodes (double line eclipse with broken outer line) and five output nodes (double line eclipse with solid outer line) that make up this OOBN's interface. All input nodes are from the human factors OOBN subnetwork: *Prey poaching*, *Human habitat impact*, *Land use* and *Cheetah removal*. The output nodes are *Prey availability* and *Intraspecific density*.

Human habitat impact (output node from the human factors OOBN) influences prey densities indirectly due to overgrazing from livestock, which in turn contributes to bush encroachment (de Klerk 2004).

Land use (output node from the human factors OOBN) and *Vegetation structure* are also expected to affect available habitat for cheetah, and carrying capacities. Cheetahs prefer habitat patches with grassy cover and high visibility (Muntifering et al. 2006). *Intraguild density* and available space affect *Intraspecific density* of cheetahs (Kelly et al. 1998). *Intraspecific density* and *Intraguild density* are assessed to only modestly affect *Prey availability*. In addition, the type of *Land use* affects the *Intraguild density* or numbers of larger predators (specifically lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*)) that would compete with cheetahs in three ways: a) reducing the amount of prey available, b) scavenging kills from cheetahs and c) killing cheetah cubs (Laurenson et al. 1995, Durant 2000).

Direct *Cheetah removal* by humans (output node from the human factors OOBN), both legal (trophy hunting, reported removal of problem

animals) and illegal will have a substantial effect on the density and abundance of cheetahs. The level of removals of cheetahs within Namibia is poorly understood. While the quota of 150 cheetahs per annum for trophy hunting (CITES 1992) is almost never met, the levels of illegal removal remain largely unknown. Furthermore, excessive human pressures would affect preferred cheetah habitat (*Vegetation structure* and *Available space*), *Prey availability* and *Intraspecific density*.

Biological factors OOBN

The biological OOBN subnetwork shown in Fig. 6 contains eleven key nodes with the interface consisting of four input nodes and three output nodes. The biological factors were designed around *Health*, *Genetics*, *Stress* and behavior (*Female mate choice*). Ecological factors influencing the biology of the cheetah were identified as *Prey availability*, which was assessed to have a stronger impact if it dropped to a critical level, and *Intraspecific density*. Crucially, all biological factors fed directly into *Mortality* and *Recruitment* to reflect that these two factors, in addition to *Immigration-emigration*, define population growth or decline, and ultimately, the

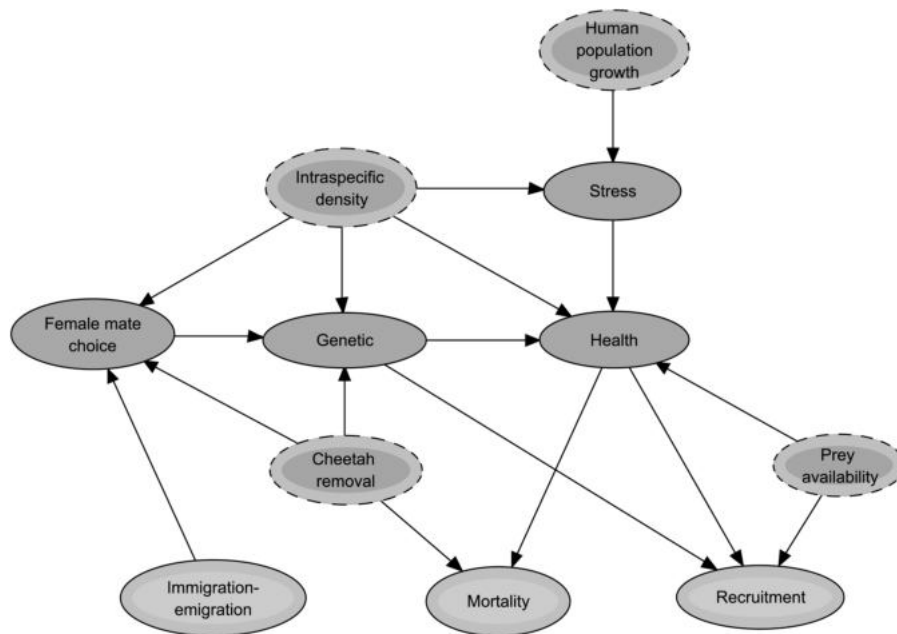


Fig. 6. Biological factors OOBN subnetwork showing four input nodes (double line eclipses with a broken outer line) and three output nodes (double line eclipse with solid outer line) that make up this OOBN's interface. Input nodes *Human population growth* and *Cheetah removal* are from the human factors OOBN and input nodes *Intraspecific density* and *Prey availability* are from the ecological factors OOBN. The output nodes are *Immigration-emigration*, *Mortality* and *Recruitment*.

viability of the free-ranging cheetah population in Namibia.

Cheetahs are known for their low genetic variability (O'Brien et al. 1983, O'Brien et al. 1985, Menotti-Raymond and O'Brien 1993, Castro-Prieto et al. 2011). However, there is no evidence that this directly impacts on *Recruitment* (successful pregnancies and survival of cubs to adulthood) (Wachter et al. 2010) and *Health* (general health regarding disease, injury, genetic defects and energy turnover) of free-ranging cheetahs (Laurenson et al. 1992, Laurenson 1994, Marker and Dickman 2003, Munson et al. 2005, Thalwitzer 2007, Thalwitzer et al. 2010). Thus, for the biological factor subnetwork, low genetic variability (*Genetic*) was not considered to cause any major genetic defects through deleterious alleles in the gene pool or any critically low functional genetic diversity. A decrease in species-specific low genetic variability due to changes from incoming nodes in the biological factor subnetwork was assumed to eventually lead to significant genetic defects if the negative effects were strong. Such a scenario would affect

Mortality, and consequently population growth. Since *Genetic* variability evaluated the risk for loss of genetic variants, an increase in the number of genetic variants was not considered in the model as it depends on mutation. *Health* was determined to be influenced by disturbance of the homeostasis due to aversive stimuli (*Stress*), *Intraspecific density* and *Prey availability* (output nodes from the ecological factors OOBN). *Prey availability* was assessed to have a strong impact on *Health* and *Recruitment* if it dropped to a critical level.

Females of a large number of species choose sires of their offspring in a non-random way, selecting males with traits signaling male quality (Harvey and Bradbury 1991). For example, in the Serengeti National Park in Tanzania, female cheetahs seem to prefer sires holding a territory compared to males roaming in large home ranges (Gottelli et al. 2007). Territorial males are in better physical condition than non-territorial males (Caro 1994). For this study, it was assumed that Namibian cheetah females preferably choose males that occupy territories, and the fluctuation

Table 3. Entropy values for the nodes in the combined OOBN. The entropy value for the target node (*Free-ranging cheetah population viability*) is shown in italics at the top of the table as a reference for the values of the other nodes. The entropy can be considered as a measure of how ‘uninformative’ a variable is. Therefore the larger the value, the more random the distribution (Kjaerulff and Madsen 2007).

Node	Value
<i>Free-ranging cheetah population viability</i>	0.692
Legislation implementation	0.303
Land Use	0.489
Environmental education	0.500
Local community awareness	0.579
Farmer education	0.611
Social impacts	0.636
Plant biomass production	0.642
Cheetah removal	0.653
Human habitat impact	0.662
Health	0.663
Livestock & wildlife management	0.675
Recruitment	0.682
Prey poaching	0.689
Genetic	0.691
Female mate choice	0.692
Human population growth	0.692
Stress	0.693
Mortality	0.693
Immigration-emigration	0.693
Vegetation structure	0.866
Rain	0.867
Intraguild density	0.927
Intraspecific density	0.929
Available space	0.975
Prey availability	1.066
Human cheetah conflict	1.079
Economic benefits	1.098

of such males was considered to be crucial for the mate choice exercised by females from the available number of males within their range (*Female mate choice*).

The fluctuation of males occupying territories was considered to be influenced by three factors: *Cheetah removal* (output node from the human factors OOBN), *Intraspecific density* (output node from the ecological factors OOBN) and *Immigration-emigration* (a factor representing the quantitative difference between immigrating and emigrating cheetahs). *Cheetah removal* on commercial farmland usually occurs at marking trees within territories (Marker-Kraus et al. 1996) and hence the likelihood of capturing a cheetah there is increased. The sex-ratio of cheetahs removed by this technique is heavily biased towards males (approximately 95% males vs. 5% females) (Marker-Kraus et al. 1996). As a result, large

numbers of potential sires, including males favored by females are removed. This leads to a higher turnover of males and thus an increased number of males available to females to select from. This scenario was considered to increase opportunities for females to exercise mate choice.

Cheetah removal was assumed to increase the number of dead adult male and female cheetahs (*Mortality*) and to potentially eliminate genetic variants from the cheetah population, hence decreasing genetic variability. Increased opportunities for females to exercise mate choice was assumed to increase genetic variability, since females might choose different partners for consecutive litters, or have multiple-paternity litters (Gottelli et al. 2007). It was not known how many potential partners were available in the range of a Namibian cheetah female, but it was assumed that a higher turnover of males leads to increased partner changes. Thus, from the *Genetic* node point of view, there was a negative, direct effect from the *Cheetah removal* node and a positive, indirect effect via the *Female mate choice* node. For the model the positive effect was assessed to be slightly stronger than the negative effect. Direct effects of *Human population growth* on biological factors were considered to be minor, however they were considered to affect the viability of the free-ranging cheetah population indirectly through *Human habitat impact* and *Prey poaching*.

Integrated OOBN

Finally, the combined integrated OOBN (Fig. 3) was updated to include the latest versions of the subnetworks, so that the validation and evaluation of the complete model could be performed. This included performing sensitivity analysis and scenario testing, to aid the future strategy for data collection, research, and refinement or extension of the integrated OOBN model and subnetworks.

Sensitivity analysis

Table 3 shows the calculated entropy for the variables in the combined OOBN. The larger values represent the more random variables, with the probability mass distributed more evenly between the states of those nodes. Therefore the largest possible value is attained for a uniform distribution across the states of the

node (Kjaerulff and Madsen 2007).

Another measure of evidence sensitivity is mutual information, which is listed in Table 4. The mutual information between the target node, *Free-ranging cheetah population viability*, and the other nodes in the OOBN is representative of the amount of information shared between the target node and each of the variables. The greater the value the bigger the amount of information shared. However, it is important to bear in mind that the depth of the network will affect the amount of information shared with the target node. This explains why nodes such as *Human cheetah conflict*, which may have been deemed to have a marked affect on the cheetah population viability, has a relatively small value. In other words, those nodes that are further removed from the target node, would have smaller values. Table 4 shows that *Mortality* and *Recruitment* share the most information with *Free-ranging cheetah population viability*, followed by *Health* and *Prey availability*. On the other hand *Free-ranging cheetah population viability* appears to be independent of *Environmental education* and *Human population growth*.

Scenario testing

When the combined OOBN was run, the probability that the free-ranging cheetah population in north-central Namibia would be viable was reported as 52.4% (Table 5), a very slender margin between being viable and unviable. Thus, if the current level of conservation activities continues and everything else remains largely unchanged, then the free-ranging population in north-central Namibia is practically equally likely to be viable or unviable. This means that the population continues to be under threat, especially if the status quo changes due to unforeseen circumstances or if some of the undesirable trends persist or increase.

The experts were interested in exploring the effect that several different scenarios may have on the viability of this population. The posterior probabilities for the nodes of interest are shown in Table 5 prior to any evidence being added to the OOBN. These values therefore formed the basis for comparison of the predicted probabilities from the scenarios. The following four scenarios were proposed by the expert team and tested on the combined OOBN model.

Table 4. Mutual information between the hypothesis variable (*Free-ranging cheetah population viability*) and each of the variables listed in the table. They are ordered in descending order so that those variables sharing most information with the target node are at the top of the list (Kjaerulff and Madsen 2007)

Node	Value
Mortality	0.0774
Recruitment	0.0759
Health	0.0253
Prey availability	0.0243
Plant biomass production	0.0137
Immigration-emigration	0.0051
Cheetah removal	0.0037
Rain	0.0031
Genetic	0.0022
Female mate choice	0.0011
Economic benefits	0.0006
Intraspecific density	0.0005
Vegetation structure	0.0002
Human cheetah conflict	0.0002
Farmer education	0.0001
Land use	0.0001
Stress	0.0001
Human habitat impact	0.0001
Intraguild density	0.0000
Social impacts	0.0000
Legislation implementation	0.0000
Available space	0.0000
Livestock & wildlife management	0.0000
Prey poaching	0.0000
Local community awareness	0.0000
Environmental education	0
Human population growth	0

1. *Cheetah removal from farmlands ceases.*—Farmers are interested in how much the cheetah population would grow if cheetahs were not shot anymore (farmers of the Seeis Conservancy, *personal communication*). Although the OOBN cannot predict the increase in cheetah population numbers, we can enter evidence into the network to represent this scenario. Setting the probability of *Cheetah removal* decreasing to 100% represents that we are certain that cheetah removal is decreasing. When we set this probability in the OOBN and propagate the information through the model, the probability of a viable population increases from 52.4% to 58.1%. This behavior suggests that, based on the constructed model and inputs, it is a worthwhile strategy to target a change in farmer attitudes. The model predicts that a decrease in cheetah removal will be associated with a substantially higher probability of economic benefits to farmers, increasing from 34.6% (Table 5) to 56.9% and with an increased probability of farmer education from 30.0%

Table 5. Posterior probabilities of selected nodes of the combined OOBN. The target node, *Free-ranging cheetah population viability*, has a probability of 52.4% of being viable (gain) and 47.6% of declining (loss).

Key factor (node)	Node state	Probability (%)	Node state	Probability (%)	Node state	Probability (%)
Free-ranging cheetah population viability	Gain	52.4	Loss	47.6		
Cheetah removal	Decrease	35.9	Increase	64.1		
Economic benefits	High	34.6	Medium	32.0	Low	33.4
Environmental education	Yes	20.0	No	80.0		
Farmer education	Yes	30.0	No	70.0		
Genetic	Increase	46.4	Decrease	53.6		
Health	Increase	62.2	Decrease	37.8		
Human habitat impact	Positive	37.5	Negative	62.5		
Human cheetah conflict	Low	37.1	Moderate	38.6	High	24.3
Livestock & wildlife management	High	40.5	Low	59.5		
Mortality	Increase	50.6	Decrease	49.4		
Plant biomass production	Sufficient	65.8	Insufficient	34.2		
Prey availability	Abundant	44.1	Sufficient	32.6	Insufficient	23.3
Rain	High	8.0	Average	61.0	Low	31.0
Recruitment	Increase	57.4	Decrease	42.6		

(Table 5) to 39.0%. Furthermore, the model indicates that if removal of cheetahs ceased, this will be associated with a reduced chance that genetic variability will decrease over time (47.6% probability that genetic variability will decrease as opposed to the previous 53.6%). Moreover, the predicted increase in cheetah population is expected to be associated with only a very small drop in the probability that prey availability will be abundant (a drop from 44.1% (Table 5) to 43.4%).

2. Increased farmer and environmental education.—One conservation management strategy to combat free-ranging cheetah population decline is to target both farmer and environmental education, especially in those areas which fall into the home ranges of the cheetahs of the free-ranging population. If the OOBN is updated with the ideal situation of 100% coverage of farmer and environmental education in north-central Namibia, the probability that the free-ranging cheetah population is viable is predicted to increase only marginally to 53.5%. This outcome was contrary to expectation. On closer analysis of the OOBN, we observed that these two nodes are far removed from the model end-point. This is bound to have a diluting effect on the target node and consequently it may be of greater interest to observe how this scenario affects other key nodes which are known to be influential in their effect on the population viability, such as cheetah removal, human cheetah conflict, and wildlife and livestock management. The probability that cheetah removal will decrease was predicted to

substantially improve from 35.9% (Table 5) to 47.8%. Furthermore, a full coverage of farmer and environmental education was associated with a large reduction in human cheetah conflict from 37.1% for low conflict (Table 5) to 61.1%, and a substantial increase in wildlife and livestock management from 40.5% for high management (Table 5) to 65.0%. Another positive outcome was an accompanying large increase in human habitat impact from 37.5% positive impact (Table 5) to 64.7%, which is known to be one of the major contributors to the worldwide decline in free-ranging cheetah populations (GCCAP 2002). This suggests that education may not have a strong direct impact on cheetah population viability, but that it is expected to sustain positive trends in the influential factors which are widely acknowledged to improve free-ranging cheetah population viability.

3. Climate change.—Namibia has periodic drought cycles which are accompanied by decreased prey availability and less tolerance of predators by farmers (Marker et al. 2007). Climate change in Namibia is expected to see an increase in temperature and a reduction in rainfall (Thuiller et al. 2006). By entering evidence of low rainfall into the OOBN, the cheetah population viability is predicted to decline (probability of population being viable is 46.6%). If we include further evidence of insufficient plant biomass as a consequence of climate change, the model predicts a more dramatic fall to 40.9%, which bodes ill for the free-ranging cheetah population. This represents a percentage

decrease of 21.9% on the original probability of population viability and is likely to be accompanied by insufficient prey (probability of insufficient prey predicted to rise from 23.3% to 65.3%) and a decline in cheetah population health (probability of health deteriorating predicted to change from 37.8% to 65.7%).

4. *Disease outbreak.*—The free-ranging Namibian cheetah population is in good health status despite being in regular contact with various viral pathogens (Munson et al. 2004, Thalwitzer et al. 2010). Although the cheetah experts therefore felt that an outbreak of infectious disease would be unlikely in the free-ranging cheetah population, they were interested in modeling this scenario. Evidence of decreased health of the free-ranging cheetah population was entered into the OOBN which predicted a devastating effect on the viability of this population, causing it to drop to 38.0%. It would be prudent therefore for conservation organizations, and government and research institutions to closely monitor the health of this free-ranging cheetah population to pre-empt any possible health issues and if evidence of a disease outbreak is detected, then early intervention would be possible, preventing any deleterious consequences.

DISCUSSION

This study demonstrates the successful application of the IBNDC approach to create an integrated BN model design within an object-oriented (OO) framework. The IBNDC heuristic was applied at the CCF BN modeling workshop where three independent OOBN subnetworks were constructed in parallel. Although each subnetwork focused on a different aspect of the free-ranging cheetah population in north-central Namibia, information flow between the OOBNs was possible through the three expert-defined interfaces. Each interface isolated the inner workings of one subnetwork from the other subnetworks. Therefore, changes could be made to one subnetwork without adversely impacting on another subnetwork. This facilitated the parallel development of three OOBN subnetworks (human, ecological and biological) for subsequent integration into a combined OOBN. This feature is particularly appealing when

modeling environmental issues of concern which involves several distinct domain expert groups. The IBNDC approach makes efficient use of their time by allowing them to work concurrently, yet independently, and then exchanging knowledge and performing cross validation, evaluation and scenario testing on the integrated network.

Furthermore, the continual development cycle of the IBNDC is appealing and relevant to multi-disciplined ecological issues such as species conservation enabling the perpetual refinement and development of integrated OOBNs as new data and knowledge comes to light. The integrated OOBN constructed for the free-ranging cheetah population in north-central Namibia represents the current expert knowledge, data and modeling for this population and may readily be extended to different spatial and temporal scales (Johnson et al. 2010a).

The sensitivity analysis of the combined OOBN indicated the need for research to focus on the quantification of the *Mortality* and *Recruitment* nodes in order to improve the estimates of the viability of the free-ranging cheetah population. The parent nodes *Cheetah removal*, *Health*, *Genetic* and *Prey availability* are therefore a priority as they affect the conditional probability distributions of *Mortality* and *Recruitment*. Additionally, the scenario testing confirmed observed trends and suggested increased focus on health monitoring, changing farmer perceptions and continued efforts in farmer and environmental education.

The OOBN model created as a result of the workshop and the subsequent refinement by the expert teams has largely been populated with expert opinion and in accordance with the IBNDC development cycle may be regarded as an initial baseline model of the current cheetah population viability in north-central Namibia. The model should be reviewed and adapted as more data, supplementary modeling, and new research become available. Furthermore, it is common practice in BN modeling to use fewer states for the initial model, which may then be refined in subsequent versions to improve the predictive accuracy of the model output (Marcot et al. 2006). In the model presented here, the nodes had generally only two or three states. The most influential nodes should be further investigated and additional statistical modeling may be

used to complement the integrated OOBN model.

It is important to note that even though the integrated OOBN model generates a single probability for each of the states of the cheetah population viability node, it does not give a definitive answer of what state the node is in. Therefore when using the BN model for inferencing such a scenario testing, the probability mass around the states of the target node is of foremost interest – are we more or less certain that the node is in a particular state? The OOBN model is able to represent many scenarios of interest, but care needs to be taken to ensure that it is not used to assess queries which are outside of the scope and context of the model. For example, the expert team was interested in exploring the impact of ungulates migrating to water points as a means of survival. Farmers are creating more permanent water holes, making water freely available to them. Consequently the ungulates roam near the water points and do not need to migrate. This increases the survival rate of the offspring and populations build up around these water points (G. Roeber, CCF Farmer Education Coordinator, *personal communication*). This farmer activity is creating an artificial availability of prey which would otherwise be accompanied by higher rainfall and consequently a greatly improved plant biomass production in the integrated OOBN model. The model should therefore be updated to include the factors and interactions of this farmer activity before doing inferencing to explore the effects on cheetah population viability.

It would be useful for future iterations of the integrated OOBN to model long term cheetah population viability. The model presented here aimed to assess whether the current free-ranging cheetah population was viable and a continually growing cheetah population may introduce other issues (Lubben et al. 2008). Extinction probabilities are positive functions of population dynamic factors such as growth rates, density dependent carrying capacities, resource bases, and current (initial) population size. Population viability analyses generally rely on inferences from stochastic population dynamic model followed by calculation of average time to extinction, probability of extinction in a given time period, or some other quantity of management concern

(Pettorelli and Durant 2007). Including the output from these models would enhance the existing OOBN model.

Other enhancements to the initial model would be to consider integrating Geographic Information System (GIS) maps to quantify nodes that are spatial and to explore representing the output from the model in a GIS map which will highlight areas of concern for cheetah population viability (Johnson et al. 2012).

Although this OOBN structure and quantification is specific for the cheetah population in north-central Namibia, lessons learned through this study have widespread applications in other places where conservation on private land is critical to the maintenance of viable populations of large carnivores and in those areas most critical for future cheetah conservation.

ACKNOWLEDGMENTS

We wish to thank Cheetah Conservation Fund for hosting the workshop and for the excellent hospitality. We also wish to thank Anne-Marie Stewart for her invaluable help in organizing the workshop and her constructive comments in the workshop and on the paper, and Burton Gaiseb for his participation in the workshop and in the human factors subnetwork. For helpful comments and information on farmer practices we thank Gunther Roeber. We gratefully acknowledge the financial support provided by the Australian Research Council's International Linkage Grant and the Messerli Foundation in Switzerland.

LITERATURE CITED

- Barton, D. N., S. Kuikka, O. Varis, L. Uusitalo, H. J. Henriksen, M. Borsuk, A. de la Hera, R. Farmani, S. Johnson, and J. D.C. Linnell. 2012. Bayesian networks in environmental and resource management. *Integrated Environmental Assessment and Management* 8:418–429.
- Bednarski, M., W. Cholewa, and W. Frid. 2004. Identification of sensitivities in Bayesian networks. *Engineering Applications of Artificial Intelligence* 17:327–335.
- Booch, G., R. A. Maksimchuk, M. W. Engle, B. J. Young, J. Conallen, and K. A. Houston. 2007. *Object-oriented analysis and design with applications*. Third edition. Addison-Wesley Professional, Massachusetts, USA.
- Caro, T. M. 1994. *Cheetahs of the Serengeti plains: group living in an asocial species*. University of Chicago Press, Chicago, Illinois, USA.

- Castro-Prieto, A., B. Wachter, and S. Sommer. 2011. Cheetah paradigm revisited: MHC diversity in the world's largest free-ranging population. *Molecular Biology and Evolution* 28:1455–1468.
- Chankong, V., and Y. Y. Haimes. 1983. *Multiobjective decision making: theory and decision making*. North-Holland, New York, New York, USA.
- CITES. 1992. Quotas for trade in specimens of cheetah. Pages 1–5. *in* Eighth Meeting of the Convention of International Trade in Endangered Species of Wild Fauna and Flora, Kyoto, Japan. <http://www.cites.org/eng/cop/08/doc/E-22.pdf>
- de Klerk, J. N. 2004. *Bush encroachment in Namibia*. Solitaire Press, Windhoek, Namibia.
- Durant, S. M. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology* 11:624–632.
- GCCAP. 2002. Global Cheetah Action Plan Review final workshop report. Page 78 *in* P. Bartels, V. Bouwer, A. Crosier, D. Cilliers, S. M. Durant, J. Grisham, L. Marker, D. E. Wildt, and Y. Friedmann, editors. *Global Cheetah Conservation Action Plan—Workshop*. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA.
- Gottelli, D., J. Wang, S. Bashir, and S. M. Durant. 2007. Genetic analysis reveals promiscuity among female cheetahs. *Proceedings of the Royal Society B* 274:1993–2001.
- Hanssen, L., and P. Stander. 2004. Namibia large carnivore atlas. Predator Conservation Trust, Windhoek, Namibia. http://www.desertlion.info/reports/atlas_july2004.pdf
- Harvey, P. H. and J. W. Bradbury. 1991. Sexual selection. Pages 203–233 *in* J. R. Krebs and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific, Oxford, UK.
- Henriksen, H. J., P. Zorrilla-Miras, A. de la Hera, and M. Brugnach. 2012. Use of Bayesian belief networks for dealing with ambiguity in integrated groundwater management. *Integrated Environmental Assessment and Management* 8:430–444.
- Hugin. 2007. Hugin Expert A/S, Aalborg, Denmark. <http://www.hugin.com/>
- Jensen, F. V., and T. D. Nielsen. 2007. *Bayesian networks and decision graphs*. Springer, New York, New York, USA.
- Johnson, S., F. Fielding, G. Hamilton, and K. Mengersen. 2010a. An integrated Bayesian network approach to *Lyngbya majuscula* bloom initiation. *Marine Environmental Research* 69:27–37.
- Johnson, S., S. Low-Choy, and K. Mengersen. 2012. Integrating Bayesian networks and geographic information systems: Good practice examples. *Integrated Environmental Assessment and Management* 8:473–479.
- Johnson, S., and K. Mengersen. 2012. Integrated Bayesian network framework for modeling complex ecological issues. *Integrated Environmental Assessment and Management* 8:480–490.
- Johnson, S., K. Mengersen, A. De Waal, K. Marnewick, D. Cilliers, A. M. Houser, and L. Boast. 2010b. Modelling cheetah relocation success in southern Africa using an Iterative Bayesian Network Development Cycle. *Ecological Modelling* 221:641–651.
- Kauffman, M. J., M. Sanjayan, J. Lowenstein, A. Nelson, R. M. Jeo, and K. R. Crooks. 2007. Remote camera-trap methods and analyses reveal impacts of rangeland management on Namibian carnivore communities. *Oryx* 41:70–78.
- Kelly, M. J., M. K. Laurenson, C. D. FitzGibbon, D. A. Collins, S. M. Durant, G. W. Frame, B. C. R. Bertram, and T. M. Caro. 1998. Demography of the Serengeti cheetah (*Acinonyx jubatus*) population: the first 25 years. *Journal of Zoology* 244:473–488.
- Kjaerulff, U. B., and A. L. Madsen. 2007. *Bayesian networks and influence diagrams*. Springer, New York, New York, USA.
- Koller, D. and A. Pfeffer. 1997. Object-oriented Bayesian networks. Pages 302–313. *in* Thirteenth Annual Conference on Uncertainty in Artificial Intelligence (UAI-97), Providence, Rhode Island, USA.
- Korb, K. B. and A. E. Nicholson. 2004. *Bayesian artificial intelligence*. Chapman & Hall/CRC, Boca Raton, Florida, USA.
- Laskey, K. B. 1995. Sensitivity analysis for probability assessments in Bayesian networks. *IEEE Transactions on Systems, Man and Cybernetics* 25:901–909.
- Laurenson, M. K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *Journal of Zoology* 234:387–408.
- Laurenson, M. K., T. M. Caro, and M. Borner. 1992. Female cheetah reproduction. *National Geographic Research & Exploration* 8:64–75.
- Laurenson, M. K., N. Wielebnowski, and T. M. Caro. 1995. Extrinsic factors and juvenile mortality in cheetahs. *Conservation Biology* 9:1329–1331.
- Lauritzen, S. L., and N. A. Sheehan. 2003. Graphical models for genetic analyses. *Statistical Science* 18:489–514.
- Lubben, J., B. Tenhumberg, A. Tyre, and R. Rebarber. 2008. Management recommendations based on matrix projection models: The importance of considering biological limits. *Biological Conservation* 141:517–523.
- Marcot, B. G., J. D. Steventon, G. D. Sutherland, and R. K. McCann. 2006. Guidelines for developing and updating Bayesian belief networks applied to ecological modeling and conservation. *Canadian Journal of Forest Research* 36:3063–3074.
- Marker, L. 2002. Aspects of cheetah (*Acinonyx jubatus*) biology, ecology and conservation strategies on Namibian farmlands. Dissertation. University of

- Oxford, Oxford, UK.
- Marker, L., A. Dickman, C. Wilkinson, B. Schumann, and E. Fabiano. 2007. The Namibian cheetah: Status Report. CAT News, Special Edition 3:4–13.
- Marker, L., A. J. Dickman, R. M. Jeo, M. G. L. Mills, and D. W. Macdonald. 2003a. Demography of the Namibian cheetah. *Biological Conservation* 114:413–425.
- Marker, L., M. G. L. Mills, and D. W. Macdonald. 2003b. Aspects of the management of cheetahs trapped on Namibian farmlands. *Biological Conservation* 114:401–412.
- Marker, L. L., and A. J. Dickman. 2003. Morphology, physical condition and growth of the cheetah (*Acinonyx jubatus jubatus*). *Journal of Mammalogy* 84:840–850.
- Marker, L. L., J. R. Muntifering, A. J. Dickman, M. G. L. Mills, and D. W. Macdonald. 2002. Quantifying prey preferences of free-ranging Namibian cheetahs. *South African Journal of Wildlife Research* 33:43–53.
- Marker-Kraus, L., D. Kraus, D. Barnett, and S. Hurlbut. 1996. Cheetah survival on Namibian farmlands. Cheetah Conservation Fund, Windhoek, Namibia.
- Menotti-Raymond, M., and S. J. O'Brien. 1993. Dating the genetic bottleneck of the African cheetah. *Proceedings of the National Academy of Sciences USA* 90:3172–3176.
- Munson, L., L. Marker, E. Dubovi, J. A. Spencer, J. F. Evermann, and S. J. O'Brien. 2004. Serosurvey of viral infections in free-ranging Namibian cheetahs (*Acinonyx jubatus*). *Journal of Wildlife Diseases* 40:23–31.
- Munson, L., K. A. Terio, M. Worley, M. Jago, A. Bagot-Smith, and L. Marker. 2005. Extrinsic factors significantly affect patterns of disease in free-ranging and captive cheetahs (*Acinonyx jubatus*) populations. *Journal of Wildlife Diseases* 41:542–548.
- Muntifering, J. R., A. J. Dickman, L. M. Perlow, T. Hruska, P. G. Ryan, L. Marker, and R. M. Jeo. 2006. Managing the matrix for large carnivores: a novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling. *Animal Conservation* 9:103–112.
- National Planning Commission. 2004. Namibia Vision 2030: policy framework for long-term national development. Office of the President, Windhoek, Namibia. <http://www.npc.gov.na/vision/pdfs/Summary.pdf>
- Neapolitan, R. E. 1990. Probabilistic reasoning in expert system applications. Wiley, New York, New York, USA.
- Nghikembua, M. T. 2008. Quantifying farmers' perceptions and willingness; as well as availability of encroaching aboveground Acacia bush biomass on CCF commercial farmlands in north central Namibia. Mini thesis research report. University of the Free State, Bloemfontein, South Africa.
- O'Brien, S. J., M. E. Roelke, L. Marker, A. Newman, C. A. Winkler, D. Meltzer, L. Colly, J. F. Evermann, M. Bush, and D. E. Wildt. 1985. Genetic basis for species vulnerability in the cheetah. *Science* 227:1428–1434.
- O'Brien, S. J., D. E. Wildt, D. Gildman, C. R. Merrill, and M. Bush. 1983. The cheetah is depauperate in genetic variation. *Science* 221:459–462.
- Onisko, A., and M. J. Druzdzel. 2011. Impact of quality of Bayesian network parameters on accuracy of medical diagnostic systems. Pages 135–148 in AIME'11 Workshop on Probabilistic Problem Solving in Biomedicine (ProBioMed-11), in conjunction with the Thirteenth Conference on Artificial Intelligence in Medicine (AIME-2011).
- Pastor, O., J. Gomez, E. Insfran, and V. Pelechano. 2001. The OO-Method approach for information systems modeling: from object-oriented conceptual modeling to automated programming. *Information Systems* 26:507–534.
- Pearl, J. 1988. Probabilistic reasoning in intelligent systems. Morgan Kaufmann, San Francisco, California, USA.
- Pearl, J. 2000. Causality: models, reasoning, and inference. Cambridge University Press, Cambridge, UK.
- Pettorelli, N., and S. M. Durant. 2007. Family effects on early survival and variance in long-term reproductive success of female cheetahs. *Journal of Animal Ecology* 76:908–914.
- Pollino, C. A., A. K. White, and B. T. Hart. 2007a. Examination of conflicts and improved strategies for the management of an endangered Eucalypt species using Bayesian networks. *Ecological Modelling* 201:37–59.
- Pollino, C. A., O. Woodberry, A. Nicholson, K. Korb, and B. T. Hart. 2007b. Parameterisation and evaluation of a Bayesian network for use in an ecological risk assessment. *Environmental Modelling & Software* 22:1140–1152.
- Purchase, G. K., L. Marker, K. Marnewick, R. Klein, and S. Williams. 2007. Regional assessment of the status, distribution and conservation needs of cheetahs (*Acinonyx jubatus*) in southern Africa: Summary of Country Reports. CAT News, Special Edition 3:44–46.
- Tang, Z., X. Huang, and K. Bagchi. 2009. Agent-based intelligent system modeling. Pages 51–57 in J. Rabuñal Dopico, J. Dorado and A. Pazos, editors. *Encyclopedia of artificial intelligence*. Hershey, Pennsylvania, USA.
- Taroni, F., C. Aitken, P. Garbolino, and A. Biedermann. 2006. Bayesian networks and probabilistic inference in forensic science. John Wiley & Sons, Chichester, UK.

- Thalwitzer, S. 2007. Reproductive activity in cheetah females, cub survival and health in male and female cheetahs on Namibian farmland. Dissertation. Free University Berlin, Berlin, Germany.
- Thalwitzer, S., B. Wachter, N. Robert, G. Wibbelt, T. Müller, J. Lonzer, M. Meli, G. Bay, H. Hofer, and H. Lutz. 2010. Seroprevalences to viral pathogens in free-ranging and captive cheetahs (*Acinonyx jubatus*) on Namibia farmland. *Clinical and Vaccine Immunology* 17:232–238.
- Thuiller, W., G. F. Midgley, G. O. Hughes, B. Bomhard, G. Drew, M. C. Rutherford, and F. I. Woodward. 2006. Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology* 12:759–776.
- Uusitalo, L. 2007. Advantages and challenges of Bayesian networks in environmental modelling. *Ecological Modelling* 203:312–318.
- van der Gaag, L. C., S. Renooij, and V. M. H. Coupe. 2007. Sensitivity analysis of probabilistic networks. Pages 103–124 in P. Lucas, J. A. Gámez, and A. Salmerón, editors. *Advances in probabilistic graphical models*. Springer, Berlin, Germany.
- Varis, O. and S. Kuikka. 1999. Learning Bayesian decision analysis by doing: lessons from environmental and natural resources management. *Ecological Modelling* 119:177–195.
- Wachter, B., S. Thalwitzer, H. Hofer, J. Lonzer, T. Hildebrandt, and R. Hermes. 2010. Reproductive history and absence of predators are important determinant of reproductive fitness: the cheetah controversy revisited. *Conservation Letters* 4:47–54.
- Woodroffe, R., L. G. Frank, P. A. Lindsey, S. M. K. ole Ranah, and S. Romañach. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: a case-control study. *Biodiversity and Conservation* 16:1245–1260.