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Research Article

Breaking through Artificial Disciplinary Barriers; Guidelines for applying Bayesian Networks to the Ecology Discipline

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Abstract

Object Oriented Bayesian Networks (OOBNs) are a semi-quantitative modeling approach that can be utilized to represent complexities of management tradeoffs and spillovers within a conservation and ecological context. However, computation expense and gradual learning curve result in their underutilization in ecological and environmental disciplines. This is despite the reoccurring need for decision-makers to adapt wildlife management protocols while constraint by limited resources and scarce data. We provide guidelines to identifying and prioritizing uncertainties surrounding complex ecological processes. Empirical data and expert explicit understanding of uncertainties are utilized. We put forth two OOBNs, each accurately representing a snapshot of the moving parts in the complex wildebeest hybridization conservation case study in South Africa. We identifying and clustered key variables impacting the probability of hybridization in either spatial, biological, or market domains. Specifically, (i) blue wildebeest male to black wildebeest male ratio, and (ii) spatial connectivity. Ecologists facing similar constraints worldwide may utilize our stepwise procedural framework so that resources are maximized. This study promotes global collegially research by bridging the boundaries of applications across disciplines, so that their advantages may be extrapolated. The construction of the suggested prototypes is explained in detail so that they may be adapted modified to quantify similar ecology-related uncertainties worldwide.

Introduction

Anthropogenic- hybridization gives raise to conservation concerns

The harmful effects of human driven hybridization have given rise to conservation challenges surrounding many plant and animal taxa worldwide [1-3]. Genetic extinction may occur via the following processes: parental taxon extinction, reduced fitness, pure genetic lineage extinction, and/ or parental taxon displacement [4,5]. In fact, hybridization is especially problematic for rare, endangered, and endemic species that overlap with relatively abundant species [8,9]. We utilize the hybridization occurrences between the black wildebeest (Connochaetes gnou) and the blue wildebeest (Connochaetes taurinus) in South Africa to create a decision support tool for wildlife managers. Our choice of a case study reflects the scope of conservation concerns evolving from this problematic process; hybridization between the endemic black wildebeest and widespread blue wildebeest in South Africa poses a conservation threat to the genetic integrity of the former [10,11].

Historically, black wildebeest and blue wildebeest were allopatric; while the first core habitat was grasslands north of the Orange River, South Africa, the later can be found in open and bush-covered savanna habitats ranging from Central to Southern Africa [12,13]. However, recent intensive wildlife management practices, such as the translocation of black wildebeest populations, have resulted in the expansion of their distribution to extralimital habitats overlapping with that of blue wildebeest [8]. Their short evolutionary divergence enables hybridization to occur when overlapped. Fossil evidence indicates that they diverged from a common ancestor between 1- 2 million years ago, which did not allow for the development of reproductive isolation mechanisms [10,14,15]. As such, management practices that entail the juxtapositioning of species have implications for species' genetic lineage conservation.

Ecosystem decision-making in the face of imperfect information

Wildlife and land managers are faced with an ongoing dilemma; on the one horn they need to intensely manage their wildlife populations with economic profitability in mind, while on the other uncertainties resulting from scarce or even a lack of, data and limited resources impose constraints on their ability to account for tradeoffs of various management decisions. Concurrently, genetic markers that distinguish pure parental species from hybrids are lacking, and qualitative data are

imprecise [10,11]. This, in turn, influences their ability to adopt informed decisions. One consequence is that many wildlife and land management decisions being "grandfathered in" and, as such, their efficiency is not reevaluated, possibly resulting in "Type III error" [16]. And yet, management decisions with potential implications on hybridization occurrences are made despite such lack of data [8,17].

There is a consensus on the need for a novel and integrated approach to foster adaptive management while maximizing economic efficiency and conservation effectiveness. A cohesive solution recognizes spillover effects of wildlife management decisions into other domains. Similar to other ecological concerns worldwide, such guidelines need to be broad enough to ensure the conservation of the wildebeest on a metapopulation (i.e., on a national scale), yet specific enough to account for the objectives of individual stakeholders. Bayesian Networks (BN) allow for such seemingly competing model objectives.

The underutilization of BNs within the ecological discipline

Bayesian modeling is widely applied to inference probabilistic representations of uncertain knowledge in various fields including industrial, government, artificial intelligence, and medical [18-20]. However, only 4.2% of environmental studies utilized BNs during 1990-2010, indicating that BNs ability to deconstruct complexities and infer and predict trade-offs within the ecological and environmental discipline remains underexploited [21-23]. Despite their efficiency on modeling multi-faceted ecological processes leading to informed decision making [24-26]. In this study, we put forth the notion that Bayesian modeling stages correspond to integrated environmental stages and therefore, are applicable to model environmental and ecological complexities (Figure 1).

These correspond to modeling procedures and outcomes written in gray rectangles. Highlighted green boxes list corresponding stages in integrated environmental modeling semantics. Ovals list disciplinary usage and arrows indicate modeling objective utilization or disciplinary applicability.

Applicability of Bayesian belief networks to the ecological discipline

Applying BNs to articulate ecological problems is a relatively new concept; this may be in part because deriving the networks' structure while considering multiple-field domains, and populating it with expert knowledge is difficult and time consuming [27-29]. BNs enable modelers to address ecological challenges within the following working framework: problem statement identification, system conceptualization, information synthesis, adapting problem statement and management scenarios, and policy development (Figure 1). These steps correspond to the following processes in BN terminology:A priori information, supervised and unsupervised learning (i.e., parameter learning, data clustering, variable clustering, probabilistic representation modeling, causal-effects analysis, predictability, and target optimization), knowledge engineering, and Bayesian updating (Figure 1).

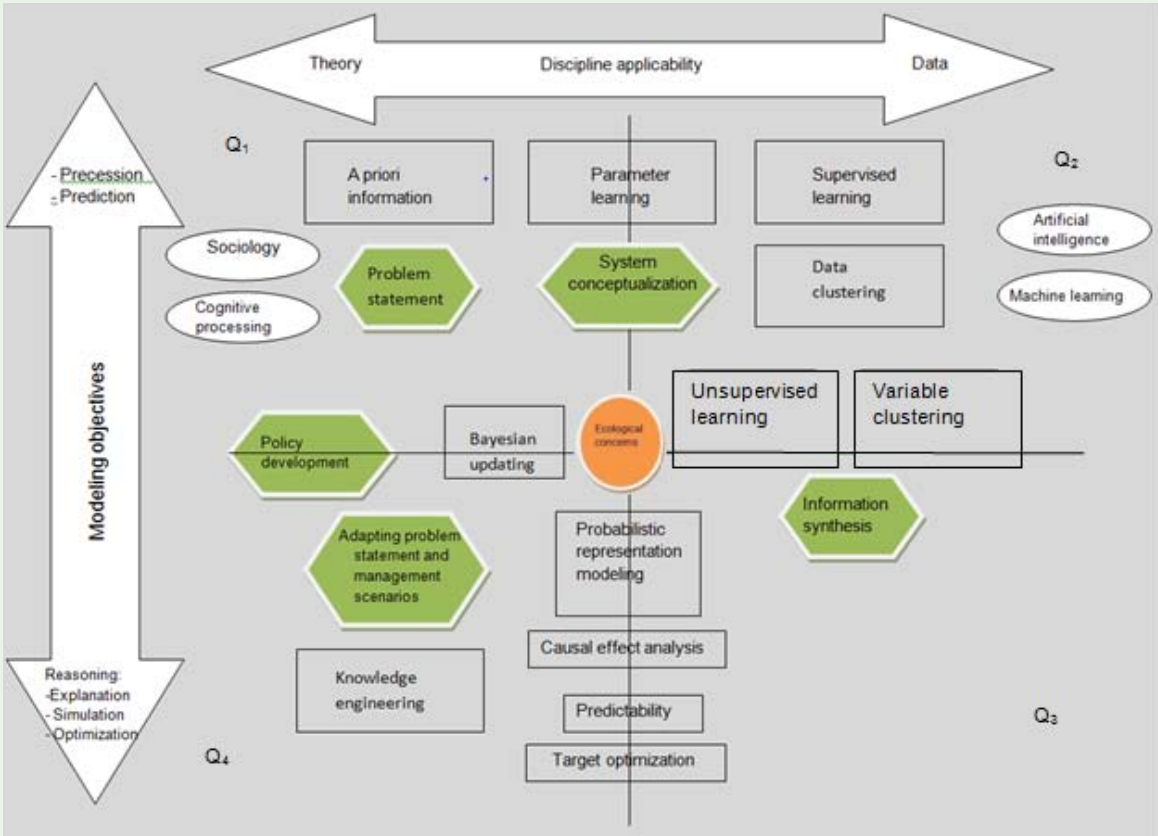

Figure 1: A continuum of Bayesian Networks' usage. Four primary modeling stages denoted by Q_{1234}.

Goals, objectives, and outline

This study illustrates the advantages in applying Bayesian modeling to the conservation discipline by considering wildebeest hybridization drivers and facilitators within their contextual ecological complexity. We show that Bayes' methods simulate alternate "real-world" scenarios, and argue that in their absence, decision makers make management decisions with incomplete information. Decision Support Systems (DSSs) are strategic frameworks designed to assist the decision maker in the decision-making process [30]. These networks are ultimately used as (DSSs) by wildlife and land stakeholders in South Africa. And because hybridization is accelerating worldwide, OOBNs serve to inform decisions globally. Thus, enabling knowledge generators and users to better understand "real-world" ecosystem complexity and interlinkage.

Our objectives are as follows: (1) to provide a working understanding of how expert knowledge may be utilized to advance informed decisions, (2) to identify key parameters that facilitate wildebeest hybridization; (3) to provide an abstract visualization that conceptualizes the multifaceted complexity, (4) to infer the relationships amongst parameters and domains, and (5) to provide DSS that identify risk assessment and wildlife management implications.

Our paper is subdivided as follows: First, we provide contextual reasoning for BN applicability to ecological problems in a background (section 2). By including concise explanations we increase the understanding of knowledge generation and slicing. We then offer detailed methods (section 3) that may be used as a stepwise guideline procedural framework to be duplicated and address similar ecological complexities elsewhere. This decreases the learning curve and computational expenses. Finally, we list our findings (section 4), discussion (section 5), and conclusions (section 6).

Background

Uncertainty inference

Bayesian inferences future uncertainties by calculating how probable specific events are and how these probabilities change contingent on every possible combination of values of parent nodes (i.e., a prioriknowledge of previous events), or given external interventions (i.e., posterior probabilities) [20,31-33]. Furthermore, uncertainty resulting from stochasticity and inference is accounted for by marginalization rather than a point estimate [34].The joint distribution of the training data, model, and observation θ, is conceptualized as follows:

$$p(\theta): p(\text{example}|\text{data}) = p(\text{example}|\text{model}) * p(\text{model}|\text{data}) \quad (1)$$

Bayes' rule calculates the posterior distribution by combining the likelihood of P (D|θ) with a priori information, as follows:

$$p(\theta|D) = \frac{p(D|\theta)\,p(\theta)}{p(D)} \quad (2)$$

Note: P denotes a set of immediate causes of parameters.

θ denotes the vector of the functional parameters linked to *P*, while *D* represents data.

Hence, the posterior is proportional to the likelihood of a priori data, therefore producing a derivative:

$$p(\theta|D)\alpha p(D|\theta)\,p(\theta) \quad (3)$$

Learning parameter from incomplete data

Probabilities incorporate the conditional probability function arguments as random variables and the product of parameter learning is an estimate of conditional probability corresponding to nodes that maximize the likelihood function [35].

To use Bays terminology, the set of parameters quantifying θ is learned from the data, so that the likelihood of the data results from the modeled joint distribution is maximized. This is written as:

$$L(\theta) = P(D|\theta) = \prod_{i=1}^{n} p(\chi_i|\theta)D = \{\chi_1, \ldots, \chi_n\}, L(\theta) \geq 0 \quad (4)$$

The *i*th training parameter is denoted by x_i .

The Maximum (log) Likelihood (ML) is a learning approximate which maximizes the likelihood of the data given the model (L(θ)). ML quantify the probability of a parameter ($p(x_i)$) given the training data (D) as follow: $p(\chi|D) \approx p(x|\theta_{ML})$. However, plugging in negative log likelihoods have the same effect as minimizing error functions, therefore solving for the likelihood derivative (log-likelihood) function is more user friendly.

$$\theta = \arg\max \theta\, L(X_\theta|D) = \arg\max \theta\, LL(X_\theta|D)\theta \leq 0 \quad (5)$$

The Product of learning is Conditional Probability Tables (CPT)

Causal links amongst discrete variables are quantified using Conditional Probability Tables (CPTs); given parents` state, the possibility that a child node will be in the roam of each possible state is calculated according to its observed frequency [32]. An a prioridistribution is needed, in order to avoid a possible zero probability assigned to a possible outcome.

CPTs may be populated from two sources: (1) data driven parameterization through machine learning, or (2) knowledge elicitation from experts. Discrete variables encode probabilities which are the model probabilities themselves. A priori data may be categorical or quantifiable [31,33].

Parameterization learning for a child node (denoted θ) with Parent nodes (denoted D) and a number of states (denoted S_θ) may be expressed as follow:

$$(S_\theta - 1)\prod_{i=1}^{D} S_i$$

However, the number of parameters increases exponentially, resulting in an expensive computational exercise. For instance,

a situation in which there are variables with n parents, and each variable has two states, 2n independent parameters is needed in order to specify its CP. This disadvantage is solvable by applying Noisy functions, serving as weighted models [34,35]. Noisy-OR is a probabilistic extension that generates CPs for an observation occurring (denoted by Y=1), across n binary nodes, as follows:

$$p(Y=1|x_1,....,x_n)=1-\Pi_{i=1}^{n}V_i\,,\,p\left(Y_i|X_i\right)=0,\text{pi}\in[0,1] \quad (7)$$

Alternatively, the Noisy-MAX is applicable to multivalued parameters, which assumes that Y has nystates [34,35]. The joint probability is written as follows:

$$p\left(Y\le y|n_1,n_2,...,n_n\right)=\Pi_i\ p\left(n_i|\,p\left(v_1\right)\right),\ \text{pi}\in[0,1] \quad (8)$$

Bayesian advantage over other environmental models

Bi-Directional flow: CPTs' primary advantage is a product of its independence: (1) models can be updated easily when data become available or policy change is needed and (2) the distribution can be populated using optimal information available for a specific node. This enables decision makers to choose the level of confidence and detail they require to make decisions [21]. Simply stated, by approaching Bayesian learning as an inference case, the training examples in the data itself are considered independent observations [32]. This is the source of the bi-directional flow.

Bidirectional flow enables top down (i.e., diagnostic/optimization reasoning), and bottom up (i.e., predictive reasoning) approaches [36,37] (Figure 2). A posterior probability incorporates propagation of uncertainty; updating posterior probabilities when new data become available triggers an update of a priori values and therefore, is especially useful and applicable to the ecological field [37-39].

Notes: θ splits network into two disjoint continuums, assuming independence. D1, D2 denote a priori evidence and serve as parent nodes to the child node denoted θ. Which in turn, serves as the parent node for θ_1 and θ_2.

The bi-directional propagation of new evidence and revision of each random variable is enabled by Pearl`s Bi-directional belief updating algorithm (PB). Mechanistically, new data is fused and propagates the resulting impact throughout the network by a belief vector constant of axioms of probability theoremfield [40,41]. Downward propagation is enabled by JPD calculations: the probability distribution quantification of all child nodes correlating to that of parent nodes, is a function of the BN structure and CPT field [36]. In the example below, the objective is to infer local computation for a single node (denoted by θ) in the schematic illustration above (Figure 2); after receiving the vector $\pi(e^+)$ updated information from parent node D_1, node θ will send to its child node θ_1 updated information. This is written as follows:

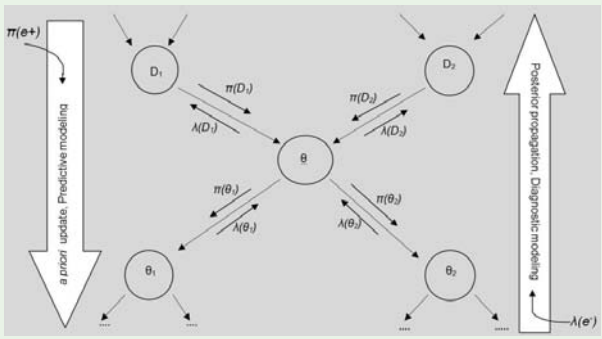

Figure 2: Schematic visualization of informational flow and Pearl's Bi-directional belief updating propagation.

$$\pi(\theta)=\Sigma_{D_1}p(\theta|D,e^+).p(D|D,e^+)=\Sigma_{D_1}p\left(\theta|D\right).\pi(\theta)=\pi(\theta)\bullet LM_{\theta|D_1} \quad (9)$$

Where $\pi(\theta)$ is multiplied by the congruent product of the likelihood matrix (LM) (I.e., the conditional probability distribution matrix between θ and D_1).

Upward propagation is enabled by setting desired nodes to a certain probability, and then evaluating their impact on probability distributions of child nodes [28].

If we continue with the same example from Figure 2, after receiving the vector $\lambda(e^-)$ with updated information from child node θ_1, parent node θ will send to its parent node D1 information. This is written as follows:

$$\lambda(\theta)=\Sigma_{\theta_1}\ p\left(e^-|\theta,D_1\right).p\left(\theta_1|\theta\right)=\Sigma_{\theta_1}\ \lambda(\theta_1).\,p\left(\theta_1|\theta\right)=\lambda(\theta_1)\bullet LM_{\theta_1}|\theta \quad (10)$$

Similarly to the vector π (θ), λ(θ) is multiplied by the congruent product of the LM between θ_1 and θ.

Moreover, posterior updates usually entail that a node receive information from multiple child nodes (i.e., multiple $\lambda(e^-)$ vectors). PB is proportional to the size of CPT and accounts for such complexity [33]. It computes BEL (θ), an additional vector that ensures that all information is congruent, thereby eliminating the possibility of accounting for specific information multiplue times [40].

$$BEL(\theta)=\alpha\lambda(\theta)\pi(\theta)\ ,\ \left\{\alpha=\left[\,p\left(e_\theta^-|e_\theta^+\right)\right]^{-1}\right\} \quad (7)$$

This bidirectional nature of BNs may provide advantages when modeling ecological complexities. Posterior updates enable decision makers to modify their networks to specifically model personalized objectives and to examine the effect of various decisions in a controlled in vitro environment before employing them in vivo (thereby promoting resource maximization and theoretical research, and allowing informed decisions). Wildlife managers can choose an optimized management practice and update CPTs as data become available so that networks remain a useful tool that reflects adaptive management. Bottom-up predictions are ideal for evaluating impact and management strategy analysis, while top-down predictions are ideal for identifying relevant parameters [32].

Simplified conceptualization: Borsuk et al. [41] suggest that BNs incorporate a series of advantages over other environmental models and support systems. Mainly, their graphical structure explicitly represents a cause-effect relationship among parameters that may be obscured in other approaches. stakeholders are able to conceptualize and evaluate interlinked relationships and management decision spillovers robustly via a Bayesian Conceptual Diagram (BCD) and a Directed acyclic graph (DAG); BCD provides a simplistic conceptualization of the query at hand while the DAG is the mathematical formulization in which nodes correspond with variables and arcs reflect qualitative dependence structure of various distributions [35,41].

Software

We used the software Netica [41], because it allows for sampling runs in real time, and the integration of confidence levels of stakeholders in their ability to accurately predict probabilistic reasoning. Netica has an identical interface for Windows and Mac, thereby enabling transferable code between these platforms. Application programmer interfaces include Java, C, C#, Com, C++, Matlab and CLisp. A free version is available which enabled the construction and evaluation of up to fifteen networks. Perching price ranges from individual use ($285) to commercial use ($785). Once the programmer defines the model structure given by experts, Netica utilizes EM algorithms to construct conditional probabilities from a given data set. Developer and contact address: Norsys Software Corp. 3512 West 23rd A venue, Vancouver, BC, Canada. (Tel. +1.604.221.2223, Fax. +1.604.221.2238). For enquiries: info@norsys.com . First available in 1995.

Methods

Study area

We surveyed South African game ranches that manage for black and blue wildebeest populations in four provinces: Limpopo, Mpumalanga, Gauteng, KwaZulu-Natal, and The Free State (Map 1).

Map 1: Surveyed regions in South Africa. Red borders indicate provinces surveyed for expert knowledge. These include Limpopo, Mpumalanga, Gauteng, KwaZulu-Natal, and The Free State.

Defining target node

Applying Bayesian modeling to ecological concerns is initiated by the definition of a target node (Figure 3). This provides focus for the modeler and clarity for the user. Genetic admixture is achieved in a finite population when hybrid individuals backcross into pure individuals and produce fertile offspring that behave in the same manner, and hybrids are not selected against [43]. This process is maintained by introgression and backcrossing [44] and can lead to the extinction of pure genetic lineages [45]. We define target nodes as hybridization, genetic admixture, or interspecies mating encounters.

Peer reviewed data and expert knowledge generation

Prior to expert knowledge elicitation, we identified known drivers affecting the occurrence of ungulate hybridization utilizing the search engine Googlescholar and various combinations of the following keywords: conservation, ecology, hybridization, ungulate hybridization, wildebeest, and wildlife management (Figure 3). Local, provincial, and state wildlife management practices were additionally reviewed.

68 stakeholders were surveyed during workshops about variables, parameters, and drivers that affect hybridization between black and blue wildebeest (Table 1). Expert knowledge served as a priori information, and the posterior probability reflected the probability that the black wildebeest and blue wildebeest will hybridize given different management scenarios. All stakeholders were users of knowledge and resources and were responsible for the decision-making process that involves strategic planning and enforcing management plans. Although stakeholders varied in their objectives, all agreed on a need to produce user-friendly management tools to bridge the gap between scientific knowledge, land-use and game-regulation needs, and private game-ranching objectives.

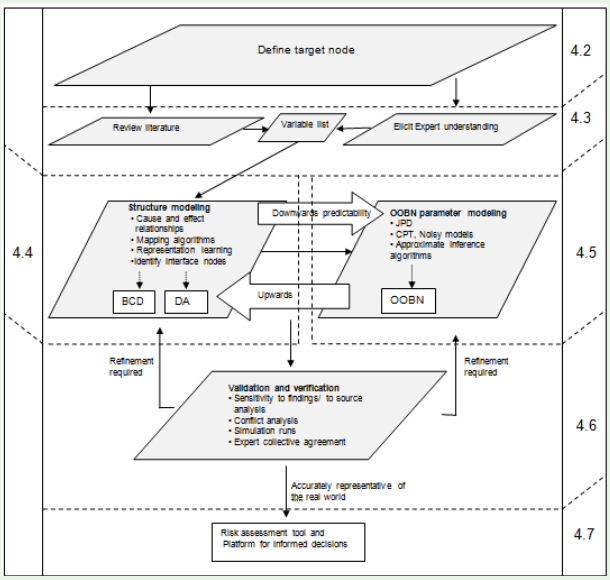

Figure 3: Flow chart of OOBN construction. Stepwise actions highlighted in gray layers. Black arrows illustrate stepwise procedure. White arrows indicate modeling directionality, while products are in white boxes. Numbers in columns (4.2-4.7) correspond to explanatory sections in text.

Table 1: List of surveyed stakeholders and their objectives. Stakeholders have a comprehensive understanding of the black wildebeest and blue wildebeest hybridization management and drivers.

Key stakeholders	Objectives
Private game owners	To manage population effectively while optimizing economic profit margins and maintaining viable populations
Private game managers	To manage population effectively while optimizing economic profit margins and maintaining viable populations
Governmental officials	To decrease hybridization rates
Scientists	To evaluate the probability of hybridization and genetic admixture under various management scenarios

Note: Respective roles and specialties of governmental officials and scientists were within land/game regulation and enforcement, as well as large mammalian biology.

Structure modeling

We first identified domains and then constructed a BCD. We simultaneously developed DAGS and BNs, followed by two OOBNs (Figure 3).

Domain identification and Bayesian Conceptual Diagram (BCD): We use parameters and variables interchangeably. Once a comprehensive list of hybridization facilitators, drivers and implications was agreed upon, we sought to identify domains. A domain is a cluster of parameters that share a commonality in structure or behavior, which provides a working interface for the programmer to interact with clusters of moving parts that differ in their predictability of hybridization, and to facilitate replication in similar ecological systems. In order to model their complexity effectively, we grouped these into three domains: biological, spatial, and market sectors.

Once parameters and domain were identified, experts collaboratively developed a conceptual representation of the relationship between variables from the aforementioned biological, spatial, and market-based domains. Parameters that result in a non-zero probability of hybridization occurrence were included. Initial BCD was presented to stakeholders for discussion and refinement. Parameters were revised, hidden, excluded, or included.

Directed Acyclic Graphs (DAGs) represent interlinkages: The BCD served as the basis for two plausible DAGs (Figure 4). We present them both to emphasize that the real world may be depicted in more than one manner.

Notes: (a) D represents a management practice (e.g., 20% increases in market demand for black wildebeest hunting). C and B represent biological and spatial management implications such as overstocking black wildebeest and not allowing for adequate wildlife fencing. A represents the probability of hybridization.

Parameter Modeling

Parameter learning and BN construction provided the basis for OOBN construction (Figure 3).

Parameterization: Acceptable ranges and probability distributions of different variables were elicited from experts and Max Log Likelihood and Noisy-MAX algorithms allowed to average different probability values for a given node and JPD to form CPTs. Because of the inherent variability of biological variables, experts were asked to consider intervals as 95% credible intervals (often incorrectly referred to as confidence intervals). This allows a parameter to have a state and quantifiable or categorical behavior. Thereby, its role within the complexity of relationships is identifiable. Finally, the parameter contains both knowledge and descriptions of its manipulation of the knowledge.

Construction of Bayesian belief networks: Expert knowledge provides a priori information, which is the basis for numerical or categorical values in a CPT. BCD and CPTs provided the platform for subnetwork structural development (Figure 3). We constructed BNs in three stages: (1) identify the set of parameters within specific domains that impact the probability of hybridization occurring between black and blue wildebeest, (2) identify the relationship among these parameters; and (3) apply CPT to quantify the links between parameters and define node states (i.e., the possible values that a variable can have). The latter stage transforms the BCD into a BN. We designed each BN to accurately represent a realistic snapshot of interactions that affect hybridization between the black wildebeest and blue wildebeest attributed to one of three domains: (1) biological, (2) spatial, or (3) market sectors.

We utilized a BN fragment (subnetwork) to describe the probabilistic relationships between connections of a domain. These connections can themselves be objects, providing a natural framework for encoding part-of hierarchies. We allowed for 1000 simulated cases generated and factored 15% of missing data in Netica. Decision nodes and utility nodes are collapsed as suggested by Nielsen & Jensen, and Lemmer&Kanal [32,46]. For example, habitat cover availability is represented as a signal node in the OOBN but in the BN framework, it has three nodes: trees, prairie (i.e., savannah), and a combination of trees and prairie. Lastly, and in light of the nature of wildlife ranching, we accounted for wildebeest movement as an implied variable within the spatial connectivity node, rather than in the biological domain.

Instance nodes served as interlinking nodes, providing a snapshot of the different BNs involved, thereby enabling their integration

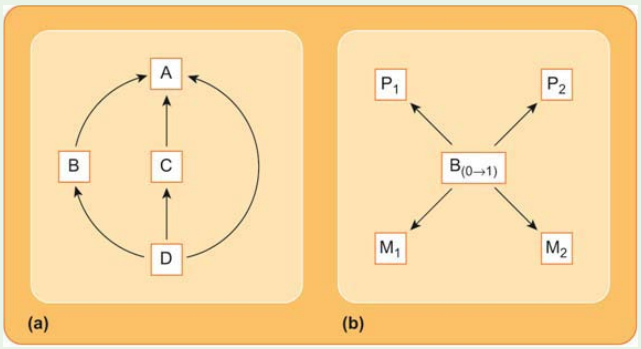

Figure 4: A skeleton Directed Acyclic Graphics (DAG) show a simplified representation of domains that act synergistically to facilitate hybridization between the black and blue wildebeest.

and an accurate representation of the multilayered real-world conservation concern in the form of an OOBN.

Validation and verification

Sensitivity to parameters and findings: We sought to determine whether the information generated might be altered by the structure of the model. Sensitivity to parameters was preformed by changing conditional probabilities and subsequently examined the accuracy and correlations in altered posterior probability distributions (Figure 3).Sensitivity to findings was preformed by changing posterior probability distributions and subsequently examined the accuracy and correlations in altered conditional probabilities. Deviations from predictions would have indicated errors in the network structure or CPTs. We did not encounter the need to adjust for such errors. Finally, whereas previous studies have employed only one of these methods, we made our sensitivity analysis more robust by adopting both.

Verification of values: As suggested by Pitchforth and Mengersen [47], we evaluate both content validity and predictive validity for expert-elicited BN validation. This enabled the production of a robust and accurate model. We sought to validate the knowledge engineering process and to enable posterior updates when data become available by "user validation", as suggested by Woodberry et al. [48]. Structured reviews were preformed; experts were asked to assess whether BNs and OOBNs represent the complexity of the wildebeest hybridization conservation concern. We calibrated networks to reflect different management scenarios and market drivers, and posterior probabilities were evaluated. If these scenarios coincided and represented expert knowledge, we concluded that they were accurate.

OOBN as Decision tools

We constructed two OOBNs that vary in their scope according to their intended audience and objective (Figure 3). An overall OOBN provides decision makers with detailed information of which drivers and variables facilitate hybridization on their game ranches. The second OOBN was constructed by an additional process of identifying and interlinking instance nodes while treating the overall OOBN as the subnet.

Results

Utilization of expert knowledge conceptualizes conservation problem and facilitates the identification of interlinked key domains and parameters

Key drivers for hybridization are clustered into following three domains: biological, spatial, and market industries. In addition, domains support inheritance of model fragments from a class to a subclass, allowing for the common aspects of related domains to be defined only once, enabling network fragments and expert knowledge to be used as the infrastructure of reusable probabilistic models that can be applied to multiple similar objects elsewhere. We utilized these domains as the infrastructure for informed decisions; stakeholders may decide to focus resources on one or more domains, while realizing spillover effects. Classifying nodes and states, and quantifying trade-offs associated with hybridization between the black wildebeest and blue wildebeest, served as the basis for a Bayesian Conceptual Diagram (BCD) formulation (Figure 5).

Note that stochasticity resulting from disease was not modeled. Variables are clustered in domains: Blue outline clusters the biological domain, yellow outline clusters spatial domain, and green outline clusters market based domain.

Based on expert knowledge, we believe that the BCD adequately represents the skeleton of causal relationships driving hybridization between the black and blue wildebeest. This abstract visualization provides wildlife managers with three utilizations: (1) to promote an understanding of which factors require attention when managing for hybridization occurrences, (2) to enable decision makers to choose the scope of their focus (i.e., one or more domains, thereby maximizing resources allocation), and (3) to identify spillover effects (Figure 5). As such, the BCD, in itself, provides the platform upon which comprehensive management guidelines may be drawn; it illustrates the specific links through which hybridization may be induced, and following deductive logic, decreased. For example, market forces drive the biological or/and spatial management practices, which in turn act as drivers for market driver and have spillover effects on species composition and abundance, and suitable habitat availability. Specifically, BCD illustrates the interlinkage between the buy/sale market and shifts in interspecies bull ration via an increase in trophy individuals (Figure 5).

Applying Bayes rule to quantify hybridization occurrences

The cyclical nature of the BCD enabled us to formulate a DAGs tailored to the specific priorities and objectives of different stakeholders (Figure 3). We converted Bayes' rule of probabilities (mainly formulas2, 3) to quantify the overall causal relationship among domains that affect wildebeest hybridization (formula 8,9). For example, let us denote two independent two market segments

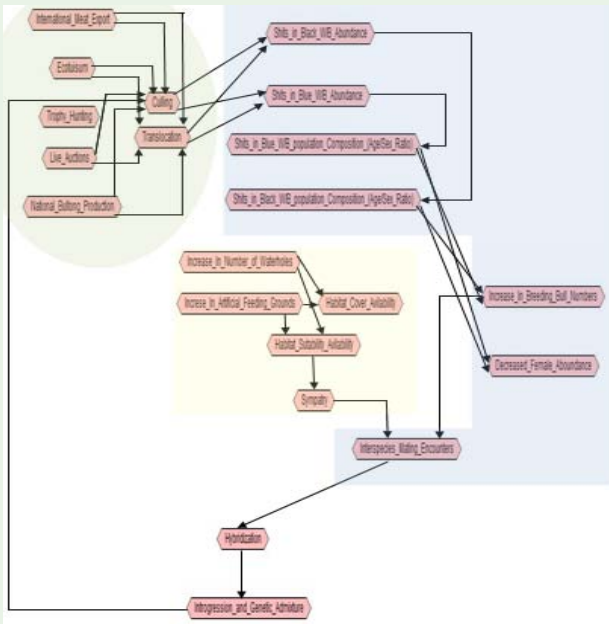

Figure 5: Bayesian conceptual diagram provides a simplified reflection of the multidimensional hybridization conservation concern. Note that stochasticity resulting from disease was not modeled. Variables are clustered in domains: Blue outline clusters the biological domain, yellow outline clusters spatial domain, and green outline clusters market based domain.

(e.g., hunting and ecotourism) as M1 and M2, and the change in the biological domain (e.g., abundance) as B_(0→1) .This yields two hybridization probabilities (denoted by P1 and P2). This is approximated as follows:

$$p\left(p_1 \middle| B_{0\to1}\right) p\left(p_2 \middle| B_{0\to1}\right) p\left(B_{0\to1} \middle| \mathrm{M}_1, \mathrm{M}_2\right) p\left(B_{0\to1} \middle| \mathrm{M}_1\right) p\left(\mathrm{M}_2\right)$$

To formulate the probability of genetic admixture and hybridization (denoted by GA and Hy), we considered all domains (B denotes biological domain, M denotes market domain, and A denotes anthropogenic-driven spatial change). We simplified the DAG shown in Figure 3 (a). This corresponds to the following formula:

$$\mathrm{p}\left(\mathrm{GA} \middle| \mathrm{Hy}_{0\to1}, B,M,A\right) = \mathrm{p}\left(\mathrm{GA} \middle| \mathrm{Hy}_{0\to1}\right) \mathrm{p}\left(\mathrm{Hy}_{0\to1} \middle| \mathrm{B,A}\right) \mathrm{p}\left(\mathrm{B,M} \middle| \mathrm{A}\right) \mathrm{P}\left(\mathrm{M} \middle| \mathrm{A}\right) \quad (9)$$

OR

$$\mathrm{p}\left(\mathrm{GA} \middle| \mathrm{Hy}_{0\to1}, B,M,A\right) = \frac{\mathrm{p}\left(\mathrm{Hy}_{0\to1}, \mathrm{B,M,A} \middle| \mathrm{GA}\right) \mathrm{p}\left(\mathrm{B,M,A} \middle\| \mathrm{GA}\right) \mathrm{p}\left(\mathrm{M,A} \middle| \mathrm{GA}\right) \mathrm{P}\left(\mathrm{A} \middle| \mathrm{GA}\right) \mathrm{P}\left(\mathrm{GA}\right)}{\mathrm{p}\left(\mathrm{Hy}_{0\to1}, \mathrm{B,M,A} \middle| \mathrm{GA}\right)},$$

$$\mathrm{p}\left(\mathrm{Hy}_{0\to1}, \mathrm{B,M,A} \middle| \mathrm{GA}\right) \neq 0$$

Note: P(GA) is the prior probability, and the initial degree of belief in GA $\mathrm{p}\left(\mathrm{Hy}_{0\to1}, \mathrm{B,M,A} \middle| \mathrm{GA}\right)$ is the conditional probability or likelihood, which represents the degree of belief in $\mathrm{Hy}_{0\to1}, B,M,A$ given that proposition GA is true.

$\mathrm{p}\left(\mathrm{GA} \middle| \mathrm{Hy}_{0\to1}, B,M,A\right)$ is the posterior probability, or the probability that GA is true after taking into account $\mathrm{Hy}_{0\to1}, B,M,A$ for and against GA.

Biological BN

We include the biological BN for the purpose of illustrating the complexity of a single domain. Additional BNs are not presented here; rather, we suggest that the process of OOBN construction as two wildlife management tools is more helpful for readers (Figures 1-3). Male blue wildebeest to male black wildebeest ratio is the key biological variable associated with the probability of wildebeest hybridization (Figure 6). Notes: BN incorporates user-friendly nodes. For example, it simplifies the process for users because they know the number of introduced black wildebeest males, rather than the percentage of introduced black wildebeest males from the entire population. Moreover, BNs conduct evaluations given management scenarios. Therefore, introgression is assumed to result in admixture and swamping. Unforeseen shifts in species composition refers to survival rate (e.g., foot and moth disease).

OOBN model predictions

OOBN provide a complete representation of the complexity of the hybridization phenomenon and its interlinking drivers, enabling transparency and tailored information according to varying objectives of different decision-making groups. The probability of hybrid swamp production is predicted primarily by a high ratio of blue male wildebeest to black male wildebeest in the biological domain, habitat connectivity availability in the spatial domain, and extractions or introductions of reproductive males following market forces in the market sector domain (Figures 6 and 7).

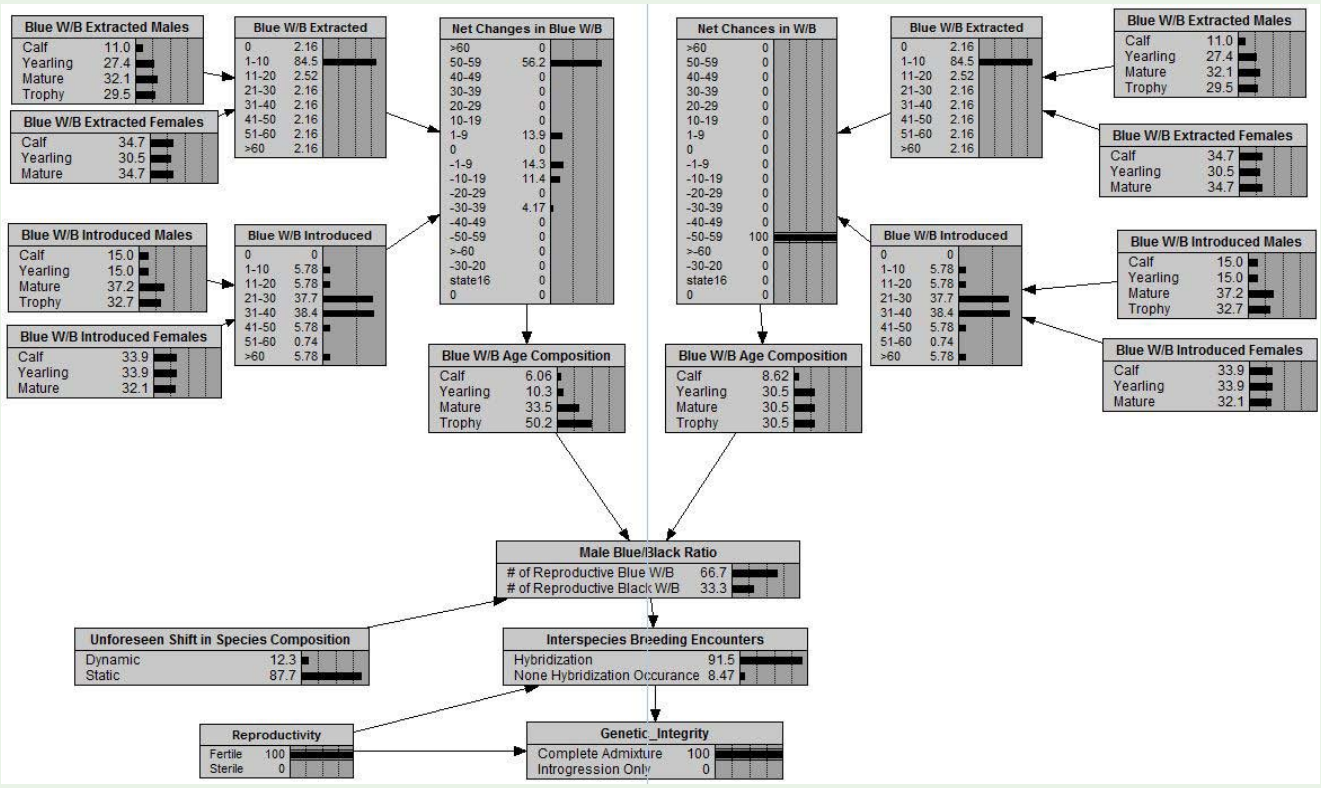

Figure 6: Bayesian belief network reflects interlinked variables in the biological domain. Nodes are titles and states are summarized. Arrows indicate causal relationships. Blue line suggests a mirror account for variables (i.e., all variables associated with blue wildebeest were additionally associated with black wildebeest).

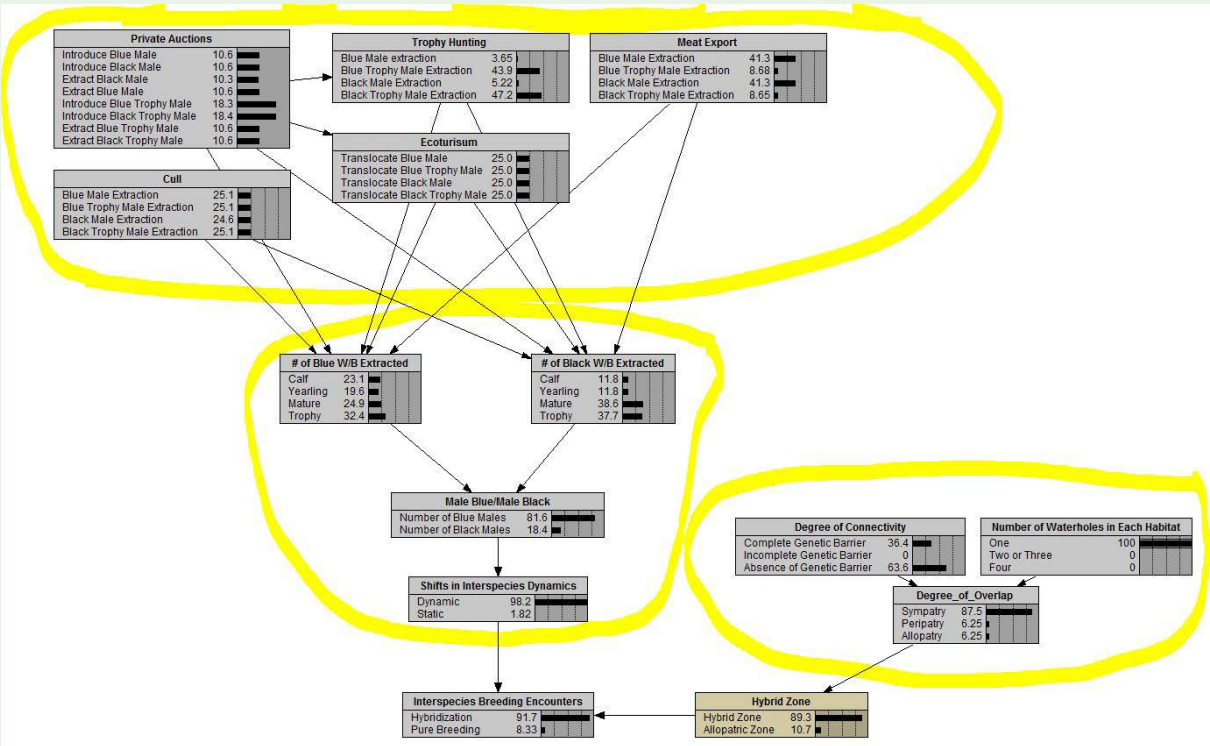

Figure 7: OOBN model mimics equalizing hierarchical subnetworks and serves as a management tool illuminating tradeoffs between domains.

Notes: In order to preserve the integrity of market role, we included a node for culling. Uniformly distributed variables are based on numbers of wildebeest translocated (i.e., extracted or introduced) in specific nodes (i.e., private auctions, cull, ecotourism). The sum of probabilities equals 100% and as such, when certain scenarios are relevant (e.g., number of water holes), the probability of alternative scenarios is 0. 1000 case simulations were run, with a 15% missing data notation. Circles indicate three primary domains.

Tradeoffs of management scenarios: Netica report indicated that 16547 conditional probability linkages were obtained and evaluated for possible fit (Figure 7). Expert knowledge constructed a scenario that entailed extractions primarily of reproductive age males, and an abundance favoring blue wildebeest, in addition to a high probability of sympatry (Figure 7). Experts advised that the combination of these factors represents the "worst-case scenario" for genetically pure black wildebeest populations. Specifically, OOBN indicates a strong

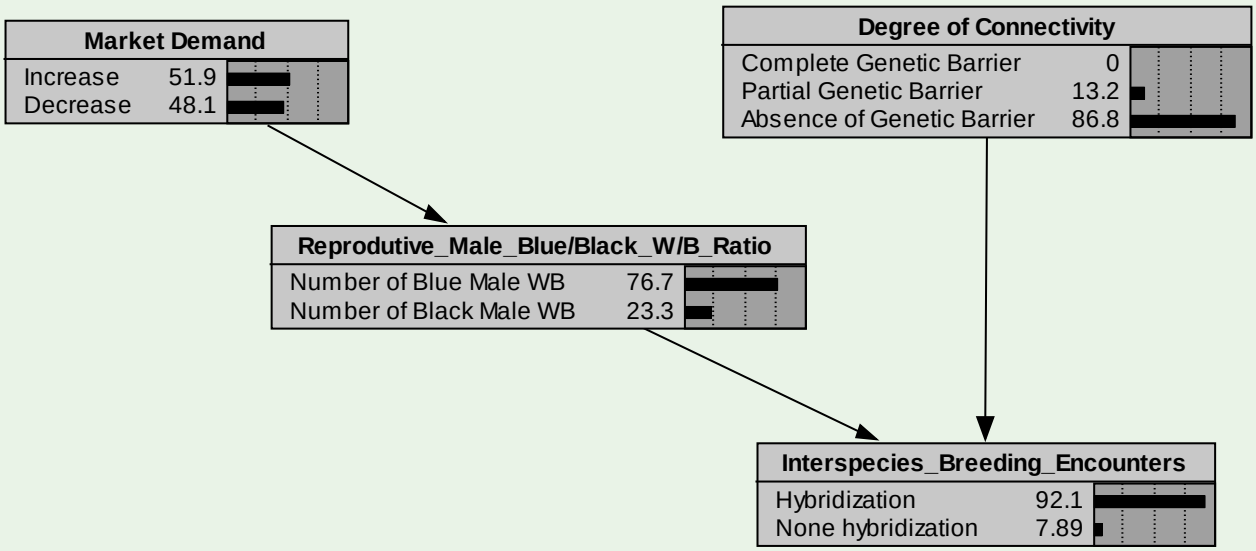

Figure 8: OOBN models ecosystem interactions encompassing "eagle's-eye" detail and acts as a risk assessment tool for resource allocation maximization.

correlation between the purchase of both blue and black wildebeest trophy males (~18% in comparison to an even likelihood of all other categories within this node) and high probability of extraction both blue and black wildebeest trophy males (43.9%, 47.2%, compared to >6% of none trophy males) and low extraction of both blue and black wildebeest trophy males resulting from the market for meat export (>9% in comparison to none trophy males). We follow the logical that this is due to the high economic investment in buying trophy males from both species in auctions that results in the targeted diminished rate of return activity (i.e., meat export, ecotourism, and trophy hunting, respectively). Moreover, the spatial domain has three significant nodes impacting hybridization: complete fence, incomplete fence, and fence absent (Figure 7 and 8). A probability ~2:1 for an absence of genetic barrier, together with only one waterhole on the grounds, yields sympatric conditions at a probability of 87.5% (Figure 7). Such a high probability of sympatry, coupled with male blue wildebeest to male black wildebeest ration of 81.6:18.4 resulted in a 91.7% probability of hybridization (Figure 7).

OOBN as a rapid assessment tool: OOBN yield a 92.1 probability of hybridization if the male blue wildebeest to male black wildebeest ratio was approximately 2:1, and there was a probability of 86.8% of an absence of sufficient barrier to gene flow (Figure 8).

Notes: Market stability is reflected by market demand, referred to as the medium point of decrease and increase (i.e., 50). Moreover, we assume that the user's intention is to assess the impact of shifts in a particular market sector on hybridization. The number of blue or black males is converted into a percentage; we argue that plugging in numbers is the most straightforward for users.

Model verification

Pearls belief propagation algorithm enables verification via probabilistic inference uses new data [40,49]. We did not encounter conflicts. We note that genetic markers that distinguish pure bred blue wildebeest from pure bred black wildebeest, or from varying hybrid generations, have not yet been identified [10,11,15,17]. As such, we used segments of knowledge, which were not utilized in the construction process. We recommend additional verification analysis when data becomes available.

Discussion

Environmental management mirrors Bayesian modeling stages

Efficient wildlife management cannot take place in a vacuum; it requires informed decisions that are within an ecosystem context. The multifaceted model structure described in this paper enabled a hierarchal breakdown and subdivision of a complex ecological system centered on a pressing conservation concern. Equally important, is that these stages correspond to procedures needed prior to the establishment and reevaluation of environmental, similar to ecological, modeling stages (Figure 1).

BCD and OOBNs highlight the need to address conservation concerns within an ecosystem context

The utilization of expert knowledge enables the construction of BCD and OOBNs. The BCD illustrates the importance of approaching the ecosystem as a whole by highlighting potentially deleterious implications of spillover effects when managing separately for domains (Figure 5). In addition, we provide a practical demonstration of how an OOBN model may be constructed and used as a DSS for wildlife managers (Figure 3). We emphasize that an efficient management plan designed to illuminate alternate management strategies that decrease wildebeest hybridization rates should consider biological, ecological, and market domains simultaneously.

The utilization of DAGs and upwards propagation

DAGs formulation incorporates the hierarchy of domain and parameter interlinkages. DAGs may be tailored to the appropriate audience and objectives. For example, if the objective is to compare the tradeoffs of two management scenarios, decision makers may utilize formula 6. Alternatively, if the objective is to quantify the probability of complete genetic admixture, decision makers may utilize formulas 8,9. Whereas formula 6 is relevant to landowners and managers, formulas 8,9 is particularly relevant to researchers and policymakers. Additionally, optimizing wildlife management scenarios maybe interpreted via posterior propagation (Figure 3). That is to say, probability of hybridization is impacted by black wildebeest relative abundance and wildlife fencing, which in turn are impacted by the hunting market sector.

OOBNs act as Decision Support Systems (DSS)

Biological Domain: Hybridization occurs as a result of mating between blue wildebeest bulls and black wildebeest cows [10]. Wildlife management practices have resulted in a shift in each population composition and abundance [8]. A decrease in male black wildebeest abundance in conjunction with the stabilization or increase in male blue wildebeest abundance increases the probability of hybridization (Figure 7). The objective of wildlife managers should be to mimic the natural population dynamics. The optimal ratio of blue wildebeest males to black wildebeest males should be kept under 0.5 to reverse stable hybridization occurrences and under 0.25 to make hybridization unlikely (Figures 6-8). A ratio of 1:1 indicates that hybridization would be maintained at an accelerating rate.

Spatial Domain and Regulations: Moreover, parapatric or sympatric conditions are largely due to economic profitability. The change in posterior probabilities for hybridization and genetic admixture proved the need to stabilize population dynamics that would mimic those found in finite populations that have continuous barriers to gene flow. In landscapes that are not altered by humans, black wildebeest are associated with trees/prairie landscapes, whereas blue wildebeest are found in prairie/tree landscapes [13]. Wildlife managers should aim for available suitable habitat, and an abundance of feeding grounds and waterholes, thereby decreasing the likelihood of intraspecies mating encounters. Moreover, structural barriers to gene flow may be the only solution to minimize intraspecies mating encounters and, as a result. Currently, regulations pose contingencies on acquiring buying, selling, and maintaining wildebeest individuals on adequate wildlife fencing. However, due to the high percentage of expert knowledge yielding the absence of complete fences as a plausible scenario, we caution about the efficacy of regulation enforcement and encourage that this be the focus of future research as suggested in previous papers [17,50].

Market Domain implications: We assumed that market variability

fell within the normal range. The effect of interventions in socio-economic parameters was not found to be strong. The reasons are primarily twofold: (1) extreme market shifts were not considered because they are not likely to occur; and (2) to represent practical reality, the model considers the effect of slight market changes on shifts in population dynamics (i.e., species abundance and composition). We had no reason to assume that the market would fluctuate dramatically and therefore, did not simulate those options. However, if the market were to act in such an unpredictable manner, the application of multiple interventions would need to be implemented simultaneously.

A 10% increase in demand in the trophy-hunting sector could be deleterious to wildebeest hybridization rates because it would result in a shift in breeding behavioral dynamics. Under natural conditions, one bull may impregnate several cows [13]. However, the presence of multiple bulls in a confined area may shift this balance. we caution against the decision to convert or direct increased livelihood to trophy hunting.

The effect of ecotourism on wildebeest hybridization was unclear, indicating that ecotourism could serve either as a catalyst for hybridization or to decrease it. We attribute this confusing finding to the attitudes of the specific experts. The sector was found to minimize hybridization in cases in which experts empathized with the ethical value of pure breeds and to promote hybridization in cases in which experts perceived the ethics of pure breeding to be secondary to revenue. We suggest green marketing, in which ranches market themselves as outfitters that place a high value on ethical breeding, thereby making them green and attractive to conservation-aware clientele.

OOBN enables risk assessment and tradeoff analysis

Bayesian networks promote adaptive management, thereby optimizing management efficiency related to conservation behavior. Consequently, the uncertainty presented at the time of modeling diminishes in light of new evidence and posterior updates [33,38]. After recalibrations, the collective expert understanding agreed that the proposed BN and OOBN model adequately reflect the complex real world. Thus, the use of interface nodes selected from individual BNs proved to be correct and efficient. Moreover, the development of a structured DSS for wildebeest population management is of high priority because it allows for more robust, informed, accountable, and strategic decisions in a setting in which quantitative data are scarce and modeling real-world complexity is limited. To quantify ecological uncertainty effectively, the widest appropriate a priori scale should be evaluated so that risks and management tradeoffs may be identified and prioritized.

We provide two OOBNs that vary in their level detail so that their adoption as DSSs may be tailored to stakeholders' objectives. We recognize that there is a need for posterior updating with data regarding hybrid individuals in order will increase model accuracy.

Finally, we perceive that simplifying the process of using a management tool will increase the likelihood that it will be used as a DSS, thereby maximizing its impact. We therefore provide a detailed decision tree that allows stakeholders to apply the most relevant OOBN (Figure 9).

Notes: Resources primarily include budget, time, and manpower. Wildebeest reside in national parks and on private game ranches.

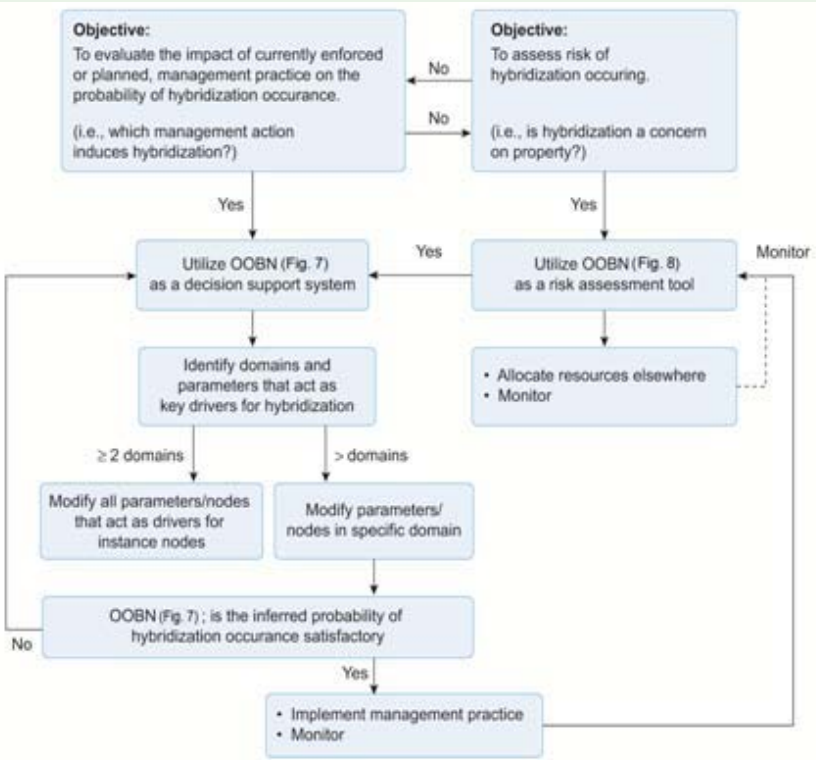

Figure 9: Decision tree designed to maximize OOBN utilization by directing decision makers to the appropriate procedure and tool.

As such, satisfactory probabilities of hybridization occurrences are defined by the model user, reflective of the objectives different stakeholders.

This decision tree transforms OOBN from a foreign concept to a more user friendly and relevant tool, thereby increasing implementation and usage. Our first OOBN (i.e., Figure 7) provides wildlife managers with a DSS for a detail tradeoff analysis, while our proposed second OOBN (i.e., Figure 8) is offered as a risk assessment tool that maximizes resource allocation by allowing knowledge generators and users to assess the probability that their currently enforced management practices facilitate hybridization and are in need of restructuring and adaptation.

The applicability of OOBNs as DSS is worldwide

We demonstrate that OOBNs illuminate decision-making tradeoffs, thus serving to promote informed decisions. Moreover, Bayesian modeling mimics the human cognitive thought process [51]. As such, the probability of it being employed is increased due to its intuitive nature. Equally important, we provide the much needed theoretical background and outlined the process of OOBN construction so that it may be used to address similar conservation concerns worldwide with relative ease. The bidirectional nature of OOBNs may be exploited (Figures 2 and 3); decision makers may plug in a zero probability of hybridization as a posterior probability and adopted a priori values as targeted objectives.

OOBNs are utilized as DSSs to promote informed decisions

Finally, in order for OOBNs to act as a DSS model, they must reasonably represent the outcome of different decisions [24,30]. Decision makers can then transform OOBNs into regional DSSs by simulations hypothetical scenarios with specific information (Figure 1). Our prototypes are practical and standardized decision-making; they can be implemented elsewhere worldwide to address conservation issues stemming from similarly complex ecological and human dimension issues.

Conclusion

Bayesian modeling is applicable to decision-making processes that address probability inference, using the knowledge of prior events to predict future events [52]. We innovatively applied it to quantify ecological uncertainty stemming from wildebeest hybridization. We show how expert knowledge can be utilized to identify domains and infer the probability that biological, spatial, and market-based drivers affect wildebeest hybridization rates. We show that BCD is an effective tool that provides decision makers with a conceptualize real-world complexity, and that the hierarchical nature of interlinked subnetworks allows for a logical and accurate construction/breakdown of the problem and cross-usage of data (Figures 5,7 and 8).

Although the reasons for decreasing wildebeest hybridization may differ among stakeholders, the primary aim is universal. Governmental officials encounter the need for allocating significant expenditure in extreme cases in which a population has undergone genetic admixture. A primary example is the culling of entire populations in the case of the Abe Bailey Nature Reserve, where wildebeest were observed to be the product of varying degrees of introgression [27,10,17]. Given that the black wildebeest survived two bottlenecks [14], culling at such magnitudes is not only resource consuming, but may also have a negative effect on the regional metapopulation structure. On a smaller scale, we suggest that game owners consider green packaging. That is, international tourists and hunters are more likely to prioritize their experience with private game reserves or outfitters if they are perceived to place a higher dollar amount on the intrinsic value of genetically pure populations, which may prove to yield increased revenue. Hence, this study is applicable and crucial to all stakeholders who share the mutual aim of decreasing hybridization rates.

In our research field, wildlife managers and owners advised that a detailed user-friendly tool would best serve as a structured DSS if it could quantify the impact of specific management actions. Thus, we put forward an OONB as such a framework (Figure 7). By contrast, government officials argued that the OOBN model was most helpful as a structured risk assessment tool that would assist them in the decision to allocate resources efficiently (Figure 8). Most comments reinforce the significant advantages embedded in an all-encompassing multifaceted model that illuminates management tradeoffs. It is logical to assume that wildlife managers and owners are most concerned with daily wildlife management decisions and implications, whereas government officials are greatly concerned with obtaining an eagle's-eye approach to the problem, which considers the effect of market segments and spatial allocation (Table 1). Lastly, we provide a structured decision tree for standardization of the decision-making process and maximum efficiency by clarifying the process needed (Figure 9).

The ratio between male blue wildebeest and male black wildebeest and the degree of species sympatry are the primary drivers of hybridization (Figure 5). Wildlife management practices should be adapted to reduce biological and spatial variables contributing to these drivers. In addition, the impact of shifts in various market sectors may determine the dynamics of introductions and extractions (e.g., translocation and culling events), and as such, have a direct impact on population dynamics and the interspecies male ratio.

Lastly, stakeholder participation is key to validating such models. We strongly recommend increasing confidence by strengthening collaboration among decision makers to allow for exchange of information in order to make DSSs more robust as data become available. As new research evolves, BNs and OOBNs can be revisited and refined. Nevertheless, there is a need currently for decisions regarding the management of wildebeest on private ranches in South Africa [8]. Hence, we argue that the suggested OOBNs could be used as a pathway toward milestone productive decisions, whereas specific BNs could be used to guide management. Lastly, the figures were presented in order of development to enable the process of OOBN reconstructions (Figure 3). This structure enables the application of innovative solutions to ecological predicaments worldwide.

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