Evaluating simple Bayesian Belief Network (BBN) models in predicting the effects of human activities on Species at Risk

Final Report

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Summary

1) In Canada, activities that might affect species which are listed under the federal Species at Risk Act require a permit. These permits are only issued, if the activity does not jeopardize the survival or recovery of a listed species. But the impact of human activities on populations in the wild are notoriously difficult to predict.
2) Simple BBN models have been designed as a tool for estimating the effects of management activities on species at risk. This is the first time such BBN models were developed to be applicable to groups of species with similar life history characteristics. These models work by predicting the probability of a change in the population growth rate as a consequence of a change in the vital rates (survival and fecundity), due to management measures.
3) To evaluate the effectiveness of these BBN models, different impact scenarios were simulated in BBN models and in selected single species population viability analysis (PVA) models. The resulting changes in the population growth rate given by each model type were compared against each other. Here, 9 different BBN models for groups of species with similar life histories were tested against 10 single species PVA models.
4) The results show that most simple BBN models for species with similar life history characteristics do not perform best for the species they were designed for. However, due to a lack of available and usable PVA studies and the limited time of the project, only one to two single species PVAs have been tested per BBN model. Further PVA models should be tested against corresponding BBN models to substantiate these initial results.

Keywords

Bayesian Belief Networks, RAMAS Metapop, Population viability analysis, Species at Risk, conservation biology, population growth rate, management impacts.

Introduction

In Canada, activities which may affect species that are listed under the federal Species at Risk Act (SARA) require a permit from the respective authorities (Environment Canada 2003; Nantel et al. 2005). Permits can only be issued if the activity will not jeopardize the survival or recovery of a listed species. Allowable activities include scientific research about the conservation of the species, activities that benefit the species, and activities whose effects on the species is incidental (Environment Canada 2003).

It is a widespread problem that wildlife conservation and development activities frequently counteract each other. It is also often the case that it is difficult to estimate the effects of such activities on populations in the wild. Seldom there is enough information on population viability on which to base scientifically sound decisions and to gather such information is costly and time intensive. But wildlife managers are routinely required to make decisions, often without sufficient knowledge about possible consequences.

A simple Bayesian Belief Network (BBN) model for groups of species with similar life history characteristics (Table 1) has been designed to estimate the effects of activities on the demography of SARA listed species (Nantel et al. 2005). The general idea behind the model is to have a consistent and easily applicable tool at hand that assists in making management decisions and which is based on empirical data.

The advantages of such BBN models would be that they provide tools for decision making in the presence of uncertainty and incomplete knowledge and that each decision is based on the same criteria or variables to ensure consistency (Nantel et al. 2005). Furthermore BBNs assist in clarifying structural and quantitative relationships among variables (Marcot et al. 2001).

In Ecology BBN models have been applied and tested in various cases, as for example in single species population management (Marcot et al. 2001; Lehmkuhl et al. 2001), in assessing the viability of salmonids (Lee & Rieman 1997), in river restoration management (Adriaenssens et al. 2004) or in evaluating the impacts of logging on rain forests (Crome et al. 1996). In the few cases in which BBNs were used to model the impact of management activities on species viability, they focussed on single species. So far, no BBN models have been developed that are applicable to a group or type of species with similar life-history.

Bayesian Belief Networks were named after Reverend Thomas Bayes (1702-1761), a British theologian and mathematician, who established a basic rule of probability, the Bayes Rule: $p(B|A) = p(A|B) \times p(B) / p(A)$,
where p(B|A), the probability of B given that A has occurred depends on the probability of A (p(A)) and B (p(B)) divided by the probability of A given that B has occurred (p(A|B)) (Norsys 2005).

A BBN is a causal network within which selected input variables influence the outcome states of downstream parameters. The causal relationship between these factors can be determined and updated by the user. The results are given as probabilities of predicted outcomes. An advantage of BBNs is that they can be updated when more information about variables and their effects are available. Also, expert knowledge can be included in addition to quantitative data (Marcot et al. 2001; Nantel et al. 2005). In the simple BBN models for groups of species, the outputs are presented as the likelihoods of a change in the population growth rate λ, which is influenced by changes in vital rates, such as fecundity and the survival of yearlings, juveniles or adults.

Here we evaluated the effectiveness of generic BBN models in predicting the effects of changes in the vital rates on the growth rate of populations by comparing the BBN outputs with those of population viability analyses (PVAs) from different published and unpublished sources. PVA comprises a variety of methods to estimate the survival capacities of populations and to evaluate the human and natural threats that populations are facing. With sufficient demographic and environmental data on populations of endangered or threatened species incorporated into PVA models, biologists can use PVAs as tools in wildlife management and to estimate the effects of management measures or other interventions that affect populations. Outputs of PVA models are typically risks of extinction and population decline, probability of recovery or time to extinction. By incorporating uncertainty through demographic and/or environmental stochasticity, these models can account for natural and human induced fluctuations in the abundance of species (Akçakaya & Sjögren-Gulve 2000).

However, PVAs have their limitations. One is that for many species, demographic data is scarce or totally missing. Furthermore PVA models tend to focus on single species (Akçakaya & Sjögren-Gulve 2000) and they have been subject to debate regarding their accuracy in predicting survival probabilities of populations (Brook et al. 2000; McCarthy et al. 2001; McCarthy et al. 2003). PVAs will never be able to offer absolute predictions because of the complexity of ecological systems and the paucity of accurate data. But it has been shown that the relative predictions of PVAs sufficiently match reality to be able to apply them in conservation biology (Brooks et al. 2000). Nevertheless PVAs should be used with caution and their predictions should be viewed in relative rather than in absolute terms (Akçakaya & Sjögren-Gulve 2000).

In this study population projections based on single species PVAs in RAMAS Metapop and R were compared to outputs of the BBN models. We assumed that the RAMAS Metapop and R outputs represent realistic predictions of the change in λ. To our knowledge this is the first attempt at predicting the effects of management measures on the viability of species by using a Bayesian Belief Network that can be applied to more than one species.

Table 1 BBN models for different species groups with respective case study and PVA reference. PVA Species 1 to 7 were modelled in RAMAS Metapop. PVA Species 8 and 9 (plants) were modelled in R.

BBN models and tested Species

	BBN model	PVA species	Scientific Name	Family	Order	Model Reference
1	Long lived birds	Whooping Crane	*Grus americana*	Gruidae	Gruiformes	Tischendorf 2004
2	Whales	Beluga Whale	*Delphinapterus leucas*	Monodontidae	Cetacea	Richard *et al*. 2003
3	Snakes	Massasauga Rattle Snake	*Sistrurus catenatus*	Colubridae	Squamata	Brennan 2004
		Eastern Black Rat Snake	*Elaphe obsolete*	Colubridae	Squamata	Brennan 2004
4	Turtles	Green Sea Turtle	*Chelonia mydas*	Cheloniidae	Chelonia	Chaloupka 2004
5	Long lived large terrestrial mammalian carnivores	Steller Sea Lion	*Eumetopias jubatus*	Otariidae	Carnivora	Gerber 2004
6	Short lived birds	Seaside Sparrow	*Ammodramus maritimus*	Emberizidae	Passeriformes	Shriver *et al*. 2004
7	Long lived medium sized mammalian herbivores	Turkish Mouflon	*Ovis gmelinii anatolica*	Bovidae	Artiodactylae	Sezen *et al*. 2004
8	Perennial shrubs	Mountain Golden Heather	*Hudsonia montana*	Cistaceae	Violales	Morris & Doak, 2002
9	Perennial herbaceous monocarpic plants	Meadow Thistle	*Cirsium scariosum*	Asteraceae	Asterales	Nantel, unpublished data

Methods

To evaluate simple BBN models for groups of species with similar life history characteristics, single species PVA case studies for species which are native to Canada or which are related to species occurring in North America were used (table 1).

To evaluate the efficiency of simple BBN models in predicting the effect of human activities on species at risk:
1) Eight RAMAS Metapop and two models in R were used to simulate 20 different population management scenarios over 2, 5 and 8 years. The models were run for a period of 60 years with population management initiated in year 50.
2) The standard deviation values of the trajectory summary of RAMAS Metapop, which presents the relative abundance of a population, was used to calculate the upper and lower bound changes in the population growth rate due to management.
3) The effect of harvest and introductions on wildlife populations was simulated in the BBN species group models by changing the vital rates of the different life stages. The effects of the simulations were shown as a probabilistic change in the growth rate λ.
4) The results of the BBN and the single species PVA models were compared by calculating the spherical pay-off in Netica (Norsys Software Corp.). To compare the overall fit of the BBN models, each single species PVA outcome was tested against all 9 BBN species group models.

Bayesian Belief Network , Netica (Norsys Software Corp.)

A Bayesian Belief Network is a causal network that describes logical or causal relationships between variables, which impact on the probability of output states of certain parameters (Marcot et al. 2001). A BBN consists of different nodes, each representing a variable, which are interconnected via directed links. Nodes can only be linked in one direction, thus that node A (parent) influences node B (child), but not vice versa. Parent nodes can influence child notes either by causing a child node, by partially causing or predisposing a child node and by being functionally related or statistically correlated. Child nodes can also be imperfect observations of parent nodes (Nantel et al. 2005). For every child node a conditional probability table (CPT) has to be generated, which defines the likelihoods or conditional probabilities of each outcome of node B, depending on the states of its upstream parent nodes, also known as prior or unconditional probabilities (Marcot et al. 2001; Nantel et al. 2005).

Once the conditional probability tables are set, the BBN can be updated through the user by entering values for a node as findings. The program will then calculate the new values for the child nodes by using specific algorithms.

Simple BBN models for groups of species

Each simple BBN model is build up out of 5 input nodes, which influence the state of the output node Lambda (see figure 1). These input nodes describe changes in vital rates of species from one year to the next, such as survival of yearlings, juveniles and adults and fertility (average number of offspring that survives the first year). Vital rates can be increased or decreased from insignificant (0-1%) to low (1-10%), moderate (10-50%) or large (50-100%). The duration of changes in the vital rates can be determined through the fifth input node, as either short (1-3 years), medium (3-6 years) or long (6-10 years).

The conditional probability table for these models was built in Netica with the function, learning from cases. The cases were generated by using an R script (R Development Core Team, 2005), which was programmed to simulate a large number of combinations of percentages of increase and decrease in vital rates, based on empirically derived transition matrices. For any given species, one transition matrix was used to generate many thousands of combinations of values for the possible changes in the growth rate values. The final BBN models for species groups with different life history characteristics were then produced by repeating the simulations with population matrices of species with different life history characteristics (Nantel et al. 2005).

The following algorithm was used for generating the cases on which the CPTs of the models are based: $B = (aFA + bYA + cJA + dMA) + A$, where B is the perturbed matrix and A is a transition matrix. F, Y, J and M describe binary matrices of the same dimensions as A with 1s in places, where A contains values for fertility rates, yearlings', juveniles' and adults' survival and growth rates, and 0s in all other places; a, b, c and d describe the proportional rate of increase or decrease and range from -1 to 1.

Simple form of Matrix A:

$$\begin{bmatrix} 0 & 0 & F_a \\ S_y & S_j & 0 \\ 0 & G_j & S_a \end{bmatrix}$$

F_a = fecundity rate of adult

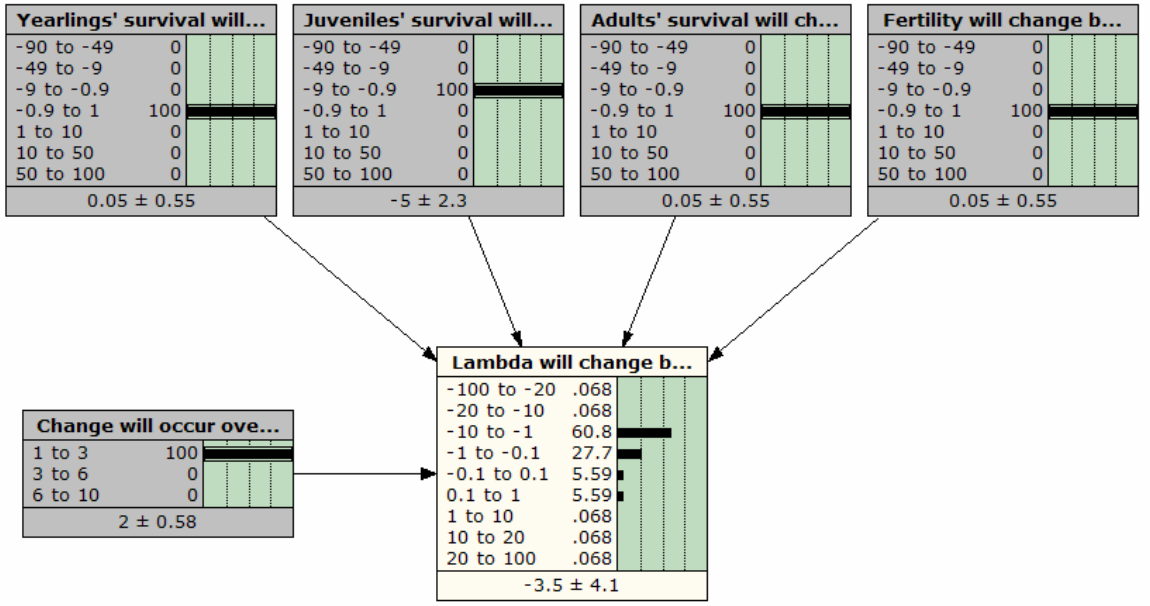
$S_{y,j,a}$ = survival rate of yearlings, juveniles or adults

G_j = growth rate of juveniles

Cases were simulated by changing the values of a, b, c and d, independently and in sequence. For each combination the change in the growth rate λ was calculated, each over a range of years (x).

The percentage change in the population growth rate was computed as:
$\Delta\lambda = 100 * (\lambda - \lambda_1^x)/ \lambda_1^x$, where λ_1^x is the dominant eigenvalue of A, raised to the power x, which is the number of years the effect on the vital rates will last. λ was calculated as:
n(t + x)/n(t), the number of individuals x years into the future, divided by the number of individuals at the start. The growth rate was computed this way, because using the dominant eigenvalue of B would assume that the population reaches a stable stage structure, whereas the simulated disturbances destabilize the population structure.
To calculate Δλ, the population size n had to be projected x years into the future, which was done by using the perturbed matrix B: $n(t + x) = B^x n(t)$, where n is the sum of n_i, the number of individuals in each stage class i (Nantel et al. 2005).

BBN model parameters were based on data of species that were not used for validation in this study
For list of species that were used to build BBN models see Annex 3.



Yearlings' survival will...	
-90 to -49	0
-49 to -9	0
-9 to -0.9	0
-0.9 to 1	100
1 to 10	0
10 to 50	0
50 to 100	0
0.05 ± 0.55	

Juveniles' survival will...	
-90 to -49	0
-49 to -9	0
-9 to -0.9	100
-0.9 to 1	0
1 to 10	0
10 to 50	0
50 to 100	0
-5 ± 2.3	

Adults' survival will ch...	
-90 to -49	0
-49 to -9	0
-9 to -0.9	0
-0.9 to 1	100
1 to 10	0
10 to 50	0
50 to 100	0
0.05 ± 0.55	

Fertility will change b...	
-90 to -49	0
-49 to -9	0
-9 to -0.9	0
-0.9 to 1	100
1 to 10	0
10 to 50	0
50 to 100	0
0.05 ± 0.55	

Change will occur ove...	
1 to 3	100
3 to 6	0
6 to 10	0
2 ± 0.58	

Lambda will change b...	
-100 to -20	.068
-20 to -10	.068
-10 to -1	60.8
-1 to -0.1	27.7
-0.1 to 0.1	5.59
0.1 to 1	5.59
1 to 10	.068
10 to 20	.068
20 to 100	.068
-3.5 ± 4.1	

Figure 1 User interface of a simple BBN model. Given here is an example of the BBN model for snakes. The growth rate lambda is affected by changes in the vital rates: Yearling survival, juvenile survival, adult survival and fecundity (mean number of offspring that survives their first year). Here, a low reduction in juvenile survival (-9% to -0.9%) over 1 – 3 years produces a probability of 60.8 % that the growth rate will decrease between -1% and -10% with a mean of -3.5 and a standard deviation of 4.1.

Simulating the effects of management activities on the population growth rate in BBN

To be able to directly compare the outputs, the same combinations of population management were used as in RAMAS and R. Population management was simulated as high (50-100%) or low (1-10%) decreases or increases in vital rates, which corresponds to a harvest or introduction of 75% and 5%

respectively, of yearlings, juveniles or adults in RAMAS Metapop and R. Changes in the vital rates were repeated for the short (1 – 3 years), medium (3 – 6 years) and long (6 – 10 years) time period corresponding to (see Annex 1).

RAMAS Metapop (Akçakaya 2002b)

RAMAS Metapop is a population viability analysis tool that can be used to evaluate risks of extinction and risks of decline of populations in a non-spatial or spatial context. In a spatial context it assesses the viability of populations that are connected via exchange of individuals, so called metapopulations, by taking into account dispersal patterns and distance between populations.

The PVA program includes a number of variables to describe environmental and species specific factors which affect the survival of populations, such as density dependence, age or stage structure, mating system, catastrophes and demographic stochasticity. It also has the option for a focussed population management by harvesting or introducing individuals from or to selected populations and life stages (Akçakaya 2002b).

Simulating in RAMAS Metapop (version 4.0)

To simulate the impact of activities on the viability of certain species, demographic population models from various sources were used (Annex 2). The effects of activities were simulated by applying the population management function of RAMAS Metapop. Negative impact was simulated as harvest and positive impact as introductions. Individuals were harvested from or introduced to populations annually for 2, 5 and 8 years. The models were run for 60 years with 3000 iterations. Population management was started in year 50. Populations were harvested for 75% and 5% of yearlings, juveniles and adults separately and in paired combinations. Altogether 20 different management scenarios were simulated for each time span. Introductions were calculated manually based on the abundance of individuals of each stage in the last year before population management started. In spatial models, introduced individuals were equally distributed among subpopulations. In age-structured models as well as in stage structured models with more than 3 stages (yearlings, juveniles and adults), first year stages were defined as yearling; stages that did not reproduce were defined as juveniles and all reproductive stages were classified as adults.

The original settings of the PVA models presented in this study were not changed. Only where initial harvest was included within the model, it was run both with and without initial harvest (Steller Sea Lion). For the Whooping Crane spatial model, the initial population size was raised from 53 (Pop1) to 500 (Pop2), due to very low abundances in year 49. RAMAS case studies with a spatial population structure were modelled as spatial and aspatial populations. The aspatial populations were generated by adding all individuals of the subpopulations into one large population.

Simulating in R version 2.1 (2005)

Plant case studies were simulated in R using a model developed by Morris & Doak (2002) based on vital rates. Harvest and introductions were performed in the same combinations as above. Each simulation was repeated 500 times.

Elements of stage-based transition matrices were first decomposed into their component, binomial, vital rates. Data from marked plants were used to estimate average and variance of those vital rates for each species. The variance was then corrected for demographic stochasticity, using Kendall's method (Kendall 1998) for survival and growth probabilities, and using Akçakaya method (Akçakaya 2002) for fertility values. Population projections were run by random selection of vital rates from beta distribution (for survival and growth probabilities) and from lognormal distribution for fertility values, keeping the observed within year and between year correlations among vital rates. Harvest and introduction of a given percentage of one or more specific life stages were simulated at year 50 and percentage change in stochastic population growth rate for the duration of the simulated management activities was calculated as with the RAMAS models. Models were programmed in the R language (R Development Core Team 2005), using MATLAB program "VitalSim" (with component functions) of Morris and Doak (2002) as pseudo-codes, modified to include harvest and introduction of individuals.

For information on model characteristics of case studies, see Annex 1.

Computing the percentage change in the growth rate (λ) in RAMAS and R

The percentage change in λ was computed to estimate the demographic effect of management activities. A high negative value indicates a large decrease in the population abundance and thus a strong negative effect on population survival, whereas a positive value points to an increase in the population size and a positive impact on the viability of a given population.

In RAMAS Metapop, the change in λ was calculated from the "trajectory summary". This summary provides the average population size and the standard deviations of the population size for the 60 years which the model projected into the future. Because of environmental and/or demographic stochasticity, most population trajectories show a large variation in population sizes. To take this variation into account, the upper and lower bound standard deviation values were chosen to calculate the ranges of change in the growth rates after harvest or introduction (figure 2).

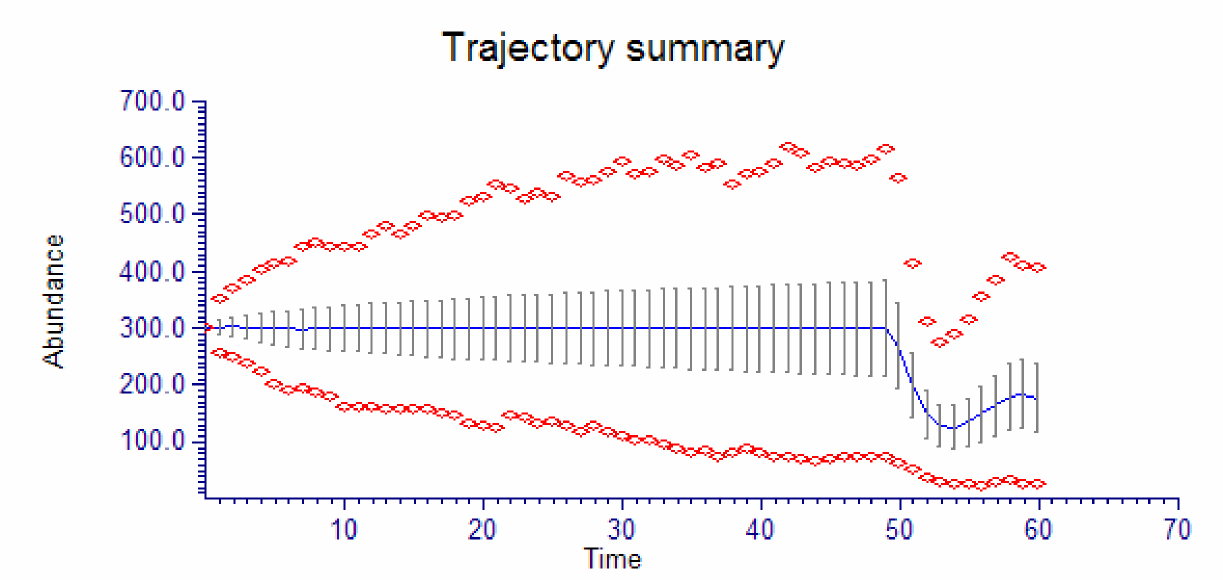


Figure 2 Trajectory summary of Black Rat Snake PVA. Population management (harvest of 75% of adults) was started in year 50 for two years. Line shows the average population size with standard deviation represented by vertical lines and lowest and highest values by squares (from RAMAS Metapop).

The percentage change in the population growth rate was calculated by determining the actual growth rate after population management started:

$\lambda_{after} = N(t + x)/N(t)$,

where N(t + x) is the population size in the last year of impact and N(t) the abundance in the last year before population management started (here year 49); and the geometric mean of the growth rate of the years before population management:

$\lambda_{before} = (\lambda_1 * \lambda_2 * \ldots * \lambda_n)^{1/n}$,

where λ_1 is the growth rate from year 0 to year 1, λ_2 the growth rate from year 1 to year 2 and so on, with n = 49. The final percentage change in the growth rate is then calculated as:

$\Delta\lambda = 100 * ((\lambda_{after} - \lambda_{before}) / \lambda_{before})$.

In R, the change in the population growth rate was calculated in the same way.

Comparing the outputs of RAMAS Metapop and R against the simple BBN models

The BBN model results were compared to the PVA results by using the spherical pay-off, which describes the overall fit of the predicted changes in λ for each BBN model compared against the results of the models in RAMAS or R. It can take values between 0 and 1, where 1 signifies a perfect fit and 0 no fit at all.

To compare the predicted changes in the population growth rate, the RAMAS results for each species were compiled in case files as described in Netica (Netica 2005) and were tested against all BBN models by using the 'test against case files' function. The spherical pay-off is calculated as: SPO = MOAC [Pc / sqrt (∑ [j=1 to n] (Pj^2))], where MOAC is the 'mean over all cases'; Pc, the probability in BBN for the correct state given by RAMAS or R (figure 1, Pc = 60.8%, if RAMAS would predict a change in λ between -1 and -10%) and Pj the probability for state j (Netica 2005). The basis for the spherical pay-off calculations is the confusion table, which summarizes the fits of all values (Table 2). For each PVA model, 120 values for Δλ were tested, which correspond to 20 different combinations of changes in the vital rates (population management) multiplied by 3 different time periods and with two outcomes (the lower and upper bound standard deviation of the change in the growth rate).

Table 2 Example of a confusion table for the BBN Snake model and the Black Rat Snake aspatial RAMAS model. Categories -20 to -100 until 20 to 100 describe the possible ranges for the change in the growth rate (from -100% to +100%). The shaded diagonal shows the amount of cases where the RAMAS outcomes matched the predictions of the BBN model. The confusion table builds the basis for the calculations of the spherical pay-off.

Confusion Table

Actual RAMAS outcome	Predicted by BBN								
	-100 to -20	-20 to -10	-10 to -1	-1 to -0.1	-0.1 to 0.1	0.1 to 1	1 to 10	10 to 20	20 to 100
-100 to -20	41	5	0	0	0	0	0	0	0
-20 to -10	5	4	2	0	0	0	0	0	0
-10 to -1	0	1	14	0	0	0	0	0	0
-1 to – 0.1	0	0	0	0	0	0	0	0	0
-0.1 to 0.1	0	0	0	0	0	0	0	0	0
0.1 to 1	0	0	0	0	0	0	0	0	0
1 to 10	0	0	0	0	0	0	10	2	1
10 to 20	0	0	0	0	0	0	0	2	2
20 to 100	0	0	0	0	0	0	0	4	27

Results

Ten PVA studies in RAMAS Metapop and R have been compared against 9 different BBN models for groups of species with similar life history characteristics (see Annex 2). The results are presented in the following sections.

Spherical pay-off

The fit of the BBN model outcomes against the actual predictions of RAMAS or R is comprised in the value of the spherical pay-off, which was calculated for all BBN – PVA combinations (table 3). The spherical pay-off for a single species PVA and its corresponding BBN model are shaded in grey. Values close to one signify a high overlap between RAMAS/R and BBN results.

The best fit is found for the BBN snake model (SPO between 0.8051 and 0.8248), followed by the long lived birds BBN (SPO between 0.7166 and 0.8125), the BBNs for short lived birds (SPO = 0.6438 & 0.7518), for large terrestrial mammalian carnivores (SPO = 0.6492 & 0.7036) and for whales (SPO = 0.6778). Both BBN plant models, which were simulated in R, show a particularly low fit (plant 1: SPO = 0.4856; plant 2: SPO = 0.4339).

To determine whether a BBN model for a specific group of species performs best for the species it was build for, each BBN model was tested against all single species PVA models. As Table 3 shows, only the snake model (BBN model 3) and the model for short lived birds (BBN model 6) perform best for the species they were built for. Other models show the highest overlap for species that do not belong to their group. When the performance of each BBN model with regard to a particular species is compared, then the long lived birds model and the perennial shrubs model perform best for their corresponding species. However, the plant models' overall performance is relatively poor (SPO between 0.2933 and 0.4856). The RAMAS snake models show the highest concordance with their corresponding BBN model, but the snake BBN does not achieve the best overall match for the two snake species compared to other BBN models that were tested against the RAMAS snake studies. Other BBN models perform as well for the snakes as the actual snake BBN. Interestingly most BBN models show their highest overlap for the RAMAS snake models (BBN models 1, 2, 4, 5, 8 and 9).

SPHERICAL PAY-OFF

		BBN Model								
Species	**PVA Model**	**LLB**	**Whl**	**Snk**	**Trt**	**LMC**	**SLB**	**MHR**	**PL1**	**PL2**
Whooping Crane	Pop1 aspatial	0.725	0.6916	0.6433	0.6602	0.7164	0.5545	0.5886	0.5934	0.6106
	Pop2 aspatial	0.7166	0.7057	0.5987	0.6476	0.7147	0.6062	0.6307	0.6133	0.5976
	Pop2 spatial	0.8125	0.7951	0.6993	0.7449	0.8038	0.6713	0.6946	0.6801	0.6743
Beluga whale	aspatial	0.6925	0.6778	0.5933	0.6146	0.6704	0.5383	0.5474	0.5869	0.5661
Black Rat Snake	aspatial	0.8337	0.7958	0.8237	0.7486	0.8201	0.6409	0.6509	0.7201	0.685
	spatial	0.8359	0.8076	0.8051	0.7505	0.8235	0.6558	0.6826	0.7535	0.6818
Massasauga Rattle Snake	aspatial	0.8408	0.8075	0.8248	0.7692	0.8296	0.6535	0.6738	0.7418	0.7314
	spatial	0.8364	0.8039	0.8225	0.7642	0.8255	0.6506	0.6677	0.7355	0.7235
Green Sea Turtle	Pop1 aspatial	0.5947	0.5665	0.6158	0.5869	0.5921	0.4457	0.4862	0.4944	0.5632
	spatial	0.5947	0.5665	0.6158	0.5869	0.5921	0.4457	0.4862	0.4944	0.5632
Steller Sea Lion	Pop1	0.7202	0.6776	0.7057	0.6402	0.7036	0.5353	0.5571	0.5664	0.6259
	Pop2	0.6612	0.6293	0.6366	0.5914	0.6492	0.5025	0.5138	0.5237	0.6009
Seaside Sparrow	aspatial	0.6901	0.6927	0.6359	0.6319	0.6719	0.6438	0.6153	0.603	0.6248
	spatial	0.7917	0.7972	0.6972	0.7088	0.7771	0.7518	0.7275	0.7035	0.6762
Turkish Mouflon	aspatial	0.7754	0.7499	0.733	0.6931	0.776	0.6364	0.6666	0.6477	0.6231
Mountain Golden Heather	aspatial	0.3906	0.4015	0.2933	0.3247	0.3902	0.4512	0.4713	0.4856	0.3113
Meadow Thistle	aspatial	0.4534	0.4402	0.4406	0.4178	0.4365	0.3579	0.3551	0.353	0.4339

Table 3 Spherical Pay-off between BBN results and PVA modelling results. Values close to 1 indicate a good overlap for the predicted changes in λ between the BBN and RAMAS or R results. Each species group specific BBN model was tested against every single species PVA model. Highlighted values show the spherical pay-off between a single species PVA model and its corresponding BBN model. BBN models: LLB = Long lived birds: Whl = Whales; Snk = Snakes; Trt = Turtles; LMC = large terrestrial mammalian carnivores; SLB = short lived birds; MHR = medium sized terrestrial mammalian herbivores; PL1 = plants of group 1; PL2 = plants of group 2. Case studies were modelled as non-spatial single populations and where possible as spatial metapopulations. Whooping crane, Pop1: initial popl.size = 53; Pop2: initial popl. Size = 500. Green Sea Turtle: Due to different vital rates between populations only one population (heron_wistari) was modelled as a non-spatial population. Steller Sea Lion, Pop1: with initial harvest of pups; Pop2: without initial harvest of pups**.**

Performance of right versus wrong BBN models

A boxplot was generated to estimate whether the spherical pay-off indicates a better fit (SPO close to 1) for the right combinations (shaded values in Table 3) than for all wrong combinations.

As figure 3 shows, the spherical pay-off between right and wrong combinations lay within similar ranges (mean (right BBN) = 0.69; mean (wrong BBN) = 0.63). These results suggest that BBN models specific for one group of species do not perform generally better for species they were developed for than for any other species tested here. Because the sample size of tested PVA studies per BBN model was very low (between 1 and 2) and thus not representative, the BBN models were not compared one by one to evaluate their performance with corresponding and non-corresponding PVA studies.

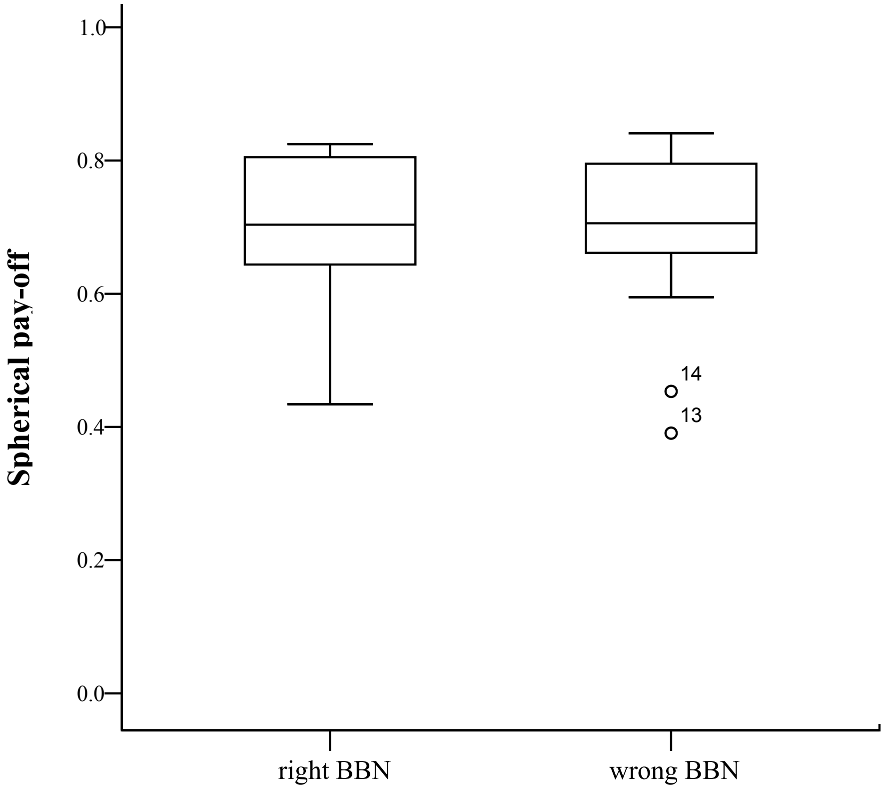


Figure 3 Boxplot showing the range of the spherical pay-off of the right BBN models (shaded values in Table 2) versus the wrong BBN models for single species PVA models (all other values) based on all BBN – PVA model combinations of Table 2.

Performance of spatial versus aspatial cases studies

It was assumed that aspatial models perform better than spatial models because simple BBN models do not take spatial patterns into account. Thus a boxplot was generated to determine if the spherical pay-off between aspatial and spatial PVA models (figure 4) differs significantly. However, the graph shows that BBN models perform slightly better for spatial models than for aspatial models (mean (spatial) = 0.71; mean (aspatial) = 0.67). A Wilcoxon Signed Rank Test for paired cases displayed a significant difference (p = 0.001) between the spherical pay-off of aspatial and spatial models. For this test only single species case studies with both spatial and aspatial RAMAS models were used.

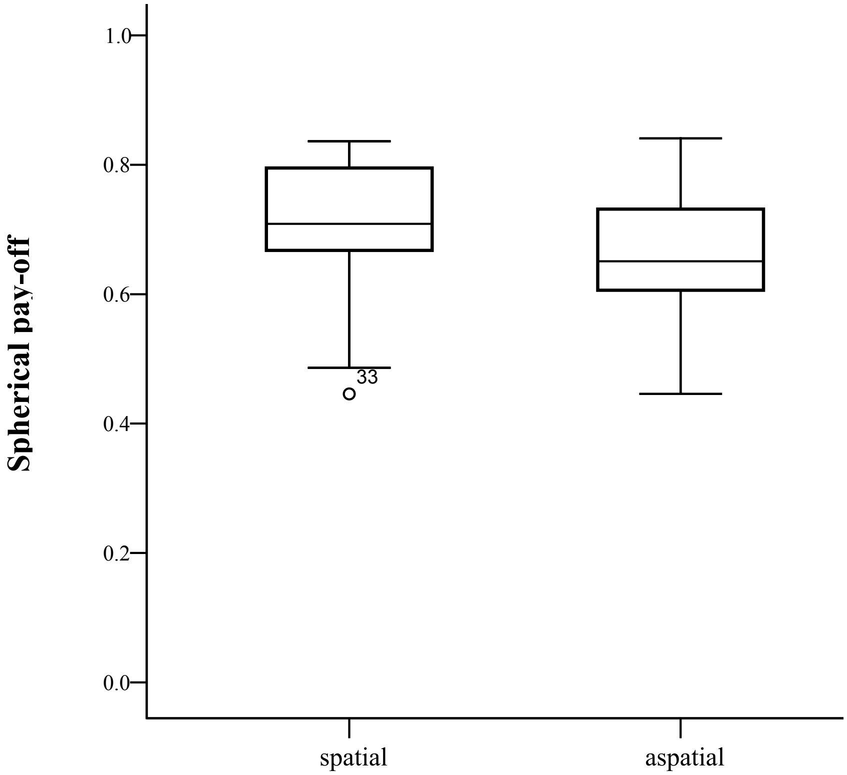


Figure 4 Boxplot showing the range of the spherical pay-off of spatial versus non-spatial PVA models based on BBN – PVA model combinations from case studies with spatial and aspatial single species PVAs (Whooping Crane, Black Rat Snake, Massasauga Rattle Snake, Green Sea Turtle & Seasside Sparrow).

Discussion

The results show that the performance of BBN models differ from model to model, ranging from a high (SPO ≈ 0.82) to a low fit (SPO ≈ 0.43). Only two BBN models perform better than all other BBN models for the species they were designed for (long lived birds, perennial plants) and also only two BBN models perform better for the species they were developed for than for all other species (snakes, short lived birds). Snakes show an overall good performance for any BBN model, which raises the question what characteristic responses on harvest and introduction make them perform best for most species group models.

When comparing the overlap in the spherical pay-off between BBN models and spatial versus aspatial PVA models, spatial models achieve a significantly better overlap. This was not expected because spatial models contain information on single populations within a metapopulation, which is not included within the BBN models. A possible explanation is that if dispersal capacity between subpopulations is high and environmental stochasticity affects subpopulations in a similar way, subpopulations might react like one big population. But the results obtained here should be viewed with caution because of the small number of single species PVAs that were tested against each BBN model. The small sample size of case studies is mainly due to a lack of available and suitable PVA data and the limited amount of time for the analysis. The study included only 10 PVA studies that were compared against 9 BBN models, thus only one to two PVA studies were available to be tested against its corresponding BBN model. For a more meaningful outcome, the number of PVA case studies per BBN models should be increased.

However, most simple BBN models show an overlap of 60% or more for their species. This leads to the question of how the threshold should be defined: When is the spherical pay-off actually too low to classify a simple BBN model as accurate enough in predicting changes in the population growth rate? This should be determined to finally evaluate the efficiency of simple BBN models.

To test the effects of human impact on the population abundance, individuals were harvested or introduced from or to distinct life stages (yearlings, juveniles, adults) in RAMAS and R. Harvest or introduction were high (75% of the abundance of a certain life stage) or low (5% of the abundance of a certain life stage) and it was assumed that these values correspond to a high change (50% to 100%) or a low change (1% to 10%) respectively, in the survival rate of a selected life stage in the simple BBN models. But the values that were used in RAMAS and R represent only the averages of the ranges in the BBN models. It is not known whether increases or decreases in the abundance of certain life stages close to for example a 100% or close to 50% would produce a similar change in the population growth rate as the 75% value. To explore if the average values for harvest and introduction chosen in this study actually lead to a good estimate of the average change in the population growth rate, values from the edges of the 1% - 10% and 50% - 100% vital rate ranges of the BBN models should be tested in RAMAS and R.

Management measures in the form of harvest and introduction were carried out only for high (75%) and low (5%) impact. These values were chosen to get a feel for what the effects of relatively low and relatively high impact would be on the change in the population growth rate. However, human impact, that requires assessment, will often have a medium impact on a population of concern. For future work it would be interesting to simulate the effects of medium harvest or introductions in RAMAS or R and to compare the resulting $\Delta\lambda$ with those of the simple BBN models.

To assess the effectiveness of simple BBN models it was assumed that the PVA studies in RAMAS and R deliver realistic results for the change in the growth rate as reactions on different management scenarios. But this strongly depends on data quality and quantity of PVA studies. To account for uncertainty in PVA parameters, the upper and lower bound standard deviation of the trajectory summary were used to calculate the change in the population growth rate λ. But by using the standard deviation of the projected abundances for calculating the change in λ, only the extreme upper and lower values were tested against the BBN models. This might not reflect the actual distribution of possible changes in the growth rate. Further values within the ranges of change in the growth rate given by RAMAS, like the average population growth rate, should be tested against the results of the corresponding simple BBN model. Another point that would be interesting to test is whether the simple BBN models tend to under- or overestimate the changes in the growth rate as predicted by the PVA models.

In this study the calculation of the percentage change in the growth rate takes only the decline of the population size into account that occurs during harvest, but it does not give information on how harvest or introduction would influence the population size for a certain time span after human intervention. Thus nothing is assumed about any long time changes in the population size, but possible effects of impact on populations might change significantly a few years later. However, uncertainty in the estimates of population abundances rises, the farther these are projected into the future and simple BBN models were designed to estimate only the immediate impact of a management activity on a species at risk, because SARA listed species are by definition already threatened or endangered or at risk of decline (Environment Canada 2003), so that any further harm should be avoided.

An initial requirement of BBN models is that it has to be known which life stages will be affected by a human activity and to which degree (high, medium or low). The impact of any human activity has then to be translated into changes in vital rates. This requires some initial knowledge about the distribution of a population and habitat requirements. However, due to the coarseness of the degree to which a certain life stage or life stages can be affected (change in vital rate from: 1% – 10%, 10% - 20% and 20% - 100%) it is easy for wildlife managers to choose possible scales of the effect and to model different scenarios in the BBN models.

This study offers a first impression on the performance of the newly developed simple BBN models for groups of species with similar life history characteristics. The results suggest that overall there is low specificity of a model for the species it was designed for. Few models perform best for the species that belong to the life history group they were built for. But even though the specificity of BBN models seems to be low, the fit of the models is higher than 60% for most of the right BBN-PVA combinations. Also, due to the small sample size of PVAs tested per BBN model, the results are not sufficiently representative and future work should include to test further PVA studies against the BBN model predictions to produce a more general assessment.

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Human impact scenarios

	RAMAS / R (harvest (-) or introduction (+) of)	**BBN** (change in survival rate of)
1	yearling / - 5%	yearling / - 0.9% to - 9%
2	yearling / - 75%	yearling / - 49% to - 90%
3	yearling / + 5%	yearling / + 1% to + 10%
4	yearling / + 75%	yearling / + 50% to 100%
5	juvenile / - 5%	juvenile / - 0.9% to - 9%
6	juvenile / - 75%	juvenile / - 49% to - 90%
7	juvenile / + 5%	juvenile / + 1% to + 10%
8	juvenile / + 75%	juvenile / + 50% to 100%
9	adult / - 5%	adult / - 0.9% to - 9%
10	adult / - 75%	adult / - 49% to - 90%
11	adult / +5%	adult / + 1% to + 10%
12	adult / + 75%	adult / + 50% to 100%
13	yearling / - 75% & juvenile / - 75%	yearling / - 49% to - 90%; & juvenile / - 49% to - 90%
14	adult / - 5% & juvenile / -5%	adult / - 0.9% to - 9% & juvenile / - 0.9% to - 9%
15	yearling / - 5% & juvenile / - 5%	yearling / - 0.9% to - 9% & juvenile / - 0.9% to - 9%
16	adult / - 5% & juvenile / - 75%	adult / - 0.9% to - 9% & juvenile / - 49% to - 90%
17	adult / - 75% & juvenile / - 5%	adult / - 49% to - 90% & juvenile / - 0.9% to - 9%
18	yearling / - 75% & juvenile / - 5%	yearling / - 49% to - 90% & juvenile / - 0.9% to - 9%
19	juvenile / + 5% & adult / + 75%	juvenile / + 1% to + 10% & adult / + 50% to 100%
20	juvenile / + 75% & adult / + 5%	juvenile / + 50% to 100% & adult / + 1% to + 10%

Annex

Annex 1 Combinations of harvest and introductions (RAMAS / R) and changes in vital rates (BBN). The table shows 20 different impact scenarios that have been simulated for 3 different time spans (RAMAS/R: 2, 5 & 8 years; BBN: 1-3, 4-6 & 7 to 10 years). Example: the harvest of -5% of yearlings in RAMAS or R was assumed to equal a reduction of the survival rate of yearlings of about -0.9% to -9% in BBN.

Annex 2 PVA characteristics of case study models.

Case study	Density dependence	Spatial / aspatial	Environmental Stochasticity	Demographic Stochasticity	Age /Stage structure	Catastrophe	PVA Model computed in
Whooping Crane	Ceiling	both	+	+	age	-	RAMAS METAPOP
Massasauga Rattle Snake	Ceiling	both	-	+	stage	-	RAMAS METAPOP
Eastern Black Rat Snake	Ceiling	both	-	+	stage	-	RAMAS METAPOP
Steller Sea Lion	Ceiling	aspatial	+	+	age	affects abundances	RAMAS METAPOP
Green Sea Turtle	Scramble Allee	both	+	+	stage	affects abundances	RAMAS METAPOP
Beluga Whale	Ceiling	aspatial	+	+	stage	-	RAMAS METAPOP
Turkish Mouflon	Scramble	aspatial	+	+	age	affects abundances	RAMAS METAPOP
Seaside Sparrow	Ceiling	both	+	+	stage	affects vital rates	RAMAS METAPOP
Mountain Golden Heather	none	aspatial	+	-	stage	-	R
Meadow Thistle	none	aspatial	+	-	stage	-	R

	Pine Barrens boneset (*Eupatorium resinosum*)	Byers & Meagher 1997
	Pitcher's thistle (*Cirsium pitcheri*)	Bell et al. 2003
Species Group for BBN	**Species matrices used**	**Source**
Long-lived birds	Atlantic Puffin (*Fratercula arctica*)	Saether & Bakke 2000
	Black-legged Kittiwake (*Rissa tridactyla*)	Saether & Bakke 2000
	Cory's Shearwater (*Puffinus diomedea*)	Saether & Bakke 2000
	Eurasia Oystercatcher (*Haematopus ostralegus*)	Saether & Bakke 2000
	Mute Swan (*Cygnus olor*)	Saether & Bakke 2000
	Northern Fulmar (*Fulmarus glacialis*)	Saether & Bakke 2000
	Northern Gannet (*Morus bassanus*)	Saether & Bakke 2000
	Parasitic Jaeger (*Stercorarius parasiticus*)	Saether & Bakke 2000
	South-Polar Skua (*Catharacta maccormickii*)	Saether & Bakke 2000
Snakes	Broad-headed snake (*Hoplocephalus bungaroides*)	Webb et al. 2002
	Small-eyed snake (*Cryptophis nigrescens*)	Webb et al. 2002
Turtles	Blanding's turtle (*Emydoidea blandingii*)	Congdon et. 1993
	Desert tortoise (*Gopherus agassizii*)	Wisdom et al. 2000
	Kemp's Ridley turtle (*Lepidochelys kempii*)	Gerber & Heppell 2004
	Loggerhead sea turtle (*Caretta caretta*)	Crouse et al. 1987
	Snapping turtle (*Chelydra serpentine*)	Cunnington & Brooks 1996
Large carnivorous mammals	Black bear (*Ursus americanus*)	Heppell et al. 2000
	Harbor seal (*Phoca vitulina*)	Heppell et al. 2000
	Northern sea lion (*Eumetopias jubatus*)	Heppell et al. 2000
	Northern fur seal (*Callorhinus ursinus*)	Heppell et al. 2000
Whales	Gray whale (*Eschrichtius robustus*)	Heppell et al. 2000
	Killer whale (*Orcinus orca*)	Brault & Caswell 1993
	Sei whale (*Balaenoptera borealis*)	Heppell et al. 2000
	Short-finned pilot whale (*Globicephala macrorhynchus*)	Heppell et al. 2000
Large herbivorous mammals	Dall's sheep (*Ovis dalli*)	Heppell et al. 2000
	Elk (*Cervus elaphus elaphus*)	Dixon et al. 1997
	Red deer (*Cervus elaphus*)	Heppell et al. 2000
	Reindeer (*Rangifer tarandus*)	Heppell et al. 2000
Short-lived birds	Cliff Swallow (*Petrochelidon pyrrhonata*)	Saether & Bakke 2000
	Eastern Kingbird (*Tyrannus tyrannus*)	Murphy 2001
	House Martin (*Delichon urbica*)	Saether & Bakke 2000
	Meadow Pipit (*Anthus pratensis*)	Saether & Bakke 2000
	Pied Flycatcher (*Ficedula hypoleuca*)	Saether & Bakke 2000
	Prairie Warbler (*Dendroica discolor*)	Saether & Bakke 2000
	Red-eyed Vireo (*Vireo olivaceus*)	Noon & Sauer 1992
	Song Sparrow (*Melospiza melodia*)	Saether & Bakke 2000
	White-crowned Sparrow (*Zonotrichia leucophrys*)	Saether & Bakke 2000
	Wood Thrush (*Catharus mustelinus*)	Saether & Bakke 2000
Plant group 1	American Ginseng (*Panax quinquefolius*)	Nantel et al. 1996
	Common boneset (*Eupatorium perfoliatum*)	Byers & Meagher 1997
	Divaricate sunflower (*Helianthus divaricatus*)	Nantel & Gagnon 1999
	Fragrant sumac (*Rhus aromatica*)	Nantel & Gagnon 1999
	Wild ginger (*Asarum canadense*)	Damman & Cain 1998
Plant group 2	Mariposa lily (*Calochortus obispoensis*)	Fiedler 1987
	Mead's milkweed (*Asclepias meadii*)	Bell et al. 2003

Annex 3 Species transition matrices used to build BBN models for groups of species with similar life history characteristics

Annex 3 continued…

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