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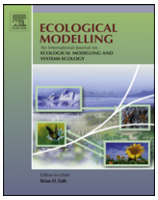

Short communication

Reducing matrix population models with application to social animal species

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ABSTRACT

Stage-structured matrix models are commonly used to inform management decisions for species with complex life cycles. These models require information on the number or proportion of individuals in each stage. However, complex life cycles, such as those in species exhibiting a complex social organization, can make these data difficult to obtain. The discrete time structure of matrix models makes them reducible, meaning that full models can be simplified by removing some stages. We illustrate the method by reducing the life cycle of wolf (*Canis lupus*) on which culling and conservation plans often lead to controversial debates. Starting from a 4-stage matrix incorporating social stages, we obtained several reduced models of increasing simplicity all showing similar demographic outcomes to the full model. We found that asymptotic growth rates of reduced models were in close agreement with empirical data. Our approach can offset the lack of information on individual stage abundance and therefore be valuable when using matrix models for wildlife management when data on certain stages are sparse.

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1. Introduction

Matrix population models are widely used in ecological modelling. In stage-structured models, individuals are assigned to different stages (e.g., morphological for insects or phenological for plants) and all individuals within a same stage are assumed to be identical (Birt et al., 2009). Matrix models are commonly used in demographic studies to obtain estimates of the asymptotic population growth rate, population size and stable stage distribution (Caswell, 2001). When used in decision theory, population matrix models can be combined with an optimization procedure to choose between alternative management strategies (Haight et al., 2002; Chadès et al., 2011).

Matrix models are parameterized with demographic rates such as fertility or survival, which require calibration from data that are sometimes difficult to collect in the field (Gimenez et al., 2012). Social species are typical examples of complex life cycles for which data can be hard to obtain. Social species are organisms living in groups of more or less interactive and related individuals that maintain common social behaviours within and across groups (Wilson, 1975). Neglecting the social structure in a matrix model can lead to biased estimation of population trends and consequently misinform management decisions and negatively impact species conservation (Brault and Caswell, 1993; Carroll et al., 2003). It is therefore important that the complexity of a population matrix model reflects the species biology while staying within the scope of available empirical data.

In this note, we demonstrate how matrix reduction can be used to simplify demographic models so that they can match the available data. Reduction of a stage-structured model consists in removing certain stages of the life cycle and merging transitions between them without affecting the population dynamics (Caswell, 2001; Wielgus et al., 2001). By doing so, demographic parameters remain the same and the only information that is lost is the number of individuals belonging to life stages that were collapsed (Caswell, 2001). A reduced matrix provides a simpler model while maintaining the biological integrity of a full stage-structured model it is issued from. Hence it allows focusing on life stages easy to monitor and manage. We showcase the approach using a case study on wolf population dynamics.

2. Materials and methods

2.1. A four-stage model reflecting wolf social organization

The wolf (*Canis lupus*) is a social species living in packs. A pack is a breeding unit, generally composed of a dominant male and a dominant female (the alpha pair) – the only pair of breeders – and their offspring of several generations. When juveniles reach their complete sexual maturity between 1 and 3 years of age, they tend

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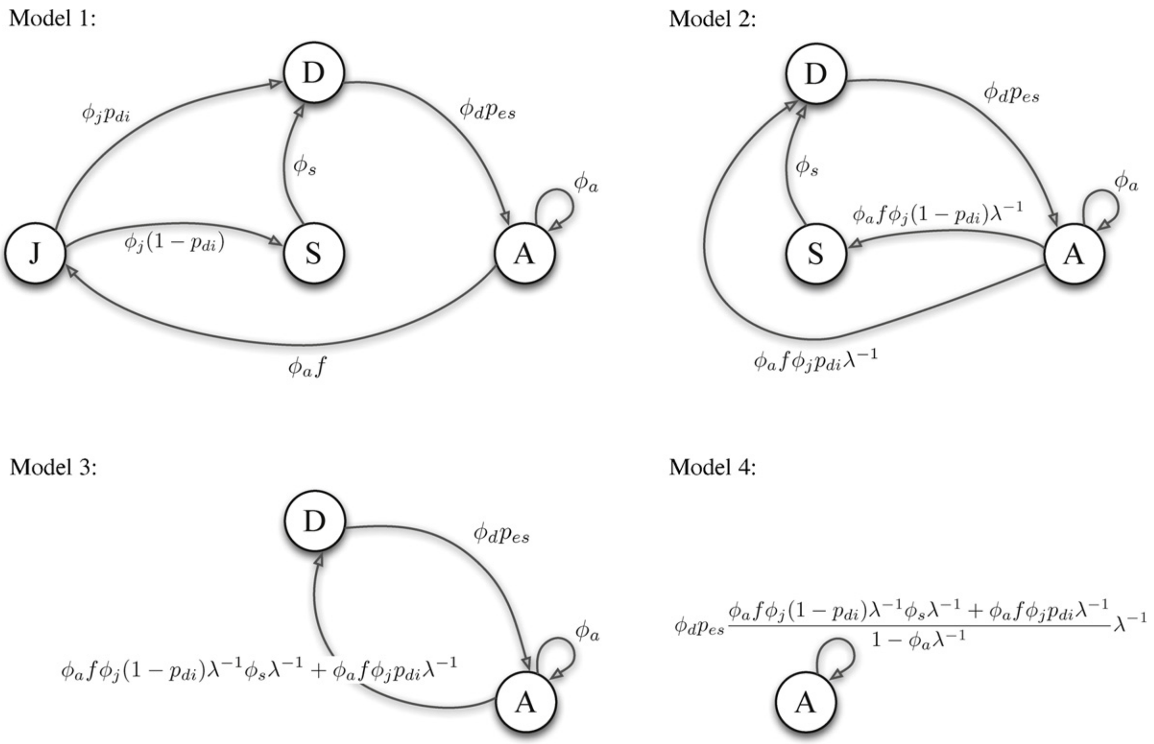

Fig. 1. Complete wolf life cycle graph of model 1, structured in 4 stages (J for juveniles, D for dispersers, S for subordinates and A for alpha) and *z*-transformed life cycle graphs in models 2, 3 and 4. Parameters notations are: *f* for fertility rate; φ_j, φ_d, φ_s and φ_a, respectively, for survival rate of juveniles, dispersers, subordinates and alphas, p_{di} and p_{es} for the probability of dispersing and of establishing a new pack and finally λ for asymptotic growth rate.

to disperse and to establish a new pack in another territory. In the present study, we considered a female-only pre-breeding model organized in four stages: juveniles, dispersers, subordinates and alphas (see model 1 in Fig. 1). Only the alpha female breeds, producing a single litter of pups every year. Those pups later become juveniles, which may not be fully sexually mature and will either disperse or become subordinates. After reaching sexually maturity, individuals disperse and look for a mate to establish a new pack (Mech and Boitani, 2003). Subordinates consist of sexually mature individuals that have not dispersed yet and are inhibited from breeding by the alpha's presence (Zimen, 1975). As most individuals disperse within 3 years, there are few subordinates above that age. For simplicity we assume that an alpha never looses its status and that all subordinates disperse before 3 years. We also assume that subordinates never directly transition to being an alpha because subordinates rarely become dominant in their natal pack.

2.2. Model calibration

Our model has four parameters that allow individuals to move from one stage to another: survival and dispersal probabilities, per capita fertility rate of female alpha and probability to establish a new pack. We run simulations over a mortality gradient ranging from 0 to 0.8 with an increment of 0.01 (Appendix 1). For each value of the mortality gradient, we run 10,000 Monte Carlo iterations in which survival probabilities are drawn in a normal distribution with a mean equal to the complementary of mortality rate and a standard deviation (SD) of 0.1. This value reflects uncertainty in survival and is estimated from a capture–recapture analysis on the French wolf population (Cubaynes et al., 2010). Because most wolf surveys estimate individual mean survival whatever their social status is, we follow the same approach in our simulations and give the same value to survival of different stages (Mech and Boitani, 2003; Fuller, 1989). We also run supplementary simulations with the more biologically realistic assumption of survival rate differing across stages (MacNulty et al., 2009) and find that our conclusions are not affected by this assumption (Appendix 2). In these simulations, for each step of the mortality gradient, we investigate different survival rate of juveniles and dispersers, always by setting them at a lower rate of the alpha survival. Per capita fertility rate (*f*) is the average number of births per breeder and per year. Since our model includes only females, *f* is set to the average litter size divided by 2. Empirical studies on wolf populations suggest that litter size varies from 4 to 9 pups (Mech and Boitani, 2003; Fuller, 1989; Miller et al., 2002; Webb et al., 2011). We therefore draw fertility rate from a uniform distribution varying from 2 to 4.5. Annual dispersal rate (p_{di}) in natural populations generally varies between 0.10 and 0.40 (Mech and Boitani, 2003; Fuller, 1989; Webb et al., 2011), and 10,000 values of this parameter are drawn from a uniform distribution between 0.1 and 0.4. Dispersal is usually regarded as a single individual looking for a mate in a buffer zone from 5 to 70 km outside the territory boundaries (Fuller, 1989). Beyond this range, individuals are regarded as emigrants and below as transients still belonging to the pack (Messier, 1985). Solitary wolves that survived but did not manage to establish a new pack are regarded as emigrants having left the population. Most of wolf studies using radio-telemetry data show that between 0 and 25% of the wolf population manage to settle new packs each month (Fuller, 1989; Keith et al., 1983). Averaging this estimation on the year and for the disperser population only, we set the pack establishment parameter p_{es} to vary uniformly between 0.3 and 0.7.

2.3. Deterministic structure of the four-stage model as the basis for reduction

First, we consider a deterministic version of the four-stage model described above (model 1) as the framework for application of transformation rules for life-cycle graphs (Caswell, 2001; e.g., Chapron et al., 2008; Wielgus et al., 2001). The population dynamics follows an exponential growth via a discrete-time Markov chain model (Heppell et al., 2000) formalized as $N_{t+1} = AN_t$ where N_t and N_{t+1} are, respectively, vectors of abundance in each stage at time t and $t + 1$ and A is the stage projection matrix representing the wolf life cycle:

$$A = \begin{bmatrix} 0 & 0 & 0 & f \cdot \varphi_a \\ \varphi_j \cdot p_{di} & 0 & \varphi_s & 0 \\ \varphi_j \cdot (1 - p_{di}) & 0 & 0 & 0 \\ 0 & \varphi_d \cdot p_{es} & 0 & \varphi_a \end{bmatrix}$$

where φ_a, φ_j, φ_d and φ_s are the alpha, juvenile dispersers and subordinates survival probabilities.

2.4. The z-transformed method for reduced life cycle graphs

Before reducing a life cycle, the model needs to be z-transformed, which consists in multiplying λ^{-1} to parameters of a transition from one stage to another where λ is the asymptotic population growth rate, calculated from the dominant value of the eigenvector of the deterministic projection matrix of model 1 (Heppell et al., 2000). Caswell's characteristic equation states that the determinant of a z-transformed matrix for reduced life cycle is equal to 0. In other words, the sum of all life cycle loops must be equal to 1, with a loop being a path starting from one stage and going back to that same stage.

For a stage-structured matrix model the characteristic equation can be formulated as

$$\sum_i L(i) = 1$$

with $L(i)$ standing for the ith loop of the z-transformed life cycle graph.

For instance in model 1, there are 3 loops, and any of these 3 are disjoint since they are all going through the alpha state:

$$L(1) = \varphi_a \cdot \lambda^{-1}$$

$$L(2) = p_{di} \cdot \varphi_j \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-3}$$

$$L(3) = ((1 - p_{di}) \cdot \varphi_j \cdot \varphi_d \cdot \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-4})$$

The exponent of the inverse of the asymptotic growth rate in each loop reflects how many years are required for an individual to go from one stage to another. In our case, a four-stage z-transformed model must verify:

$$\begin{aligned} &\varphi_a \cdot \lambda^{-1} + p_{di} \cdot \varphi_j \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-3} + (1 - p_{di}) \cdot \varphi_j \cdot \varphi_d \cdot \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-4} = 1 \\ &\varphi_a + p_{di} \cdot \varphi_j \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-2} + (1 - p_{di}) \cdot \varphi_j \cdot \varphi_d \cdot \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-3} = \lambda \\ &p_{di} \cdot \varphi_j \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-2} + (1 - p_{di}) \cdot \varphi_j \cdot \varphi_d \cdot \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-3} = \lambda - \varphi_a \end{aligned}$$

which is equivalent to:

$$\frac{p_{di} \cdot \varphi_j \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-2} + (1 - p_{di}) \cdot \varphi_j \cdot \varphi_d \cdot \varphi_d \cdot p_{es} \cdot \varphi_a \cdot f \cdot \lambda^{-3}}{\lambda - \varphi_a} = 1 \qquad (1)$$

2.5. Reduction of the wolf life cycle from a four-stage model to a one-stage model

The reduction method is similar to the 'signal flow graph' method (Mason, 1953), in which we remove some categorical variable in a matrix model while preserving all its dynamic properties, in this case the asymptotic growth rate. We added uncertainty in parameter estimates to the deterministic four-stage model (model 1) and we successively reduced the life cycle stage by stage.

First, a three-stage model is considered with the juvenile stage removed (see model 2 in Fig. 1). This model accounts for the direct transition from the alpha stage to either the subordinates stage with probability of $f \cdot \varphi_a \cdot \varphi_j \cdot (1 - p_{di}) \cdot \lambda^{-1}$ or to the disperser stage with probability of $f \cdot \varphi_a \cdot \varphi_j \cdot p_{di} \cdot \lambda^{-1}$.

The following reduced model is built from the three-stage reduced model, now with the subordinate stage collapsed (see model 3 in Fig. 1). We obtained a two-stage model describing abundance of dispersers and alphas only. Individuals go directly from the alpha stage to the disperser stage with transition probability $f \cdot \varphi_a \cdot \varphi_j \cdot \varphi_s \cdot (1 - p_{di}) \cdot \lambda^{-2} + f \cdot \varphi_a \cdot \varphi_j \cdot p_{di} \cdot \lambda^{-1}$.

The last and most reduced model accounts only for the number of female alphas. The dynamics within this single stage model reflects the temporal dynamic of established packs (model 4 in Fig. 1). It is obtained by multiplying the expression for the transition between alpha and dispersers with the expression for the transition between disperser and alpha. The self-loop standing for the surviving alpha is reduced by dividing the total expression by $1 - \phi_a \cdot \lambda^{-1}$, which give an asymptotic growth rate of

$$\lambda = [\phi_a \cdot f \cdot \phi_s \cdot \phi_j \cdot (1 - p_{di}) \cdot p_{di} \cdot \lambda^{-2} + \phi_a \cdot f \cdot \phi_j \cdot p_{di} \cdot \lambda^{-1}] \cdot \left[\frac{\phi_d \cdot p_{es} \cdot \lambda^{-1}}{1 - \phi_a \cdot \lambda^{-1}}\right] \qquad (2)$$

Now multiplying both sides by λ^{-1} leads to Eq. (1), meaning that after successive stages being reduced, our transformed model still solves Caswell's characteristic equation.

2.6. Model validation

We compared model results to check that the matrix reduction did not affect population dynamics with regards to the asymptotic growth rate (Fig. 2). To do so, we calculated the median and 95% confidence interval of the exponential rate of increase obtained from the 10,000 simulations as a function of mortality rate (Fig. 2, Appendix 1). We also validate the accuracy and reliability of reducing matrix by checking that population dynamics did not differ between our models by comparing the median exponential rate of increase of the full and reduced model calculated with different survival rates across stages (Appendix 2).

To explore how well the models fit to empirical data, we graphically explored the outputs obtained with stage-invariant survival rates, and overlaid empirical rate of increase observed in many wolf populations given their estimated mortality found in the literature. We choose this representation first because mortality and growth rate are two demographic parameters common to wolf studies. Second, they are both acknowledged to be good indicators for assessing the species conservation status (Marescot et al., 2011). Empirical data were extracted from the wolf monograph by Fuller (1989) and updated with other wolf studies summarized in Mech and Boitani (2003). We also added a recent estimate of the rate of increase of the wolf population in the French Alps (Marescot et al., 2011) (Table 1). We performed a Kolmogorov test to statistically evaluate how well the models fit the data (Quinn and Keough, 2002).

3. Results

All models adequately represented wolf population dynamics. The asymptotic growth rate followed a decreasing trend along the mortality gradient and which was identical between full and reduced models and so, whether survival rate differed or not across stage (Fig. 2, Appendix 2). Asymptotic growth rate calculated from the stage model and its reduced derivatives encompass all data except one data point located at the extreme boundary of the mortality gradient. This dataset is for the East-central Yukon population that exhibited a rate of increase of −0.03 for a mortality rate of 0.60 (Hayes et al., 1991) and is beyond the upper limit of models predictions. Besides this population, most of the data points are close to

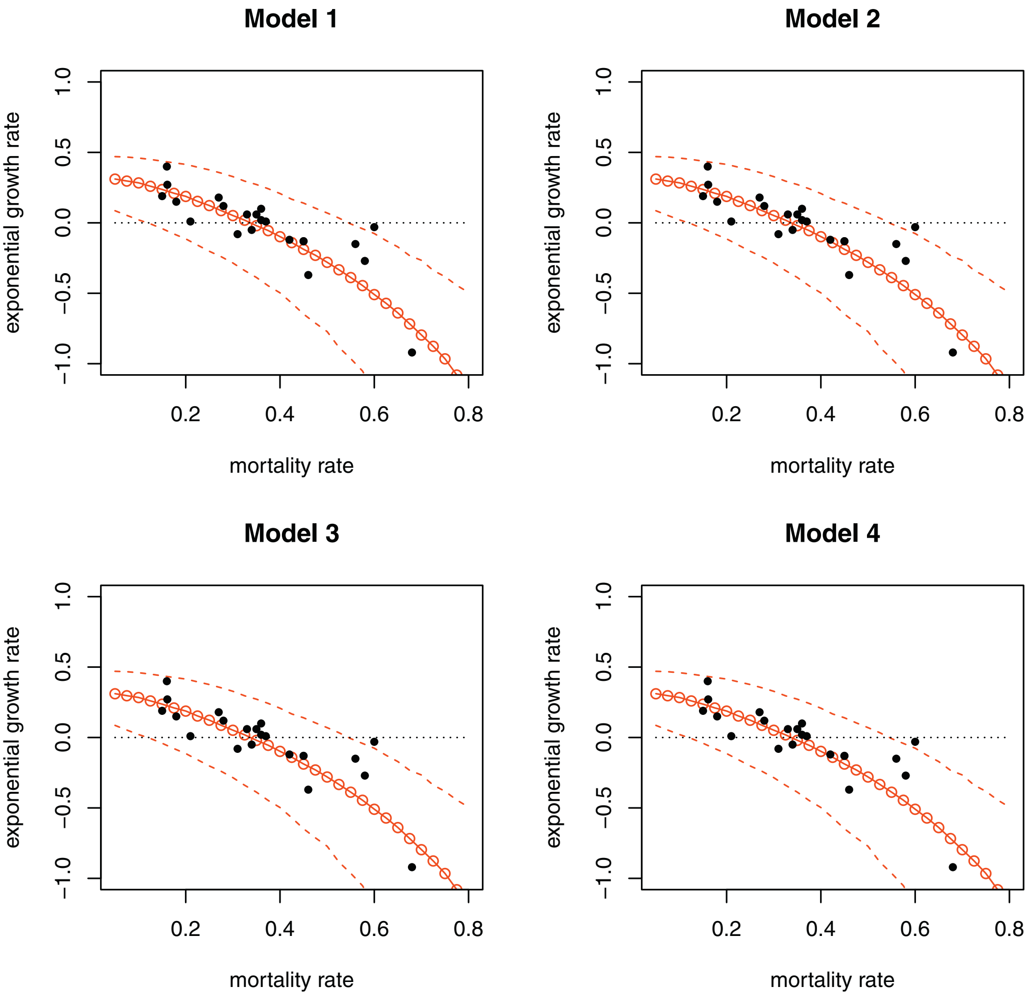

Fig. 2. Median exponential growth rate (red circles) and 95% confidence intervals, calculated in each model as a function of mortality rate and fitted to empirical data (black points) obtained mostly in Fuller (1989) review of North American wolf populations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 1
Empirical data and model results of the exponential rate of increase used for the Kolmogorov test as a function of mortality rates found in the literature.

Mortality rate	Median exponential rate of increase	Exponential rate of increase in empirical data	References[a]	Population
0.15	0.237	0.190	Fuller and Keith (1980)	Northeastern Alberta
0.16	0.227	0.400	Hayes and Harestad (2000)	East-central Yukon
0.161	0.229	0.271	Marescot et al. (2011)	French Alps
0.18	0.206	0.150	Wydeven et al. (1995)	Northern Wisconsin
0.21	0.176	0.010	Peterson (1998)	Isle Royale Michigan
0.27	0.094	0.180	Mech et al. (1998)	Denali park Alaska
0.28	0.086	0.120	Fritts and Mech (1981)	Northwestern Minnesota
0.31	0.039	−0.080	Berg and Kuehn (1982)	North central Minnesota
0.33	0.010	0.060	Peterson et al. (1984)	Kenai Peninsula Alska
0.34	−0.001	−0.050	Peterson and Page (1988)	Isle Royale Michigan
0.35	−0.022	0.060	Messier (1985)	Southwestern Quebeck
0.36	−0.033	0.020	Fuller (1989)	North Central Minnesota
0.36	−0.037	0.100	Fuller (1989)	North Central Minnesota
0.37	−0.050	0.010	Forbes and Theberge (1995)	Algonquin Park Ontario
0.42	−0.135	−0.120	Mech (1977, 1986)	North esatern Minnesota
0.45	−0.184	−0.130	Ballard et al. (1997)	Northwestern Alaska
0.45	−0.186	−0.130	Ballard et al. (1987)	South-central Alaska
0.46	−0.202	−0.370	Gasaway et al. (1983)	Interior Alaska
0.56	−0.404	−0.150	Carbyn (1980)	Southwestern Manitoba
0.58	−0.456	−0.270	Ballard et al. (1997)	Northwestern Alberta
0.6	−0.504	−0.030	Hayes et al. (1991)	Southern Yukon
0.68	−0.723	−0.920	Bjorge and Gunson (1983)	Northwestern Alberta

References cited here are issued from Table 6.8 of Fuller et al. in chapter 6 of Mech and Boitani (2003); from Fuller (1989) and from Marescot et al. (2011).

the curve representing the median exponential rate of increase. In the Kolmogorov goodness-of-fit test the null hypothesis assuming that median exponential rates of increase of a model do not differ from the ones observed in natural populations was rejected neither in the original four-stage model ($D = 0.1667$, p-value = 0.799; Table 1) nor in the reduced models that lead to the same values of asymptotic growth rates.

4. Discussion

4.1. Interpretation of results

Matrix reduction does not affect population trends since asymptotic growth rate remains the same as the juvenile, subordinate and disperser stages are successively removed from the model. Reducing a population matrix model is allowed only on a z-transformed life cycle graph for which the characteristic equation must be equal to 1 (Caswell, 2001). We perform reduction on an un-transformed graph because in our particular model starting reduction on a transformed graph or un-transformed graph was equivalent (see Eqs. (1) and (2)). When the model is fully reduced, the single loop of the alpha-only model corresponds to the asymptotic growth rate of the full un-transformed model (Eq. (2)). Hence in our specific model, multiplying the transition parameters by λ^{-1} before reduction on the full model, or after reduction on the one-stage model, is equivalent and solves the characteristic equation. We emphasize that such simplification would not be possible on a stage-structured model with disjoint loops. For instance, if emigration was not considered, the surviving dispersers that failed in settling a pack would remain in the disperser stage and because such self loop would be disjointed with the alpha self loop our approach would not be feasible.

We found that our simple reduced stage structured model adequately fits the empirical data even though it required less data than in a full age-structured model (Miller et al., 2002) or in an individual-based model (Chapron et al., 2003; Pitt et al., 2003). Our model predictions along mortality gradient covered all empirical data except the southern Yukon wolf population. We offer two explanations for this discrepancy. First, our matrix models did not account for harvest and the Southern Yukon wolf population experienced one of the strongest harvest pressures amongst the data considered (40% of the population was harvested through culling corresponding to 67% of the total mortality rate) (Hayes et al., 1991). Harvest can lead to a temporary increase of the population growth rate by decreasing competition and favouring pup production and survival, which can explain why this population is above the 95% confidence interval of models predictions (Fuller, 1989; Keith, 1983). Second, this actual population exhibits a high immigration rate, a demographic process that we chose to ignore for the sake of model simplicity.

4.2. Management implications

Evaluating the conservation status of large carnivore populations is a real challenge given the difficulty of surveying these species as well as the social and economic consequences of their colonization. The limited field data impedes a precise knowledge of their demography. In many cases of tense social contexts and serious threats of population extinction risks, important decisions need to be made quickly. These decisions often preclude using stage-structured models to evaluate the consequences of management strategies on population trends and status (DeMaso et al., 2011; Heppell et al., 2000). This is unfortunate because such models are well-suited to inform conservation decisions due to their conceptual simplicity, flexibility, ease of computation, and their ability to be directly parameterized from empirical data (Wisdom et al., 2000). However, their implementation requires calibration with demographic data that are very difficult to estimate especially for elusive, wide ranging, long-live and social species exhibiting multiple stages difficult to observe (Crouse et al., 1987; Brault and Caswell, 1993). Thus, reducing the life cycle of species is a recommended approach to deal problem of studying species with limited count data. It allows focusing on those life stages detectable *in situ* or quantifiable via field, laboratory or computing techniques, thereby allowing more efficient allocation of management and survey effort. It allows mostly focusing on which stage management actions must aim at. For instance, regarding wolf management, it might be relevant to consider a two stage model (individuals in packs and dispersers) and thus investigated the impact of removing a pack members comparing to dispersers. Because reduced models only loose information on number of individuals in particular stages and not on probabilities of transition between these stages, they are consistent with and show the exact same resulting dynamic than a complete stage model.

Optimization methods such as stochastic dynamic programming provide powerful tools for solving the optimal strategy that best achieves management objectives (Chadès et al., 2011). Considering a demographic model with few life stages when coupled with an optimization model would help to avoid a common problem in dynamic programming known as the ‘curse of dimensionality’. This difficulty arises when many state variables (e.g., life stages) are included in the model and the dimension of the state space therefore increases exponentially (Walters and Hilborn, 1978). Despite the many conveniences reduction model brings within the decision process, few matrix models have used reduction so far, and even though they are applied to species threatened of extinction, they are not dealing with social species like wolves (see Chapron et al., 2008 on tigers and Wielgus et al., 2001 on bear populations). In the case of the wolf, keeping only the breeder stage produces a model based on pack dynamic only, which can be relevant for managers. Following the population in terms of number of packs (i.e., number of alpha females) instead of number of individuals in each stage can adequately document the spatial growth of a colonizing population without corrupting estimates of the overall numeric growth. This simple approach of reducing the wolf life cycle can provide simple models to implement in a an adaptive management framework by keeping only the stage measurable in the field and regarded as important in terms of the species conservation (Varley and Boyce, 2006).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.02.017.

References

Birt, A., Feldman, R.M., Cairns, D.M., Coulson, R.N., Tchakerian, M., Xi, W.M., Guldin, J.M., 2009. Stage-structured matrix models for organisms with non-geometric development times. Ecology 90, 57–68.

Brault, S., Caswell, H., 1993. Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74, 1444–1454.

Carroll, C., Phillips, M.K., Schumaker, N.H., Smith, D.W., 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program using dynamic spatial models. Conservation Biology 17, 536–548.

Caswell, H., 2001. Matrix Population Models. Sinauer Associates, Inc., Sunderland, MA, USA.

Chadès, I., Martin, T.G., Nicol, S., Burgman, M.A., Possingham, H.P., Buckley, Y.M., 2011. General rules for managing and surveying networks of pests, diseases, and endangered species. Proceedings of the National Academy of Sciences 20, 8323–8328.

Chapron, G., Legendre, S., Ferriere, R., Clobert, J., Haight, R.G., 2003. Conservation and control strategies for the wolf (*Canis lupus*) in western Europe based on demographic models. Comptes Rendus Biologies 326, 575–587.

Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legendre, S., Clobert, J., 2008. The impact on tigers of poaching versus prey depletion. Journal of Applied Ecology 45, 1667–1674.

Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for the loggerhead sea turtle (*Caretta caretta*) and implications for conservation. Ecology 68, 1412–1423.

Cubaynes, S., Pradel, R., Choquet, R., Duchamp, C., Gaillard, J.M., Lebreton, J.-D., Marboutin, E., Miquel, C., Reboulet, A.M., Poillot, C., Taberlet, P., Gimenez, O., 2010. Importance of accounting for detection heterogeneity when estimating abundance: the case of French wolves. Conservation Biology 24, 621–626.

DeMaso, S.J., Grant, W.E., Hernández, F., Brennan, L.A., Silvy, N.J., Wu, X.B., Bryant, F.C., 2011. A population model to simulate northern bobwhite population dynamics in southern Texas. Journal of Wildlife Management 75, 319–333.

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs 105, 1–41.

Gimenez, O., Lebreton J.-D., Gaillard J.-M., Choquet R., Pradel R., 2012. Estimating demographic parameters using hidden process dynamic models. Theoretical Population Biology, doi:10.1016/j.tpb.2012.02.001.

Haight, R.G., Travis, L.E., Nimerfro, K., Mech, L.D., 2002. Computer simulation of wolf-removal strategies for animal damage control. Wildlife Society Bulletin 30, 844–852.

Hayes, R.D., Baer A.M., Larsen D.G., 1991. Population dynamics and prey relationships on exploited and recovering wolf population in the southern Yukon. Yukon Territory, Fish and Wildlife Branch, Department of Renewable Resources, Final report TR-91-1-67pp.

Heppell, S.S., Crouse, D.T., Crowder, L.B., 2000. Using matrix models to focus research and management efforts in conservation. In: Ferson, S., Burgman, M.A. (Eds.), Quantitative Methods for Conservation Biology. Springer, New York, pp. 148–168.

Keith, L.B., 1983. Population dynamics of wolves. In: Carbyn, L.N. (Ed.), Wolves in Canada and Alaska. Report Series 45. Canadian Wildlife Service, Ottawa, Canada, pp. 66–77.

Marescot, L., Pradel, R., Duchamp, C., Cubaynes, S., Marboutin, E., Choquet, R., Miquel, C., Gimenez, O., 2011. Capture-recapture population growth rate as a robust tool against detection heterogeneity for population management. Ecological Applications 21, 2898–2907.

Mason, S.J., 1953. Feedback theory: some properties of signal flow graphs. Proceedings of the IRE 44, 920–926.

Mech, L.D., Boitani, L., 2003. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago.

Messier, F., 1985. Social organisation, spatial distribution and population density of wolves in relation to moose density. Canadian Journal of Zoology 63, 1068–1077.

Miller, D.H., Jensen, A.L., Hammill, J.H., 2002. Density dependent matrix model for gray wolf population projection. Ecological Modelling 151, 271–278.

MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R., Packer, C., 2009. Predatory senescence in ageing wolves. Ecology Letters 12, 1347–1356.

Pitt, W.C., Box, P.W., Knowlton, F.F., 2003. An Individual-based model of canid populations: modeling territoriality and social structure. Ecological Modelling 166, 109–121.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.

Varley, N., Boyce, M.S., 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. Ecological Modelling 193, 315–339.

Walters, C.J., Hilborn, R., 1978. Ecological optimization and adaptive management. Marine Environmental Research 9, 157–188.

Webb, N.F., Allen, J.R., Merill, E.H., 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Canadian Journal of Zoology 89, 744–752.

Wielgus, R.B., Sarrazin, S., Ferriere, R., Clobert, J., 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. Biological Conservation 98, 293–303.

Wilson, E.O., 1975. Sociobiology: The New Synthesis. Harvard University Press, Cambridge, MA.

Wisdom, M.J., et al., 2000. Life-stage simulation analysis: estimating vital rate effects on population growth for conservation. Ecology 81, 628–641.

Zimen, E., 1975. Social dynamics of the wolf pack. In: Fox, M.V. (Ed.), The Wild Canids-Their Systematics, Behavioural Ecology and Evolution. Van Nostrand Reinhold, New York, p. 1975.