A trans-national monarch butterfly population model and implications for regional conservation priorities

KAREN OBERHAUSER,[1] RUSCENA WIEDERHOLT,[2] JAY E. DIFFENDORFER,[3] DARIUS SEMMENS,[3] LESLIE RIES,[4] WAYNE E. THOGMARTIN,[5] LAURA LOPEZ-HOFFMAN[2] and BRICE SEMMENS[6]   [1]Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St Paul, Minnesota, U.S.A., [2]School of Natural Resources and the Environment and Udall Center for Studies in Public Policy, The University of Arizona, Tucson, Arizona, U.S.A., [3]U.S. Geological Survey, Geosciences and Environmental Change Science Center, Denver, Colorado, U.S.A., [4]Department of Biology, Georgetown University, Washington, District of Columbia, U.S.A., [5]U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, U.S.A. and [6]Scripps Institution of Oceanography, University of California, La Jolla, California, U.S.A.

Abstract. 1. The monarch has undergone considerable population declines over the past decade, and the governments of Mexico, Canada, and the United States have agreed to work together to conserve the species.

2. Given limited resources, understanding where to focus conservation action is key for widespread species like monarchs. To support planning for continental-scale monarch habitat restoration, we address the question of where restoration efforts are likely to have the largest impacts on monarch butterfly (*Danaus plexippus* Linn.) population growth rates.

3. We present a spatially explicit demographic model simulating the multi-generational annual cycle of the eastern monarch population, and use the model to examine management scenarios, some of which focus on particular regions of North America.

4. Improving the monarch habitat in the north central or southern parts of the monarch range yields a slightly greater increase in the population growth rate than restoration in other regions. However, combining restoration efforts across multiple regions yields population growth rates above 1 with smaller simulated improvements in habitat per region than single-region strategies.

5. *Synthesis and applications:* These findings suggest that conservation investment in projects across the full monarch range will be more effective than focusing on one or a few regions, and will require international cooperation across many land use categories.

Key words. Bayesian stage-based matrix model, conservation prioritisation, *Danaus plexippus*, management strategies, population dynamics.

Introduction

The area occupied by overwintering eastern North American monarch butterflies has been measured since the winter of 1993–1994. Since then, this area has declined at a rate averaging ∼0.89 ha/year (or about 38–44 million monarchs/year, depending on assumptions about the density of monarch in the wintering sites; Solensky, 2004), with the lowest two population sizes recorded during the winters of 2013–2014 and 2014–2015 (Rendón-Salinas & Tavera-Alonso, 2015). These reports have precipitated a flurry of activity. In February 2014, monarchs were discussed at a meeting of the leaders of all three North American countries, resulting in a tri-national commitment to protect the species (Baker & Malkin, 2014). In June 2014, President Obama issued a memorandum calling for the restoration of pollinator and monarch habitat and the creation of a high-level U.S. Federal task force on pollinators (Office of Press Secretary, 2014). In August 2014, a coalition of non-governmental

Correspondence: Karen Oberhauser, Department of Fisheries, Wildlife and Conservation Biology, 2003 Upper Buford Circle, St. Paul, Minnesota 55108, U.S.A. E-mail: oberh001@umn.edu

organisations and citizens submitted a petition to the U.S. Fish and Wildlife Service (USFWS) to list the butterfly as a threatened species (Center for Biological Diversity *et al.* 2014). There is substantial year-to-year variation in monarch numbers, as illustrated by a return to 2010–2011 values in 2015–2016 (World Wildlife Fund-Mexico, 2016). Despite this recent uptick, monarchs face a high level of quasi-extinction risk (Semmens *et al.*, 2016, but see Flockhart *et al.*, 2015). In the U.S., funding is being amassed for conservation (e.g. National Fish and Wildlife Foundation, 2016), and Federal agencies are developing pollinator and monarch conservation action plans.

It is crucial to focus monarch habitat conservation and restoration efforts in areas where they will have the largest impact. However, ensuring that conservation efforts are efficiently directed is a challenge for monarchs because their geographical range is so large, and the geographical location of the population varies across seasons. The spatially explicit demographic model presented here addresses this need.

Spatial demographic models are essential tools for evaluating the relative efficacy of conservation measures aimed at particular life stages and habitats (Kareiva & Wennergren, 1995; Caswell, 2001). With the exception of Flockhart *et al.* (2015), who used an approach similar to ours (see below), previously-developed monarch population models have considered all breeding habitat together (Yakubu *et al.*, 2004), or modelled occupancy probability during the breeding season based on climatic and geographical variables (Flockhart *et al.*, 2013). Investigations of population declines and threats to monarchs have focused on assessing the potential impacts of climate on breeding and overwintering survival (Oberhauser & Peterson, 2003; Zalucki & Rochester, 2004; Batalden *et al.*, 2007; Zipkin *et al.*, 2012; Zalucki *et al.*, 2015a), as well as documenting a relationship between fecundity or monarch population size and breeding habitat loss (Pleasants & Oberhauser, 2013; Pleasants, 2015). Like that of Flockhart *et al.* (2015), the stage-based matrix model (Lefkovitch, 1965) presented here simulates the multi-generational annual cycle of the eastern monarch population. However, it includes more stages of the annual migratory cycle and slightly different parameter estimates.

Similar to the approach of Caswell (2001), this model allows for an examination of how different scenarios of conservation efforts could affect population viability by simulating effects of increasing survival, and migration and breeding success in different regions across the monarch's range.

Materials and methods

The matrix model considers adults overwintering in Mexico, the migration of overwintered adults to breeding grounds in the southern U.S., reproduction by these adults leading to the first generation of the year, movement of this first generation into the North Central and Northeastern breeding grounds (modeled separately), multiple cycles of reproduction in these two northern regions, and late summer/fall migration back to Mexico (Fig. 1). The model is fitted to overwintering population trends from 1993 to 2015. Because it is difficult to accurately estimate the number of monarchs during any stage of their migratory cycle, the area occupied by overwintering monarch colonies in central Mexico, where the vast majority of the population coalesces, is used as a proxy for population size (Brower *et al.*, 2012).

The model includes 34 parameters, summarised in Fig. 2 and Table 1. To balance reality and complexity, some transitions that are known to occur, but that are less important to monarch population dynamics, were not included [e.g. contributions of monarchs that breed in the southern U.S. throughout the winter (Batalden & Oberhauser, 2015; Satterfield *et al.*, 2015), and egg-laying by generation 1 females as they fly north in the spring (Malcolm *et al.*, 1987)].

To estimate the demographic parameters in the monarch annual cycle, informative priors (long-term population means and their associated uncertainty) were developed based on expert opinion elicited during in-person conversations (Sonia Altizer, Elizabeth Howard, Karen Oberhauser, John Pleasants, and Orley Taylor) and published or in review data (see Table 1). Because these priors needed to represent long-term means over broad spatial scales, and most existing data on parameter values are measured at a single location and over a short time scale, the in-person conversations with experts were structured to elicit both estimates of the parameters for which little or no data existed (e.g. migration survival) and long-term means and ranges for values for which data have limited spatial and temporal breadth. The legend for Table 1 lists the sources of parameters for which data existed and parameters for which values were based solely on expert elicitation. Elicitation of expert opinion to inform the prior distributions was conducted independent of, and before, modelling the species' demography. Expert estimates were buffered by tuning the model to the observed times series of winter population size estimates in Mexico and the total amount of egg production in the Midwest, allowing us to identify the suite of potential parameter values from which to select among the prior distributions. We elected not to use iterative elicitation because there are known biases that would need to be carefully accommodated for this method to have been used. For example, experts anchor on their initial estimate, leading to only conservative or partial revision when faced with new information (Phillips, 1964; Jacowitz & Kahneman, 1995).

Narrow ranges were assigned to the parameters for which we had more data and more expert certainty, and broader ranges to reflect higher uncertainty in other parameters (Table 1). Thus, the interval widths were mathematical reflections of the estimates elicited from the experts. As an example, several of the parameters were proportions p (e.g. survival). It is common to assume that the prior distribution for p is a beta distribution bounded between 0 and 1 (Walck, 2007). This beta distribution has two parameters, α and β, reflecting the shape and scale of the distribution (beta[α, β]). Quantifying expert opinion about p reduces to finding values for α and β. The experts provided point estimates for p which, when averaged, provide average values for α and β. They also provided lower and upper quartiles to their estimates, which, when treated as point estimates, provide the uncertainty in the beta distribution. Thus, prior distributions are a mix of individually elicited prior distributions, the average of which was the initial prior distribution. For all fecundity parameters, lognormal prior
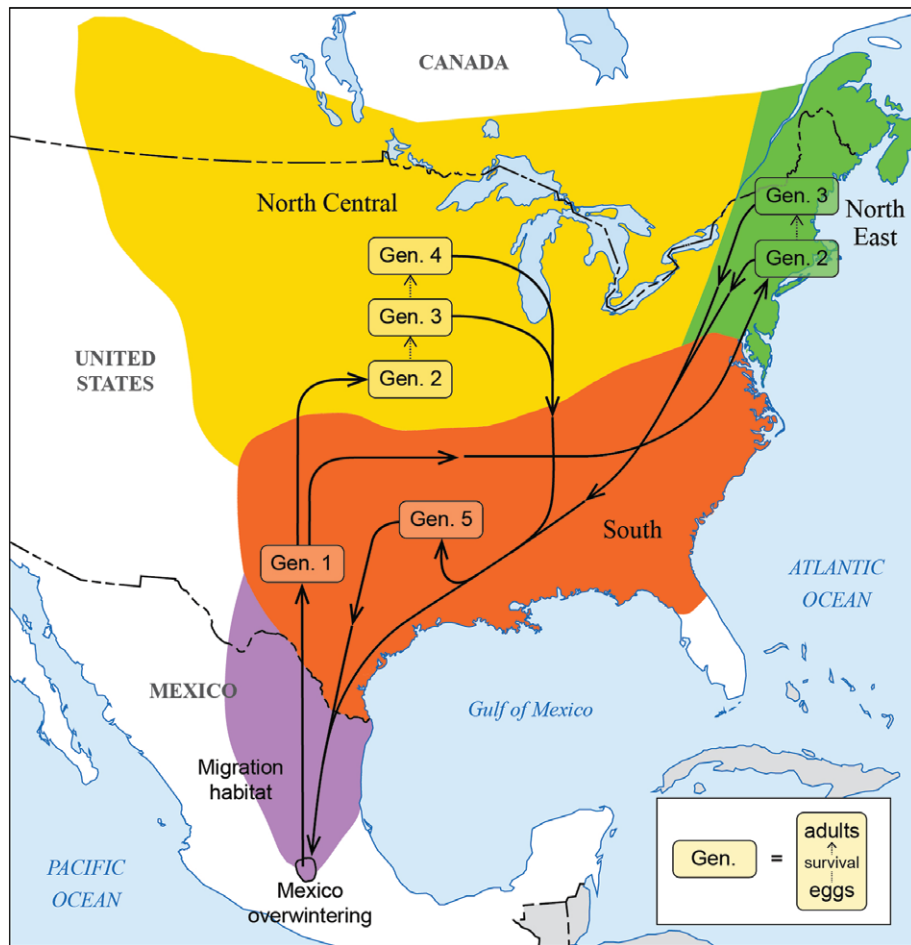
Fig. 1. Map of monarch butterfly annual migration in Eastern North America. Colours refer to regions that are treated separately in the model, and boxes and arrows refer to transitions (see Fig. 2 and Table 1).

distributions were used, and all survival proportion parameters, beta prior distributions were used (Walck, 2007). For the migration proportion parameters that involved three possible destinations (P2, P3, P5, and P6; see Table 1 and Fig. 2) Dirichlet prior distributions were used; a Dirichlet distribution is the multivariate generalisation of the beta distribution (Ng *et al.*, 2011). For all other migration proportion parameters, beta prior distributions were used (Walck, 2007).

The model accommodates the possibility that some late summer or early fall monarchs may arrive in the southern U. S. (where they may breed) or Mexico at the same time that other individuals are still breeding in the northern or southern U. S., respectively. As such, it includes parameters that 'hold' generations arriving in the south or Mexico before later generations; this is necessary because monarch generations are not synchronised, especially by the end of the summer. The model ensures that all generations involved in the fall migration undergo vital rates and migration in the same model time step by adding cells to the matrix with a value of 1. For ease of interpretation, these 'holding cells' are not illustrated in Fig. 2, but are included in Figure S3 (in Appendix S1).

Next, estimates of the monarch overwintering population size were used (1993–2015) from a Bayesian state-space first-order autoregressive model that produced estimates of the population size (Semmens *et al.*, 2016). This model used two different time series depicting temporal dynamics of the eastern migratory population of monarch butterflies: (i) the log of the total extent (ha) of overwintering forest area occupied in Mexico per year, as measured by the World Wildlife Federation-Mexico and the Monarch Butterfly Biosphere Reserve (MBBR) (Vidal *et al.*, 2014), and (ii) an estimate of the log of the total amount of egg production in the Midwest per year, using data from the Monarch Larva Monitoring Program (2015) (Pleasants & Oberhauser, 2013, estimates extended through 2014). Semmens *et al.* (2016) estimated values corrected for an observation error, but our analyses were also performed using the uncorrected values to assess the sensitivity of the model to this correction.

A Markov chain Monte Carlo approach calculated in R (MCMCpack package) (R Core Team, 2012) was used to calculate posterior probabilities for the parameters from 3 300 000 iterations after thinning the estimates by 1000 and removing the first 200 000 iterations, and used the Gelman–Rubin

Table 1. Transitions and parameters in matrix model (Fig. 2), with parameter prior distributions and baseline matrix model cell results.

Parameter(s) in matrix cells	Region of origin	Region of destination	Generation†	Season	Range of parameter prior distributions ‡	Mean of matrix cell posterior distribution (95% CI)
Winter survival and migration survival (S1 × S2)	MX	S	W	Winter/spring	S1: 0.6–0.8 S2: 0.1–0.6	0.214 (0.113–0.348)
Fecundity of overwintered females (F1)	S	S	1	Spring	F1: 100–250	172 (136–219)
Immature survival (S3)	S	S	1	Spring	S3: 0.01–0.025	0.0164 (0.0121–0.0219)
Proportion of gen1 that go to NC and migrate successfully (P1 × S4)	S	NC	1	Summer	P1: 0.7–0.9 S4: 0.6–0.9	0.612 (0.510–0.708)
Proportion of gen1 that go to NE and migrate successfully ((1−P1)×S5)	S	NE	1	Summer	P1: 0.7–0.9 S5: 0.5–0.8	0.123 (0.0770–0.183)
Fecundity of gen1 in NC (F2)	NC	NC	2	Summer	F2: 150–350	220 (157–308)
Immature survival of gen2 in NC (S6)	NC	NC	2	Summer	S6: 0.01–0.05	0.0267 (0.0154–0.0416)
Fecundity of gen2 in NC (F3)	NC	NC	3	Summer	F3: 150–350	221 (158–307)
Immature survival of gen3 in NC (S7)	NC	NC	3	Summer	S7: 0.002–0.05	0.00244 (0.0001–0.0091)
Proportion of gen3 that remains in NC × their fecundity (P2 × F4)	NC	NC	4	Summer	P2: 0.2–0.75 F4: 100–250	97.4 (35.3–162)
Proportion of gen3 that migrates from NC to Mexico and survives migration (P3 × S8)	NC	MX	3	Fall	P3: 0.1–0.6 S8: 0.6–0.8	0.237 (0.0485–0.509)
Proportion of gen3 that migrates to south and survives migration ((1−P2−P3)×S9))	NC	S	3	Fall	P2: 0.2–0.75 P3: 0.1–0.6 S9: 0.6–0.8	0.0500 (0.0010–0.276)
Immature survival of gen4 in NC (S10)	NC	NC	4	Summer	S10: 0.005–0.05	0.00623 (0.0001–0.0260)
Proportion of gen4 that migrates to Mexico and survives migration (P4 × S11)	NC	MX	4	Fall	P4: 0.85–0.99 S11: 0.7–0.8	0.697 (0.599–0.784)
Proportion of gen4 that migrates to south and survives migration ((1−P4)×S12)	NC	S	4	Fall	P4: 0.85–0.99 S12: 0.6–0.8	0.00663 (<0.00001–0.0492)
Fecundity of gen1 in NE (F5)	NE	NE	2	Summer	F5: 150–350	221 (156–309)
Immature survival of gen2 in NE (S13)	NE	NE	2	Summer	S13: 0.01–0.05	0.0269 (0.0160–0.0419)
Proportion of gen2 that stays in NE × their fecundity (P5 × F6)	NE	NE	3	Summer	P5: 0.6–0.8 F6: 150–350	172 (79.5–261)
Proportion of gen2 that migrates from NE to Mexico and survives migration (P6 × S14)	NE	MX	2	Fall	P6: 0.1–0.3 S14: 0.6–0.8	0.00570 (0.0001–0.0322)
Proportion of gen2 that migrates from NE to south and survives migration ((1−P5−P6)×S15)	NE	S	2	Fall	P5:0.3–0.9 P6: 0.01–0.4 S15: 0.6–0.8	0.0523 (0.0004–0.303)
Immature survival of gen3 in NE (S16)	NE	NE	3	Summer	S16: 0.01–0.05	0.0269 (0.0160–0.0413)
Proportion of gen3 that migrates from NE to Mexico and survives migration (P7 × S17)	NE	MX	3	Fall	P7: 0.5–0.8 S17: 0.06–0.08	0.0457 (0.0371–0.0548)
Proportion of gen3 that migrates from NE to south and survives migration ((1−P7)×S18)	NE	S	3	Fall	P7: 0.5–0.8 S18: 0.6–0.8	0.241 (0.172–0.320)
Fecundity of immigrants from NE and NC in the south (F7)	S	S	3 and 4	Fall	F7: 150–350	222 (159–309)
Immature survival of eggs in south in fall (S19)	S	S	3 and 4	Fall	S19: 0.001–0.05	0.00360 (0.0002–0.0166)
Proportion of individuals that migrate successfully from the south to Mexico (S20)	S	MX	3 and 4	Fall	S20: 0.6–0.8	0.757 (0.648–0.846)
Model parameter holding generations arriving early to south or Mexico so that all generations undergo vital rates and migration at same time step	S or MX	S or MX	2, 3, and 4	Fall	1	1

Parameter naming convention: S = survival, F = fecundity, P = proportion of population migrating. The W (Winter) 'generation' is not given a number because it can consist of multiple generations (see text for detail on how the model accommodated this biological reality). Starting with the population in Mexico, parameters of the same type are numbered sequentially. Matrix cell transitions that include parameters based solely on expert opinion are highlighted. Individual parameter values are included in SI.
MX, Mexico S, South; NE, North East; NC, North Central.
†Generation 1 refers to the first generation produced in a year (in the southern US by migrants from Mexico).
‡Sources for prior parameter values and ranges: Fecundity: Oberhauser, 1997; Immature survival: Borkin, 1982; Oberhauser *et al.*, 2001; Prysby, 2004; Calvert, 2004; Oberhauser, 2012; Nail *et al.*, 2015; De Anda & Oberhauser, 2015; Winter survival: Vidal and Rendón-Salinas 2014, Ries *et al.*, 2015; Migration survival, Transition probabilities to eastern and western breeding grounds, and Proportion of each generation that migrate vs. breed: expert conversation. Note that these ranges were identified as most likely, but that other values outside the range had non-zero probabilities.
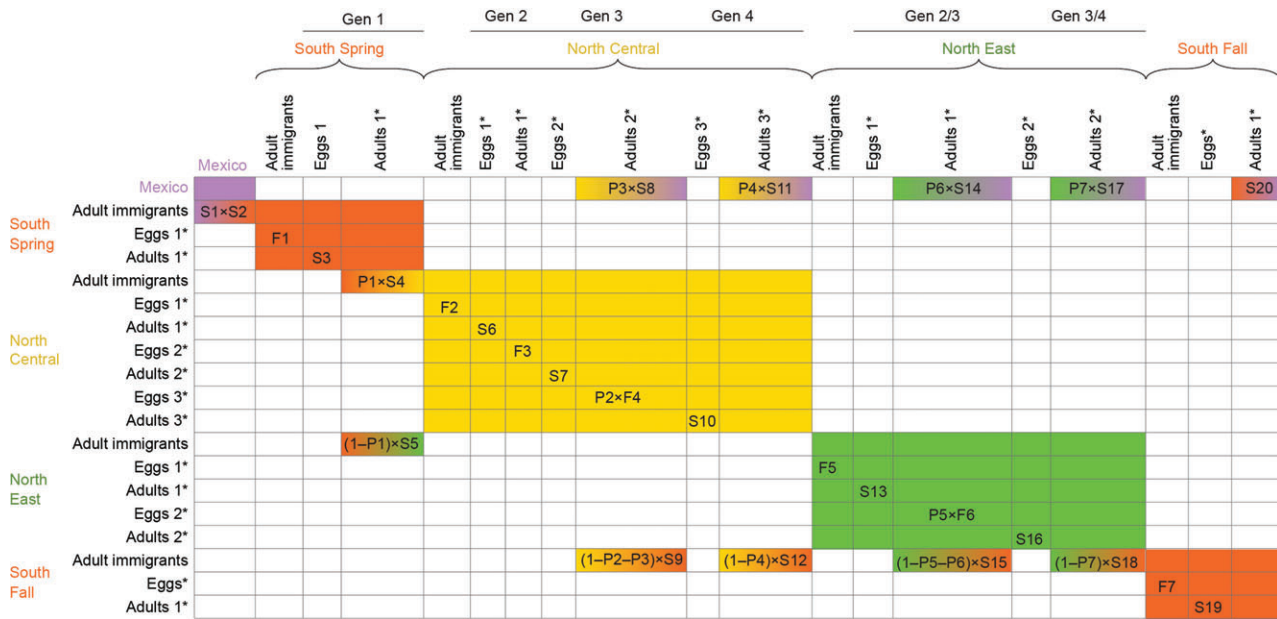
Fig. 2. Monarch butterfly matrix model. For explanations of transitions, see Table 1. Colours refer to transitions that occur regions illustrated in Fig. 1. For full matrix that includes holding cells (see text for more information), see Figure S3 in Appendix S1.

convergence diagnostic to assess model fit (Gelman & Rubin, 1992). The model accommodated a process error (or environmental variation) while finding combinations of parameters resulting in a population trajectory matching the long-term decline in the overwintering data and patterns in Midwestern egg production (see Table S3 in Appendix S1 for the full model code). It converged on all parameters except S2 (migration in the spring from Mexico to the southern U.S.). We assumed that the population is at a stable-stage distribution, such that trends in monarch abundance in Mexico directly reflect the asymptotic density-independent growth rate for the population (defined by the dominant eigenvalue of the transition matrix, λ). The basic statistical model is

$$M \times n_t = n_{t+1}$$

where M is the matrix, and n_t is the population vector at time t. This is repeated for 13 time steps to move through the annual cycle. At the 13th time step, the entire population is in the overwintering grounds. The population growth rate equals:

$$\lambda = n_{t+13} / n_t$$

Management scenario simulations

Using the model with the posterior parameter distributions (the 'baseline' model), we tested the effects of different management and conservation scenarios by simulating 11 scenarios representing various management actions (including no new actions) in different regions, or combinations of regions, relevant to the monarch life cycle (Table 2). Sensitivity analyses were performed for each model parameter and each matrix element (which could be combinations of parameters, Appendix S1) to

provide insight into the mechanisms driving the results of the scenario simulations. Because our demographic variables were measured in different units, we conducted elasticity analyses, which estimate the effect of a proportional change in vital rates on λ.

In the management scenarios, all of the parameters affected by each scenario were simultaneously increased until the mean λ exceeded 1. Draws from the posterior distribution were multiplied by $1 + p/100$ (where p = the per cent increase needed to achieve a stable population). For example, improving habitat availability and suitability in the North Central region (scenario 7) could increase parameters F2, F3, F4 (fecundity parameters), and S6, S7, S10 (survival parameters). For the breeding scenarios (scenarios 6–8), alternative scenarios were tested in which we assumed only fecundity was affected [e.g. only fecundity of generation 1 in the North Central (F2), and not immature survival of generation 2 (S6)], or that both fecundity and offspring survival were affected. While it is often the case that there is overlap between actions improving the suitability of a given habitat for both breeding and migration, the phenological availability of plant species will affect the value of the habitat for these two seasonal phases. Additionally, migration steps in the model involve movement from one region to another, and thus actions across regions (for example, parameter S8 is survival from the north central region to Mexico, and will be affected by actions in our north central, south, and Mexico regions). Thus, we opted to keep breeding and migratory scenarios separate. Three combination scenarios (9, 10, 11) using the two- (scenarios 6 and 7) and four- (scenarios 2, 3, 6, 7) most effective management scenarios were also included, as well as all seven management scenarios combined (2–8). In these combination scenarios, each of the parameters was increased by 1%. In all

Table 2. Management scenario descriptions

Scenario	Parameters increased	Mean λ	% draws with $\lambda < 1$	% increase in parameters required to achieve stable population
1. Baseline. No management	NA	0.957	71.4	NA
2. MX overwintering. Increase the quality and quantity of overwintering forests in Mexico	S1, S2	1.01	45.1	3%
3. Migration in MX and southern US. Increase nectar availability, decrease insecticide use, increase the amount of habitat in MX and southern US.	S2, S8, S11, S14, S17, S20	1.01	45.1	3
4. Migration in the North Central US. Increase nectar availability, decrease insecticide use, increase the amount of habitat in the North Central US.	S4, S8, S9, S11, S12	1.01	48.7	5
5. Migration in the North East US. Increase nectar availability, decrease insecticide use, increase the amount of habitat in the North East US.	S5, S14, S15, S17, S18	1.00	49.9	5
6. Breeding in the Southern US. Increase milkweed and nectar availability, decrease insecticide use in the southern US.	F1, S3, F7, S19	1.01	46.7	2
6a. Breeding in the Southern US – fecundity only. Management actions in 6 only increase fecundity	F1, F7	1.01	47.1	4
7. Breeding in the North Central US. Increase milkweed and nectar availability, decrease insecticide use, in the North Central US.	F2, S6, F3, S7, F4, S10	1.01	48.6	2
7a. Breeding in the North Central US – fecundity only. Management actions in 7 only increase fecundity.	F2, F3, F4	1.01	48.7	4
8. Breeding in North East region. Increase milkweed and nectar availability, decrease insecticide use in the North East US.	F5, S13, F6, S16	1.01	46.5	3
8a. Breeding in North East region – fecundity only. Management actions in 8 only increases fecundity.	F5, F6	1.00	50.5	5
Combinations of scenarios				
9. Combination of scenarios 6, 7		1.01	47.6	1
10. Combination of scenarios 2, 3, 6, 7		1.04	34.1	1
11. Combination of all management scenarios		1.07	20.7	1

scenario analyses, the resulting mean lambda, λ, and the per cent of model draws that were decreasing ($\lambda < 1$) are reported.

Results

The baseline model (with both the overwintering population data and our prior parameter estimates) was consistent with observed declines in monarch populations (Brower *et al.*, 2012; Semmens *et al.*, 2016) with declines in 71.4% of model draws (Table 2, Table S1 in Appendix S1). When the uncorrected data for overwintering colony size and egg production were used, the estimate was still < 1, but slightly higher (mean $\lambda = 0.984$, with 58.5% of model draws <1).

Parameter-specific sensitivity and elasticity

The sensitivity analyses indicated small individual contributions of any parameter to population growth (Appendix S1), which is expected, given the number of parameters that were used. Migration survival in the North in the spring (S2), fecundity (F1), and immature survival in the South during the spring

(S3) had the highest elasticity values, followed by vital rates to and in the North Central region (P1, S4, F2, S6, F3, S7).

Management scenario results

Improving breeding habitat in the South (scenario 6) or the North Central region (scenario 7) had the greatest impacts on population growth, with only a 2% increase in parameters resulting in mean $\lambda > 1$ (Table 2). The next best strategies were improving overwintering habitat in Mexico (scenario 2), migration habitat in Mexico and the South (scenario 3), and breeding in the Northeast (scenario 8), with 3% increases in parameter values leading to population growth rates >1. These results generally correspond with the sensitivity analysis.

When the top two (scenario 9, which combines scenarios 6 and 7), and four (scenario 10, which combines scenarios 2, 3, 6, and 7) most effective management scenarios were combined, increasing the affected parameters by 1% resulted in a positive growth rate ($\lambda \geq 1$), with 47.6% or 34.1% of the draws resulting in growth rates <1, respectively. When all management strategies (scenario 11) were combined, increasing the affected

parameters by 1% resulted in a growth rate of 1.07, with only 20.7% of the draws resulting in growth rates <1.

Discussion

The model results presented here help to identify the regions used during the monarch annual cycle where management actions are most likely to have large impacts on overall population dynamics. Across single regions, habitat improvements in either the Southern or North Central breeding regions lead to a stable population with the lowest increase in parameter values. However, actions across multiple regions achieved population stability when parameter values were increased by smaller amounts than any of the single-region strategies (Scenarios 9, 10, and 11). These results suggest that large-scale habitat restoration and management efforts across the breeding and migratory range is the best strategy for long-term population recovery, assuming that modest gains in vital rates everywhere will be more easily attained than dramatic gains in any single region.

Despite considerable differences in model structure, assumptions, and parameterisation, this model and the model by Flockhart *et al.* (2015) produced similar results. Flockhart *et al.* (2015) used a spatially structured, stochastic, and density-dependent periodic projection matrix model to estimate the importance of four different regions and vital rates on population abundance. Their results implicate loss of milkweed in the breeding grounds as a key factor driving monarch population decline. Our model was tuned to population growth rate, while the Flockhart *et al.* (2015) model used monarch abundance. In contrast to our model, Flockhart *et al.* (2015) included a density-dependent function linking immature survival to host plant density and a state-and-transition model to predict future land-cover types and declines in milkweed density. Our model incorporates estimates of process and measurement errors, and the parameter estimates were tuned to the observed decline in population size using a Bayesian approach. Despite these differences in analytical approach, the findings of the two studies cohere. Our goal is not to improve on the Flockhart *et al.* (2015) model, but rather to use a different approach reflecting our best understanding of monarch biology. The fact that these two analyses find similar patterns strengthens the conservation implications associated with recovery of this species.

The identification of breeding areas as drivers of population dynamics in both models suggests that these areas should be a focus of conservation efforts. Flockhart *et al.* (2015) did not compare multi-region conservation scenarios, but their perturbation analyses show that combined management actions across breeding areas have a larger demographic elasticity than any region alone (Flockhart *et al.*, 2015, Fig. 2), a finding similar to ours.

Our scenario results indicate that improving breeding habitat in the Southern and North Central regions would increase population growth rates more than improving habitat in other regions (Table 2). These conclusions, however, come with several caveats. First, the model does not provide information on the magnitude of habitat restoration that would be required

to achieve the increases in population parameters that were simulated. Further, it does not identify which of the specific actions listed in Table 2 will be most effective, nor does it provide insight into the amount of time after restoration occurs that parameter values will change. Second, our model did not take into account the fact that management scenarios in each region are achievable to varying degrees which will depend on cost, current land use, political support, and other logistical challenges. We assumed that management scenarios would occur over a large enough area in each region to increase the population parameters of the region as a whole, but more fine-grained analysis about where within the region management should occur is beyond the scope of the model. Rather, the model was developed to identify broad regions of conservation importance. Third, our model does not take into account changes in vital rates that may result from climate change. Monarch survival is likely to be affected by a changing climate in their Mexican wintering sites (Oberhauser & Peterson, 2003; Barve *et al.*, 2012); the extent of their summer breeding range could be affected by warming temperatures in their Upper Midwestern breeding range (Batalden *et al.*, 2007); and climatic variability in the southern breeding range can have large effects on summer breeding populations farther north (Zipkin *et al.*, 2012; Saunders *et al.*, 2016). Regional trends in climatic favourability are likely to affect the success of management strategies across broad geographical scales. Fourth, our parameters have varying levels of uncertainty. To account for this in the sensitivity analysis and scenarios, alterations across the entire parameter space were tested (Table 1 and Table S1 in Appendix S1). Finally, we assumed that changes in parameter values instantly affect stable-stage density-independent growth; in fact, it takes some time to equilibrate, and growth may be slower during this transient period. Thus, a sound broadly distributed programme to monitor season- and region-specific abundance patterns along with better understanding of the effectiveness of conservation action is implicated.

Given the above caveats, this study has several potential management implications. Certainly, mitigating the large declines in milkweed that have occurred in the North Central region owing to the use of genetically modified, herbicide-tolerant crops (Pleasants & Oberhauser, 2013) will be key. For example, Conservation Reserve Program (CRP) land could be improved by encouraging farmers to include forbs (including milkweed) in seed mixes for CRP and other farm conservation incentive programmes (Pleasants & Oberhauser, 2013). Roadsides have the potential to provide important habitat but are often mowed and sprayed to reduce forbs (Ries *et al.*, 2001). The models developed by Zalucki and Lammers (2010) and Zalucki *et al.* (2015a, 2015b) suggest that an important focus of monarch conservation in the vast agricultural areas of the Corn Belt should be to increase milkweed availability in the 'matrix', the land in between the remaining habitat patches, including roadsides, other right-of-way land, yards, fencerows, and marginally productive land that is currently being farmed. Recent studies, based on data from a butterfly monitoring project focused on high-quality habitat (Inamine *et al.*, 2016) and a fall monitoring programme on a Lake Michigan peninsula at the northern periphery of the breeding range (Badgett & Davis, 2015),

suggest that a lack of correlation between summer and fall monarch numbers and the size of the wintering population mean that conservation efforts should be focused on the fall migration. However, the sites on which these monitoring projects are conducted are not representative of the summer breeding population over the period during which these correlations were made (Pleasants *et al.*, 2016). Additionally, the summer and fall numbers used in these studies do not show a decline, despite the fact that the eastern migratory population is clearly declining (Semmens *et al.*, 2016). Thus, using them to represent the size of the population is problematic.

The actions necessary to increase monarch fecundity and survival in the Southern region are not as obvious. No single factor is so clearly implicated in extensive habitat loss; for example, multiple years of below-average precipitation (Brower *et al.*, 2015) may have had a larger effect on monarchs than habitat loss in this region. While more research is needed to understand the magnitude and effects of monarch habitat loss in the south, conserving and, where possible, increasing the availability of milkweed plants and nectar sources may benefit monarchs by decreasing their searching time for these resources.

In conclusion, model results presented here suggest that simultaneous restoration efforts across all regions, with a focus in the Southern and North Central breeding ranges and while also addressing other threats to monarchs, is the most effective strategy to increase the monarch population growth rate. This conclusion is robust, given that Flockhart *et al.* (2015) came to a similar conclusion using a different approach. A strategy of improving monarch habitat across a variety land-use types (e.g. CRP lands, public and private lands, roadsides, and agricultural areas) is likely to be most effective. It remains to be seen whether concerted efforts in these areas will increase vital rates to the extent required to stop monarch population declines, as the model does not provide a direct link between the specific conservation actions listed in Table 2 and vital rates. However, answering these remaining questions will take time, and given the 13–42% probability of quasi-extinction (losing the migratory phenomenon in the eastern monarch) within 10 years (Semmens *et al.*, 2016), time is of the essence. These findings suggest that the only way to lower the risk of quasi-extinction is to increase the population size, making the conservation efforts we outline here critical to ensuring the future of monarch migration in eastern North America.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12351

Appendix S1. Details on elasticity analysis and model parameters

References

Badgett, G. & Davis, A.K. (2015) Population trends of monarchs at a northern monitoring site: analyses of 19 years of fall migration counts at Peninsula Point, MI. *Annals of the Entomological Society of America*, **108**, 700–706.

Baker, P. & Malkin, E. (2014) In Mexico meeting, a show of friendship with few results on immigration and trade. *New York Times.* New York. [WWW document]. URL [WWW document]. http://www.nytimes.com/2014/02/20/world/americas/in-obama-trip-to-mexico-a-show-of-friendship-with-little-results-on-issues.html?_r=0. [accessed on 9 July 2015].

Barve, N., Bonilla, A.J., Brandes, J., Brown, J.C., Brunsell, N., Cochran, F.V. *et al.* (2012) Climate change and mass mortality events in overwintering monarch butterflies. *Revista Mexicana de la Biodiversidad*, **83**, 817–824.

Batalden, R.V. & Oberhauser, K.S. (2015) Potential changes in Eastern North Amereican monarch migration in response to an introduced milkweed, *Asclepias curassavica*. *Monarchs in A Changing World: Biology and Conservation of An Iconic butterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 215–224. Cornell University Press, Ithaca, New York.

Batalden, R.V., Oberhauser, K.S. & Peterson, A.T. (2007) Ecological niches in sequential generations of eastern North American monarch butterflies (Lepidoptera: Danaidae): the ecology of migration and likely climate change implications. *Environmental Entomology*, **36**, 1365–1373.

Borkin, S.S. (1982) Notes on shifting distribution patterns and survival of immature *Danaus plexippus* (Lepidoptera: Danaidae) on the food plant *Asclepias syriaca*. *Great Lakes Entomologist*, **15**, 199–206.

Brower, L.P., Taylor, O.R., Williams, E.H., Slayback, D.A., Zubieta, R.R. & Ramirez, M.I. (2012) Decline of monarch butterflies overwintering in Mexico: is the migratory phenomenon at risk? *Insect Conservation and Diversity*, **5**, 95–100.

Brower, L.P., Fink, L.S., Kiphart, R.J., Pocius, V., Zubieta, R.R. & Ramirez, M.I. (2015) Effect of the 2010-2011 drought on the lipid content of monarchs migrating through Texas to overwintering sites in Mexico. *Monarchs in A Changing World: Biology and Conservation of An IconicBbutterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 117–129. Cornell University Press, Ithaca, New York.

Calvert, W. (2004) The effect of fire ants on monarchs breeding in Texas. *The Monarch Butterfly: Biology and Conservation* (ed. by K.

S. Oberhauser and M. S. Solensky), pp. 47–53. Cornell University Press, Ithaca, New York.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts.

Center for Biological Diversity, Center for Food Safety, Xerces Society & Brower L.P. (2014) *Petition to protect the monarch butterfly (Danaus plexippus plexippus) under the Endangered Species Act* [WWW document]. URL http://www.centerforfood safety.org/legal-actions [accessed on 9 July 2015].

De Anda, A. & Oberhauser, K.S. (2015) Invertebrate natural enemies and stage-specific mortality rates of monarch eggs and larvae. *Monarchs in A Changing World: Biology and Conservation of An Iconic Butterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 60–70. Cornell University Press, Ithaca, New York.

Flockhart, D.T., Wassenaar, L.I., Martin, T.G., Hobson, K.A., Wunder, M.B. & Norris, D.R. (2013) Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. *Proceedings of the Royal Society of London Series B*, **280**, 20131087.

Flockhart, D.T., Pichancourt, J.B., Norris, D.R. & Martin, T.G. (2015) Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. *Journal of Animal Ecology*, **84**, 155–165.

Gelman, A. & Rubin, D. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–511.

Inamine, H., Ellner, S.P., Springer, J.P. & Agrawal, A. (2016) Linking the continental migratory cycle of the monarch butterfly to understand its population decline. *Oikos*, **000**, 001–011.

Jacowitz, K.E. & Kahneman, D. (1995) Measures of anchoring in estimation tasks. *Personality and Social Psychology Bulletin*, **21**, 1161–1167.

Kareiva, P. & Wennergren, U. (1995) Connecting landscape patterns to ecosystem and population processes. *Nature*, **373**, 299–302.

Lefkovitch, L.P. (1965) The study of population growth in organisms grouped by stages. *Biometrics*, **21**, 1–18.

Malcolm, S.B., Cockrell, B.J. & Brower, L.P. (1987) Monarch butterfly voltinism: effects of temperature constraints at different latitudes. *Oikos*, **49**, 77–82.

Monarch Larva Monitoring Program (2015) *Monarch Larva Monitoring Program*. University of Minnesota, St. Paul, Minnesota [WWW document]. URL http://www.mlmp.org/. [accessed on 9 July 2015].

Nail, K.R., Stenoien, C. & Oberhauser, K.S. (2015) Immature monarch survival: effects of site characteristics, density, and time. *Annals of the Entomological Society of America*, **108**, 680–690. DOI: 10.10 93/aesa/sav047.

National Fish and Wildlife Foundation (2016) *Monarch butterfly conservation fund* [WWW document]. URL http://www.nfwf. org/monarch/Pages/home.aspx. [accessed on 26 June 2016].

Ng, K.W., Tian, G.L. & Tang, M.L. (2011) *Dirichlet and Related Distributions: Theory, Methods and Applications*, Vol. **888**. John Wiley & Sons, Hoboken, New Jersey.

Oberhauser, K.S. (1997) Fecundity, lifespan and egg mass in butterflies: effects of male-derived nutrients and female size. *Functional Ecology*, **11**, 166–175.

Oberhauser, K.S. (2012) Tachinid flies and monarch butterflies: citizen scientists document parasitism patterns over broad spatial and temporal scales. *American Entomologist*, **58**, 19–22.

Oberhauser, K.S. & Peterson, A.T. (2003) Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 14,063–14,068.

Oberhauser, K.S., Prysby, M.D., Mattila, H.R., Stanley-Horn, D.E., Sears, M.K., Dively, G. *et al.* (2001) Temporal and spatial overlap between monarch larvae and corn pollen. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 11,913–11,918.

Office of Press Secretary (2014) *Presidential Memorandum -- Creating a federal strategy to promote the health of honey bees and other pollinators* [WWW document]. URL https://www.whitehouse.gov/ the-press-office/2014/06/20/presidential-memorandum-creating-fed eral-strategy-promote-health-honey-b [accessed on 9 July 2015].

Phillips, L.D. (1964) *Man As Transducer for Probabilities in Bayesian Command and Control Systems. Human Judgements and Optimality*. Wiley, New York, New York.

Pleasants, J.M. (2015) Monarch butterflies and agriculture. *Monarchs in a Changing World: Biology and Conservation of an Iconic Butterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 169–178. Cornell University Press, Ithaca, New York.

Pleasants, J.M. & Oberhauser, K.S. (2013) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. *Insect Conservation and Diversity*, **6**, 135–144.

Pleasants, J.M., Williams, E.H., Brower, L.P., Oberhauser, K.S. & Taylor, O.R. (2016) Conclusion of no decline in summer monarch population not supported. *Annals of the Entomological Society of America*, **109**, 169–171. DOI: 10.1093/aesa/sav115.

Prysby, M.D. (2004) Natural enemies and survival of monarch eggs and larvae. *Monarchs in A Changing World: Biology and Conservation of An Iconic Butterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 27–37. Cornell University Press, Ithaca, New York.

R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rendón-Salinas, E. & Tavera-Alonso G. (2015) *Forest surface occupied by monarch butterfly hibernation colonies in December 2015*. WWF-México, DF, unpublished, 6 pp.

Ries, L., Debinski, D.M. & Wieland, M.L. (2001) Value of roadside prairie restoration to butterfly communities. *Conservation Biology*, **15**, 401–411.

Ries, L., Oberhauser, K.S., Taron, D.J. & Rendon-Salinas, E. (2015) Connecting eastern monarch population dynamics across their migratory cycle. *Monarchs in A Changing World: Biology and Conservation of An Iconic Butterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 268–282. Cornell University Press, Ithaca, New York.

Satterfield, D.A., Maerz, J.C. & Altizer, S. (2015) Loss of migratory behaviour increases infection risk for a butterfly host. *Proceedings of the Royal Society of London Series B*, **282**, 20141734.

Saunders, S.P., Ries, L., Oberhauser, K.S. & Zipkin, E.F. (2016) Evaluating confidence in population-level predictions of population change in a migratory species. *Global Ecology and Biogeography*, **25**, 1000–1012. DOI: 10.1111/geb.12461.

Semmens, B.X., Semmens, D.J., Thogmartin, W.E., Wiederholt, R., López-Hoffman, L., Diffendorfer, J.E. *et al.* (2016) Quasi-extinction risk and population targets for the Eastern, migratory population of monarch butterflies (*Danaus plexippus*). *Scientific Reports*, **6**, 23265. DOI: 10.1038/srep23265.

Solensky, M.J. (2004) Overview of monarch overwintering biology. *The Monarch Butterfly: Biology and Conservation* (ed. by K. S. Oberhauser and M. J. Solensky), pp. 117–120. Cornell University Press, Ithaca, New York.

Vidal, O. & Rendón-Salinas, E. (2014) Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico. *Biological Conservation*, **180**, 165–175.

Vidal, O., Lopez-Garcia, J. & Rendon-Salinas, E. (2014) Trends in deforestation and forest degradation after a decade of monitoring in the Monarch Butterfly Biosphere Reserve in Mexico. *Conservation Biology*, **28**, 177–186.

Walck, C. (2007) *Handbook on Statistical Distributions for Experimentalists*. Internal Report SUF-PFY/96-01. University of Stockholm [WWW document]. URL http://www.stat.rice.edu/~dobelman/textfiles/DistributionsHandbook.pdf Search PubMed, 2001 [accessed on 26 June 2016].

World Wildlife Fund-Mexico (2016) Aumenta la superficie ocupada por la mariposa monarca en los santuarios mexicanos [WWW document]. URL http://www.wwf.org.mx/?262370/Aumenta-superficie-ocupada-por-mariposa-monarca-en-santuarios-mexicanos. [accessed on 20 March 2016].

Yakubu, A., Saenz, R., Stein, J. & Jones, L.E. (2004) Monarch butterfly spatially discrete advection model. *Mathematical Biosciences*, **190**, 183–202.

Zalucki, M.P. & Lammers, J.H. (2010) Dispersal and egg shortfall in monarch butterflies: what happens when the matrix is cleaned up? *Ecological Entomology*, **35**, 84–91.

Zalucki, M.P. & Rochester, W.A. (2004) Spatial and temporal population dynamics of monarchs down-under: lessons for North America. *The Monarch Butterfly: Biology and Conservation* (ed. by K. S. Oberhauser and M. S. Solensky), pp. 219–228. Cornell University Press, Ithaca, New York.

Zalucki, M.P., Brower, L.P., Malcolm, S.B. & Slager, B.H. (2015a) Estimating the climate signal in monarch population decline: no direct evidence for an impact of climate change? *Monarchs in A Changing World: Biology and Conservation of An Iconic Butterfly* (ed. by K. S. Oberhauser, K. R. Nail and S. Altizer), pp. 130–142. Cornell University Press, Ithaca, New York.

Zalucki, M.P., Parry, H.R. & Zalucki, J.M. (2015b) Movement and egg laying in monarchs: to move or not to move, that is the equation. *Austral Ecology*, **41**, 154–167. DOI: 10.1111/aec.12285.

Zipkin, E.F., Ries, L., Reeves, R., Regetz, J. & Oberhauser, K.S. (2012) Tracking climate impacts on the migratory monarch butterfly. *Global Change Biology*, **18**, 3039–3049.