Predicting monarch butterfly (*Danaus plexippus*) movement and egg-laying with a spatially-explicit agent-based model: The role of monarch perceptual range and spatial memory

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ABSTRACT

An ∼80% decline in the eastern population of the monarch butterfly (*Danaus plexippus*) has prompted conservation efforts to increase summer reproductive success in the Midwest United States. Implementation of conservation practices will create a patchwork of milkweed (mainly *Asclepias* spp.) habitat within agricultural landscapes dominated by corn and soybean production. Since the monarch butterfly is a vagile species, reproductive success is, in part, a function of both the amount and spatial arrangement of habitat patches in a fragmented landscape. To inform conservation planning we developed a spatially-explicit, agent-based model for summer breeding, non-migratory female monarch butterfly movement and egg-laying on an Iowa, USA landscape. Our model employs a unique movement algorithm when monarch agents encounter habitat edges that incorporates monarch perceptual range to their host plant and spatial memory of previously visited habitat. These behavioral factors are rarely incorporated into animal movement algorithms; however, they can influence estimates of resource utilization. Model exploration assessed the distribution and density of eggs laid on a spatially-explicit 148,665 ha landscape comprised of 17 land cover classes with varying milkweed densities. Uncertainty analysis was undertaken by sampling 25 combinations of perceptual range, spatial memory, flight step length and flight directionality parameters from a total of 256 (4^4) possible combinations. Movement paths simulated with our new movement algorithm show preferential use of high density milkweed areas that would not be simulated using a correlated random walk. Increasing perceptual range caused a decrease in the area used by monarch agents and caused a skewed egg distribution where most eggs were laid in relatively few habitat patches. Increasing spatial memory caused an increase in the area used but decreased the median number of eggs laid in roadside habitat. Current national and regional monarch conservation goals assume a uniform distribution of milkweed in different land cover classes. Translating these goals into spatially-explicit, heterogeneous habitat patches is essential for predicting realized fecundity in the landscape. Our model provides the foundation to link national and regional monarch conservation goals to fine scale spatial configurations of habitat patches in defined landscapes.

1. Introduction

The North American eastern population of the monarch butterfly (*Danaus plexippus*) has declined by ∼80% over the past two decades (Semmens et al., 2016). Increasing summer reproductive success in the Midwest United States has been identified as a high priority for monarch conservation (Oberhauser et al., 2017; Flockhart et al., 2015). Monarch butterflies oviposit only on milkweed species (mainly *Asclepias* spp.) and primarily common milkweed (*Asclepias syriaca*) in the Midwest (Malcolm et al., 1993). To increase monarch populations to

level that would reduce the probability of quasi-extinction by 50% over 20 years, Pleasants (2017) and Thogmartin et al. (2017) estimated that 1.3–1.6 billion additional milkweed stems need to be added to the U.S. Midwest. The current amount of common milkweed stems in the Midwest is estimated to be approximately 1.3 billion, the majority of which is in publically owned grasslands; land enrolled in conservation programs, such as the United States Department of Agriculture's Conservation Reserve Program (CRP); road Right-Of-Ways (ROWs), which are the strips of public or private property along both sides of roads that are maintained by government transportation agencies and/or private

landowners; and miscellaneous non-agricultural habitat (Pleasants and Oberhauser, 2013; Pleasants, 2017; Thogmartin et al., 2017). Analyses by Thogmartin et al. (2017) indicate that adding 1.3–1.6 billion new milkweed stems in the Midwest can only be achieved through extensive adoption of habitat restoration in primarily privately owned land in agricultural landscapes. Consequently, establishment of milkweed and forage plants in rural roadsides; marginal crop land; portions of existing CRP land, pastures and grassland; and grassy areas bordering crop fields, will create a patchwork of habitat within agricultural landscapes dominated by corn and soybean production.

Since the monarch butterfly is a vagile species that can travel up to 15 km/d (Zalucki et al., 2016), female monarch flight and ovipositing patterns and resulting egg densities in theoretical landscapes vary with different arrangements of habitat patches, even though the total amount of added habitat is held constant (Zalucki and Lammers, 2010; Zalucki et al., 2016). Because monarch reproduction is expected to be a function of both the amount and spatial arrangement of existing and new habitat, the means to predict movement and egg distribution in a spatially-explicit context is critical to understanding the strengths and limitations of conservation planning scenarios for states in the U.S. Midwest. Agent-based modeling is well-suited to address the effects of different spatially-explicit landscape configurations on animal population dynamics (DeAngelis and Mooij, 2005, Grimm et al., 2005; Railsback et al., 2006; Railsback and Grimm, 2011).

Building on previous experience with agent-based modeling of monarchs in a theoretical landscape (Zalucki et al., 2016) and *Helicoverpa* spp. in explicit Australian agricultural landscapes (Parry et al., 2017), we have developed a spatially-explicit, agent-based model for non-migratory female monarch butterfly movement and egg-laying in an Iowa, USA landscape. The model incorporates decision- and directional-based random walk flight algorithms. When the habitat is homogeneous, monarch agents move in a correlated random walk, corresponding to the directional movement described by Zalucki and Kitching (1982b). In Iowa many of these homogeneous areas are corn and soybean fields that are largely devoid of milkweed. Grasslands and pastures are also large homogeneous areas without discrete internal habitat edges, but they may have substantial milkweed populations. In these homogeneous areas, wild monarch butterflies have been observed to turn more often (Zalucki and Kitching, 1982b). We model flight patterns in different homogeneous habitat types using different assumptions of directionality; higher directionality values create straighter movement paths and lower directionality values create more tortuous movement paths. Correlated random walk algorithms are reasonable for modeling animal movement (Jones, 1977; Kareiva and Shigesada, 1983; Zalucki, 1983; Bovet and Benhamou, 1988; Turchin, 1998) in some situations and especially in homogeneous environments (Codling et al., 2008; Smouse et al., 2010). But in heterogeneous environments movement algorithms that include interactions of the animal with the environment are often needed (Johnson et al., 1992; Codling et al., 2008; Wallentin, 2017).

For decision-based flight at discrete habitat edges in heterogeneous environments, our model uses a unique random walk movement algorithm that incorporates monarch perceptual range and spatial memory. These behavioral factors are rarely incorporated into animal movement algorithms (Siniff and Jessen, 1969; Smouse et al., 2010; Zhao et al., 2015); however, the need to elucidate how these behaviors can influence resource utilization on the landscape has long been recognized (Lima and Zollner, 1996; Mueller and Fagan 2008; Mueller et al., 2011) and is a growing area of research in landscape ecology (Turner and Gardner, 2015) and spatially-explicit individual-based modeling (Wallentin, 2017; Smouse et al., 2010). Perceptual range is the distance at which animals can detect and respond to resources, such as host plants or food resources (Lima and Zollner, 1996). Perceptual range can have a substantial effect on animal movement, as animals cannot react to resources they cannot detect. Spatial memory is the ability of organisms to remember locations they have previously visited and

subsequently avoid or revisit (Smouse et al., 2010; Moorcroft, 2012).

Perceptual range and spatial memory likely have a strong effect on the distribution of monarch eggs on the landscape. Perceptual range in monarch butterflies includes olfactory and visual sensory inputs (Garlick, 2007). Visual perceptual range is likely only a few meters (Garlick, 2007). However, field observations indicate that olfactory perceptual range for nectar sources could extend hundreds of meters (Dr. Orley Taylor, pers. comm.), depending on the strength of the odor, wind speed and direction of the odor plume (Cardé and Willis, 2008). Observations reported by Fisher et al. (2017) suggest that olfactory perceptual range in monarch butterflies is 50 to ≥ 75 m.

While monarchs likely have spatial memory, the mechanisms and spatial scale of their memory is unclear. Male butterflies patrol milkweed patches or nectar sources waiting for females (Zalucki and Kitching, 1982b), suggesting they recognize "their" patches. Female butterflies, however, move extensively among habitat patches (Zalucki and Lammers, 2010, and references cited therein). Memory capabilities are well known in some insects such as honey bees (Hammer and Menzel, 1995) and learning behavior in butterflies (Lewis, 1986) and moths (Cunningham et al., 1999) has been documented. Monarch butterflies learn associations between color and nectar sources (Blackiston et al., 2011) and can remember these associations for up to three days (Rodrigues and Weiss, 2012).

By incorporating decisional and directional movement in our agent-based model we evaluate the following hypotheses:

1 Greater directionality in poor habitat results in more eggs laid on the landscape as monarch agents spend less time in poor habitat and, conversely, less directionality in good habitat results in more eggs laid as monarch agents spend more time in good habitat.

2 As perceptual range increases there is an associated increase in the number of eggs laid on the landscape because females are better able to find oviposition habitat.

3 With longer-term spatial memory of previously visited milkweed patches, female monarchs will have a greater area of habitat utilization and lay fewer eggs since they spend more time searching for new habitat patches.

We employ uncertainty analysis of the parameters used for perceptual range, spatial memory, directionality, and step length to determine the effect of parameter assumptions on model outputs (Marino et al., 2008). Uncertainty analysis provides insight into plausible values for these parameters and the design of future experimental and observational studies to improve understanding of the role these behavioral elements play in monarch movement and egg-laying in fragmented landscapes.

2. Methods

In our model each monarch agent behaves autonomously and interacts with habitat patches to probabilistically "choose" a direction to move and where to lay eggs. Our model advances the work of Zalucki et al. (2016) and Parry et al. (2017) by incorporating a novel movement algorithm. In their movement algorithm, agents choose between two adjacent habitat patches and perceptual range was simulated as either 5 or 25 m. However, monarch butterflies likely have a perceptual range of 75–400 m 50–400 m (Fisher et al., 2017, Orley Taylor, pers. comm.) and thus, in heterogeneous landscapes with small habitat patches, more than two habitat patches will likely be within range and the model described here allows agents to choose between any habitat patches within their perceptual range. Other modifications to the movement algorithm include varying directionality according to habitat quality and incorporating spatial memory of recently visited habitat patches. Whereas Zalucki et al. (2016) used a simulated model landscape, we model monarch butterfly movement and egg-laying on a spatially-explicit landscape. We describe our model for monarch butterfly

movement and egg-laying in Story County, Iowa following the ODD protocol (Grimm et al., 2006, 2010). The model is implemented in the Repast Simphony 2.3.1 platform using the Java programming language (North et al., 2013; see Supplemental material A).

2.1. Model purpose

The purpose is to model monarch butterfly movement and egg-laying on a spatially-explicit Iowa, USA landscape, to better understand the effects of landscape composition and configuration on the distribution of adult female monarchs and their eggs, with the long term goal to support evaluation of alternative conservation strategies. Our purpose here is to explore how uncertainty in monarch perceptual range, spatial memory, and directionality affect the number of eggs laid on the landscape and the habitat patches in which eggs are laid to motivate further research to refine understanding of monarch movement ecology.

2.2. Entities, state variables, and scales

The model agents represent individual female monarch butterflies. Monarch agents move around the landscape laying eggs using a programmed movement algorithm. Monarch agent movement is simulated over 10 days, the approximate egg-laying lifespan of an adult female monarch. The model is divided into time steps of one day and within each day monarch agents move a defined number of movement steps. The initial state of a monarch agent is at a random location in the study area and they hold 410 eggs that can be laid over 10 days. Monarch agent movement and egg-laying decisions are based on interactions with habitat patches. Habitat patches are delineated in a Geographic Information System (GIS). As monarch agents interact with the landscape, they make decisions to move toward patches based on the characteristics of the patch they currently occupy and other patches they can perceive.

The model was implemented for Story County, Iowa, an area of 148,665 ha ($=1486.65$ km^2; Fig. 1). We ran 25 simulations, each with a different combination of parameter values (Table 2). Values were sampled across the range of uncertainty for each parameter. In each simulation we used 10,000 monarch agents, an estimate of female monarch density obtained from a panel of experts (see Acknowledgements for the experts consulted).

2.2.1. Land cover patches

We classified the landscape into 17 land cover categories based on relative homogeneity and available data (Table 1). We created an ArcGIS polygon shapefile of land cover for import into Repast Simphony. Using the 2014 Crop Data Layer (CDL; 30 m resolution; USDA, 2014) for Story County, Iowa, USA we created eight land cover categories: corn, soybeans, forest, medium-high intensity development, low intensity development/developed open space, grass/pasture, open water/barren landscapes, and wetlands. We then converted the raster into a shapefile. In Iowa, ~12 and 4% of planted corn and soybeans, respectively, are not glyphosate resistant (USDA, 2015). Because non-glyphosate resistant corn and soybean fields have a higher density of milkweed (Pleasants and Oberhauser, 2013), we randomly selected 12% of the corn and 4% of soybean fields as being planted with non-glyphosate resistant crops.

In Iowa, roads are found along most public land survey section boundaries, resulting in a substantial number of rural roads in the state. In Story County, there are 1536 km of rural roads. Using a road shapefile, we identified all rural roads in the county by excluding roads in urban areas (defined according to an urban area shapefile), interstate freeways, and state highways. Urban roads, interstate freeways, and state highways remained in the model as low intensity development, as classified in the Crop Data Layer. Rural road ROWs are characterized by a heterogeneous distribution of milkweed and milkweed patches

(Hartzler, 2010; Hartzler, pers. comm.). In such a narrow space, this heterogeneity is likely to have important effects on monarch agent movement. We modelled this heterogeneity as continuous, adjacent 50 m square patches along each side of the roads. Using data from 2010 (Hartzler, 2010) and 2015 (Hartzler, pers. comm.), we created five categories of milkweed density for roads (see Table 1). Railroad ROWs were represented by buffering a shapefile of the railroad with a 25 m buffer. Because the step length of the monarch agent is 20–50 m (see Table 2), we processed the shapefile such that all patches are at least 50 m across in the smallest dimension.

Relative milkweed density among the 17 land-cover types was determined from literature sources and experts' best professional judgement (see Acknowledgements); a parameter representing milkweed density was assigned to each land-cover type (Table 1). Initial values of milkweed density ranged from 0 to 1 but were reduced to 10% of their original value during model calibration (see 2.6). The movement algorithm described below uses the milkweed density parameter to determine movement and egg-laying decisions. Relative milkweed density for road ROWs was determined from 2015 state-wide survey data (Hartzler, pers. comm.). Pleasants and Oberhauser (2013) provide milkweed densities for grasslands, pastures, and non-glyphosate resistance and glyphosate resistant corn and soybeans. Relative milkweed densities for railroad ROWs, other crops, forest, and low intensity development were estimated by expert professional judgement. The GIS shapefile with assigned values of milkweed density was then imported into a Repast Simphony geographic context. The model maintains a running total of the number of eggs laid in each habitat patch.

2.3. Process overview and scheduling

Each time step of the model is a day in the life of an egg-laying monarch agent. Within each time step the agents move 5.5–10 km in a sequence of 110–500 movement steps, depending on whether the step length is 20, 30, 40, or 50 m (Fig. 2). Agents have opportunities to lay eggs after each step length. The egg-laying lifespan of captive monarchs varies from 14 to 45 days (Oberhauser, 1997) and averages approximately 28 days, depending on temperature (Zalucki, 1981). Data on wild monarchs is lacking but they likely have a shorter lifespan (Zalucki and Kitching, 1984). Monarch agent movement and egg-laying is simulated for 10 days (see Table 2 for monarch parameters). On the first day of their egg-laying life, monarch agents move 10,000 m (Zalucki et al., 2016). Movement capacity is thought to decline in Lepidoptera as they age (e.g., Sappington and Burks, 2014), consequently, the distance they can move each day in the model decreases by 500 m. On the 10th day they can move 5500 m (consistent with Zalucki et al., 2016). The number of eggs potentially laid by a female monarch each day decreases over time (Zalucki, 1981; Oberhauser, 1997). In the model, on the first day agents can lay up to 50 eggs. Starting on day 2, potential eggs laid decreases by two each day and by the last day they can lay 32 eggs (consistent with Oberhauser, 2004). The total possible number of eggs that a monarch agent can lay over 10 days is 410, consistent with Urquhart's (1960) reported lifetime fecundity value of 420 eggs and Oberhauser's (2004) estimate of 300–400.

A movement submodel, described in detail in 2.7, incorporates a correlated random walk when only one habitat patch is within perceptual range and a decision-based movement when more than one habitat patch is within perceptual range. Decision-based movement includes an algorithm to choose among habitat patches using weighted probabilities of milkweed density and spatial memory. Finally, each agent has a probability of laying eggs in each movement step.

2.4. Design concepts

2.4.1. Basic principles

The monarch butterfly is a vagile species that moves extensively across the landscape (Zalucki and Kitching, 1984; Zalucki and
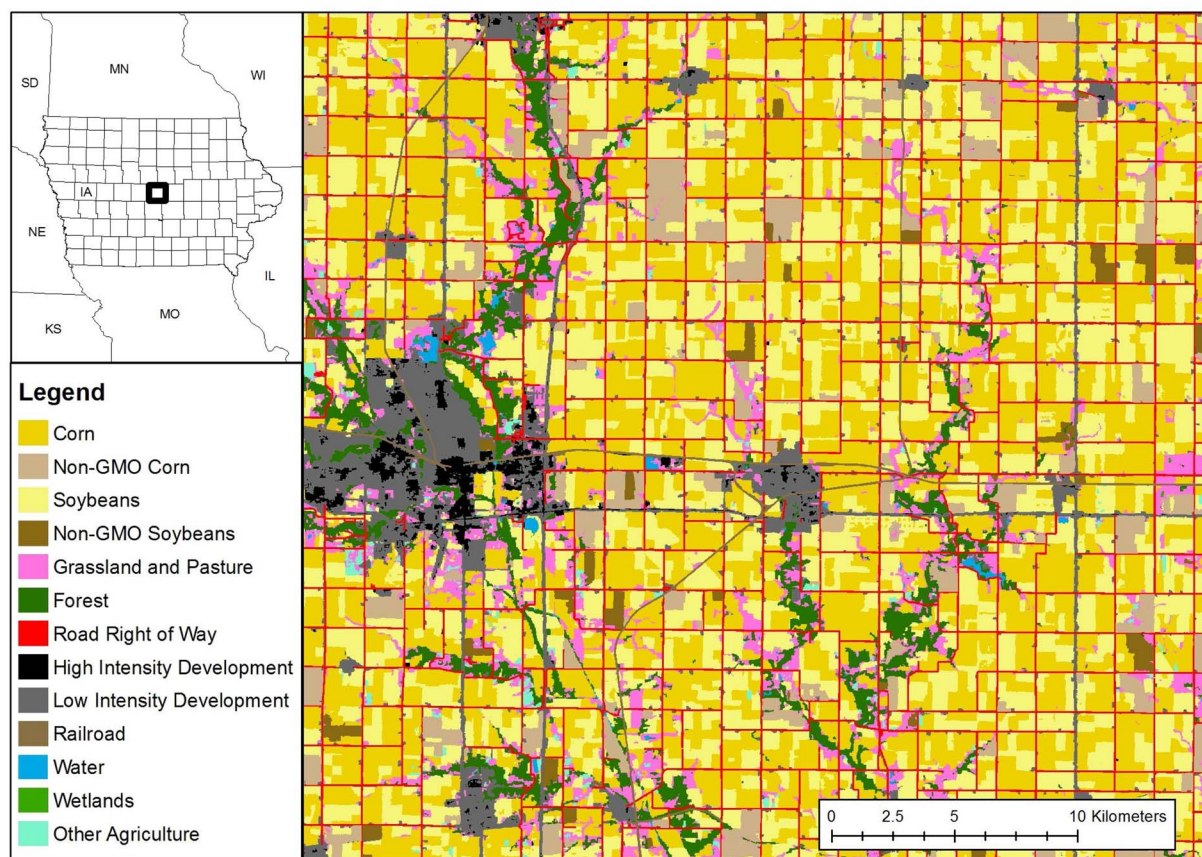
Story County, Iowa

Fig. 1. Land cover categories in Story County, Iowa, USA. Inset map shows Story County in the context of Iowa and neighboring states. Five road right-of-way categories (see Table 2) were combined for this map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Lammers, 2010). We model non-migratory generations that are resident in Iowa in July and August. Monarch butterflies attempt to maximize their fitness by laying eggs in habitat that are most likely to produce adult monarchs. Monarch agents in the model make movement decisions based on the resources they can perceive on the landscape within their perceptual range and based on which locations they have visited in the past (i.e., spatial memory). Resource distribution is modelled as habitat patches with varying attractiveness based on milkweed density.

2.4.2. Emergence

The primary emergent outputs are the monarch movement paths and the distribution of eggs on the landscape that arise from the movement behavior of the monarch agents interactions with habitat patches.

2.4.3. Adaptation

Monarch agents change their behavior based on milkweed density of habitat patches within their perceptual range. They also adapt their movement behavior according to patches they occupied during recent steps.

2.4.4. Objectives

Monarch agents' objectives are to find oviposition habitat (i.e., patches with milkweed) in the fragmented landscape and maximize their fitness by laying eggs in locations most likely to allow growth and development to the adult stage. Objectives are evaluated by determining the number of eggs laid and how those eggs are distributed on the landscape.

2.4.5. Learning

Female monarch agents remember patches they have recently occupied and have a lower probability of returning to those patches.

2.4.6. Prediction

Monarch agents do not predict future conditions over the course of their egg-laying lifetime.

2.4.7. Sensing

Monarch agents are assumed to sense milkweed using olfactory or visual cues (Bergstrom et al., 1994; Blackiston et al., 2011; Garlick, 2007). In the model, the milkweed density parameter serves as a measure of sensory input.

2.4.8. Interaction

Monarch agents do not interact. It is conceivable that in nature they interact indirectly by choosing not to lay eggs on milkweed that already have eggs; i.e., a type of density dependence. This interaction is not currently incorporated in the model, given the limited evidence of this behavior.

2.4.9. Stochasticity

Monarch agents choose which patch to move toward according to probabilities calculated for each patch within their perceptual range. Monarch agents also lay eggs at each movement step as determined by milkweed density. Monarch agents start at a randomly selected point in the landscape on day 1.

Table 1

Habitat categories for Story County with the associated milkweed density parameter, the probability a monarch agent lays eggs on a particular step. The milkweed density parameter was calibrated to 10% of its original value. "MW = 1–5 m^2" indicates a milkweed density of 1–5 m^2 occupied by milkweed per 2500 m^2 according to Hartzler (2010 and pers. comm.).

Land cover Category	Relative Milkweed Density	Cumulative Area (km^2)	No. of Patches
Road ROW MW = 60–100 + m^2	0.090	22.90	8976
Road ROW MW = 20–60 m^2	0.085	17.26	6778
Non-Glyphosate-Resistant Corn	0.085	80.20	175
Non-Glyphosate-Resistant Soybeans	0.085	17.12	54
Grass/Pasture	0.075	107.63	1920
Road ROW MW = 5–20 m^2	0.075	17.80	6987
Railroad ROW	0.050	7.06	2
Road ROW MW = 1–5 m^2	0.050	5.58	2194
Wetlands	0.020	0.29	18
Low Intensity/Open Space Dev	0.005	92.63	1260
Other-primarily alfalfa	0.005	12.01	394
Glyphosate-Resistant Corn	0.002	557.36	1280
Glyphosate-Resistant Soybeans	0.002	448.27	1292
Forest	0.002	66.08	661
Road ROW MW = 0 m^2	0	12.11	4756
Med/High Intensity Development	0	16.79	303
Water/Barren/Other	0	5.11	115
Total		1486.18	37,165

Table 2

Monarch parameters and the values or range of values used in the model.

Parameter	Value(s)/Value Range	Source
Distance moved first day	10,000 m	Zalucki & Kitching (1984)
Lifespan	10 d	Oberhauser (1997)
Eggs laid over lifespan	410	Oberhauser (2004)
Eggs laid per step	2	Zalucki & Kitching (1982a)
Step length	20–50 m	Model assumption
Directionality	0.1–0.9	Zalucki & Kitching (1982b)
Perceptual range	50–400 m	Expert estimates
Patches remembered	0–100	Model assumption
Milkweed Density	0–1	See Table 1 for details

2.4.10. Observation

The model outputs data for habitat patches and monarch agents. For habitat patches, the model outputs the number of eggs laid in each of the 37,165 patches. For each monarch agent, the model outputs the number of eggs laid each day. The model can output the location (latitude and longitude) of a monarch agent as x,y coordinates at each step to obtain movement trajectories.

We examined several metrics to describe model behavior and serve as response variables in the uncertainty analysis (Table 3). We used the x,y coordinates of each monarch agent at each step to calculate their habitat utilization distribution, which is a metric for how much of the landscape is used (Worton, 1989). This metric can be compared with empirical field data of monarch movement. We calculated the area of the utilization distribution for each monarch agent with a dynamic Brownian bridge movement model (Kranstauber et al., 2012) using the R package *move* (Kranstauber and Smolla, 2016). We used a 30 m raster, thus our utilization distribution estimate is the sum of all 30 × 30 m raster cells occupied by a monarch agent. We calculated the mean proportion of potential eggs laid per monarch agent on day five. We calculated median egg density per patch for two habitat types: grass/pasture and road ROWs with the most milkweed (Road ROW MW = 60 − 100 + m^{-2}). We chose these two habitat types for closer

examination after evaluating behavior across all habitat types. Grass/pasture patches are medium in size, are distributed somewhat randomly across the landscape, and have a high density of milkweed (Pleasants and Oberhauser, 2013). Road ROWs are considered to be an important habitat component (Kasten et al., 2016) because of their overall large area and connectivity across the state. Road ROW patches are generally small, but regularly distributed across the landscape and adjacent to other road ROW patches. Finally, we looked at total cumulative eggs laid in the entire landscape and in the high density road patches and grass/pasture patches. Because of uncertainty in parameter estimates for monarch agents, we examine only the relative number of eggs laid per land-cover type, rather than the absolute number of eggs laid.

2.5. Initialization

The model is initialized by randomly placing the monarch agents across Story County. For the uncertainty analysis, 10,000 monarch agents were used, except for the utilization distribution analysis (see below), for which 1000 agents were used. An exploratory study indicated that 10,000 agents was a sufficient sample size for egg density analyses. For example, two simulations with 10,000 agents with the same parameterization (step length = 30, perceptual range = 50, remembered patches = 0, and directionality = 0.5–0.75) resulted in a difference of 0.04% in the cumulative eggs laid in the study area (2,744,170 vs. 2,743,108) and a correlation of 0.97 for eggs laid in the 37,165 individual patches.

2.6. Input data

The model does not use input data to represent time-varying processes.

2.7. Submodels

In the movement submodel, the monarch agents' random walk is programmed as a series of steps: monarch agents choose a heading (0–360°), move the distance of the step length in that direction, choose a new heading from their new location, move the next step, and so on. Wild monarchs lay eggs singly as they move across the landscape (Zalucki and Kitching, 1982a), but the rate at which they lay eggs is unclear and likely varies with milkweed density. One of us (MPZ) collected data on eight monarchs in Florida in 1987 in a diffuse patch of milkweed in a pasture. Monarchs were followed from milkweed to milkweed as they laid eggs. Mean egg-laying rate was 0.012 eggs/m (SD = 0.006), or about 1 egg per 82 m (SD = 25.4). A straight step length in the model may represent a more convoluted path of a wild monarch, consequently we assumed that monarchs lay 2 eggs per step length, if it chooses to lay eggs on that step. Because egg-laying rate is poorly known, we make inferences about relative egg densities and postpone inference on absolute egg densities until additional experimental data and/or field observations are available. The egg-laying rate is held constant, hence step length serves as a surrogate of egg-laying rate; our uncertainty analysis evaluates this model assumption.

Agents determine the heading on which to move by evaluating the landscape (Fig. 3). Agents have a perceptual range assumed to represent the distance that they can detect milkweed plants through olfactory or visual cues (Bergstrom et al., 1994; Garlick, 2007; Rodrigues and Weiss, 2012). Wild monarchs likely use olfaction for long-range detection of milkweed, and visual cues at short distances (Garlick, 2007). The agents' field of perception is 360°, under the assumption that they can detect odor plumes from any direction. At each step, agents query the modelled landscape and determine how many patches are within the perceptual range. If no other patches are within the perceptual range, other than the currently occupied patch, the agent moves in a correlated random walk. In a correlated random walk the heading that the agent moves is determined by a change to the current heading by θ
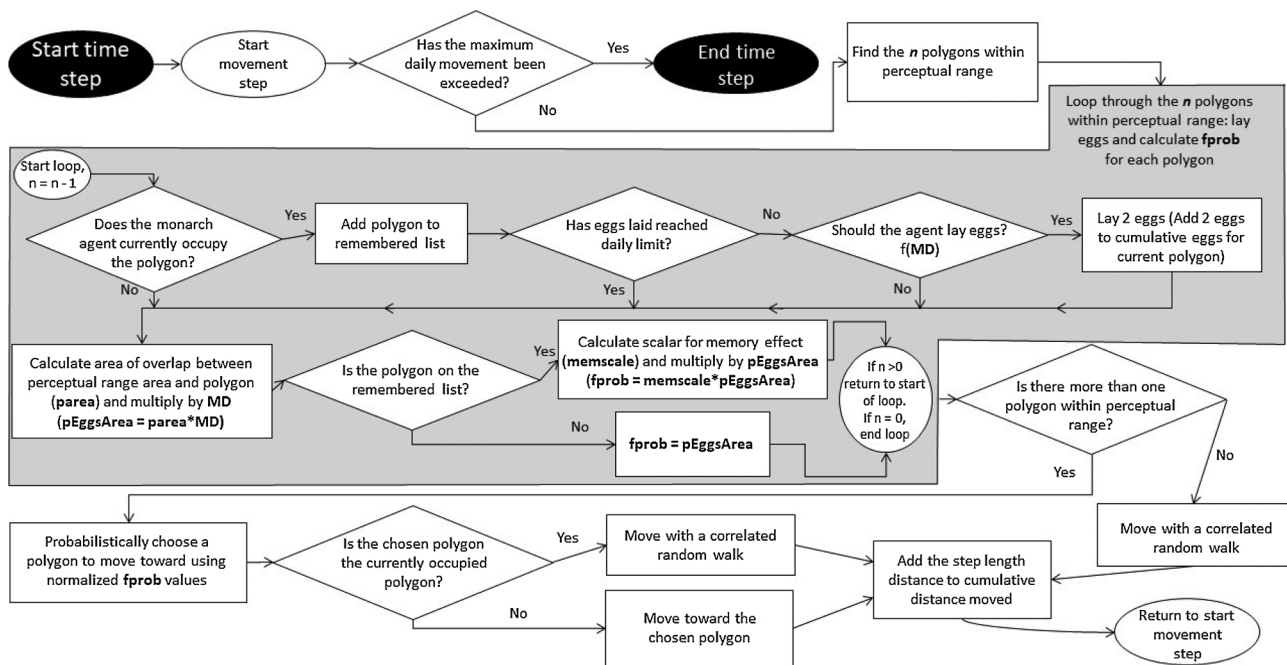
Fig. 2. Flow diagram depicting model processes and scheduling. Each time step is a day in the life of a monarch agent. Monarch agents move one step length at a time until their daily movement distance is exhausted. Model variables are in bold. **MD** corresponds to relative milkweed density in the land-cover types, and is the probability that an agent lays eggs in that patch and the basis for movement choices. **fprob** is the attractiveness, or final relative probability of moving toward a patch, before normalization. See text for calculation of **memscale**. Other variables are calculated as explained in the diagram.

Table 3
Range of parameter values used in the uncertainty analyses. Step length, patches remembered, and perceptual range are continuous variables. Directionality varies linearly from D_{min} in good habitat to D_{max} in poor habitat. Directionality was treated as a categorical variable.

Step Length (m)	Patches Remembered	Perceptual Range (m)	Range in Directionality (D_{min}–D_{max})
20	0	50	0.1–0.2
30	10	100	0.1–0.9
40	40	200	0.5–0.75
50	100	400	0.8–0.9

radians. The change in heading, θ, is determined by the formula:

$$\theta = \pm \pi R (1 - D) \tag{1}$$

where R is a random number between 0 and 1 chosen by a random number generator and D is the directionality parameter that ranges from 0 to 1. High directionality, e.g., 0.9, causes the agent to move in nearly straight lines and low directionality, e.g., 0.1, causes the agent to move in nearly random directions, resulting in very tortuous movement paths. We assume directionality increases as habitat quality decreases (Zalucki and Kitching, 1982b; Zalucki, 1983); thus, directionality for an agent is dependent on the habitat it occupies. At each step, the monarch agent queries the milkweed density of the current patch and calculates directionality according to Eq. (2):

$$D_{current} = D_{max} - MD \left(\frac{D_{max} - D_{min}}{0.09} \right) \tag{2}$$

Where $D_{current}$ is the directionality for the current patch, D_{max} is the maximum possible directionality, D_{min} is the minimum possible directionality, MD is the milkweed density parameter queried from the current patch, and the range of milkweed density values in the study area is 0.09. As an example, if directionality was set to a range of 0.5–0.75, directionality was 0.5 in the best habitat (MD = 0.09) and increased linearly to 0.75 in the poorest habitat (MD = 0).

If more than one patch is detected within the perceptual range, the

agent must choose which patch to move toward (i.e., decisional flight). Monarch agents are assumed to have a higher probability of moving toward patches with higher milkweed density, based on laboratory and greenhouse studies suggesting that increased number of milkweed plants result in an increased intensity of olfactory and/or visual cues (Bergstrom et al., 1994; Rodrigues and Weiss, 2012; Garlick, 2007).

Monarch agent attractiveness to a patch is based on the milkweed density parameter, after adjustments. An attractiveness probability is calculated for each patch within the perceptual range in a two-step process. In the first step, the milkweed density parameter for each patch is scaled according to the area of the patch within perceptual range. The model calculates the area of each patch within the perceptual range (i.e., the area of overlap between the perceptual range and the landscape patches) and multiplies that area by the milkweed density parameter. For example, if a patch covers 50% of the perceived area of the monarch agent and the milkweed density parameter for that patch is 0.1, the scaled attractiveness probability = 0.5*0.1 = 0.05. This adjustment controls for the fact that the more area of a patch is within the perceptual range, there is a greater likelihood of more milkweed providing olfactory and/or visual cues, increasing its attractiveness. Without this function, very small patches with high milkweed density are nearly exclusively chosen by the monarch agents (simulations not shown), which is not consistent with field observations that indicate the monarch is a vagile species (Zalucki and Kitching, 1982b; Zalucki and Suzuki, 1987; Ries and Debinski, 2001; Zalucki and Lammers, 2010).

Attractiveness probability is next adjusted based on the monarch agent's interaction with the patch in recent steps. It is assumed monarchs have spatial memory (Blackiston et al., 2011; Rodrigues and Weiss, 2012) and have a lower probability of returning to small patches previously visited and evaluated for oviposition potential, and thus more likely to visit habitat not yet evaluated. This behavior is realized by saving a list of the most recently visited patches. The size of the list corresponds to the spatial memory parameter. If spatial memory = 10, identification numbers of the last 10 patches visited are saved in the list (which may all be the same patch if it is a large area of habitat). At each step, the identification number of the patch occupied by the agent is added to the top of the list, and the identification number of the oldest
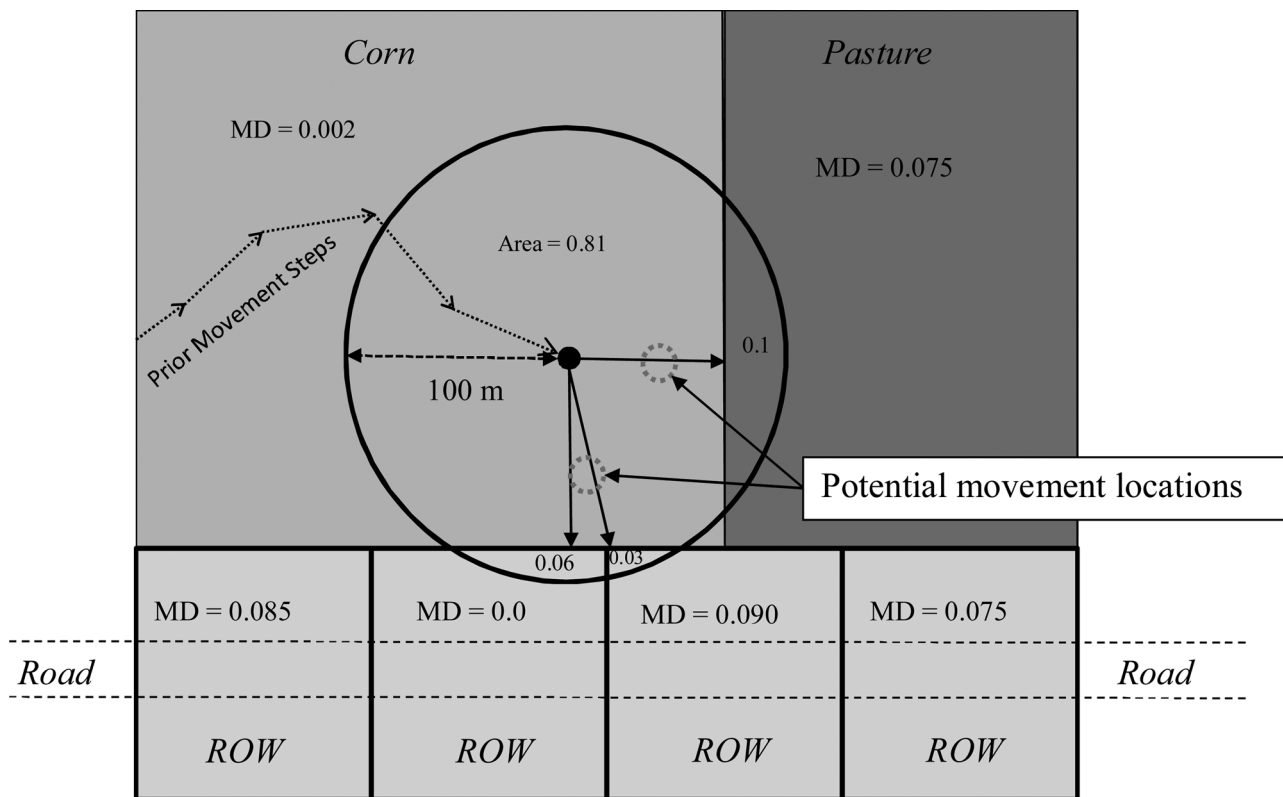
Fig. 3. Potential future movement locations for a monarch butterfly agent (black dot). The agent moves with a 50 m step length in this case. The perceptual range is 100 m; therefore, the agent must choose between the four habitat patches that it perceives. The probability that it moves toward a particular patch depends on the milkweed density (MD) parameter, the area of the perceivable patch, and whether it has visited the patch recently. If it chooses the current patch, it moves in a correlated random walk. At each step, the agent lays eggs in the current patch with probability equal to the milkweed density parameter.

patch is dropped from the list. When choosing among patches within the perceptual range, each patch is checked against the list, and the probability of moving toward a patch is reduced if it is on the list.

Under the assumption that monarchs remember relatively small patches on the landscape better than large patches, we reduce the effect of remembering patches as a function of patch area. The remembered probability is reduced by a scalar generated using the logistic Eq. (3) as

$$\frac{1}{1 + e^{-2(A-0.92)}} \tag{3}$$

where A is the area of the patch (Fig. 4). Using this equation, patches above approximately 3 ha have a scalar of nearly 1 and thus have a negligible effect when calculating attractiveness. Patches at the smallest size of approximately 0.25 ha have a scalar of 0.18. Thus there is a strong effect for small patches, which have the attractiveness probability reduced to 18% of its initial value.
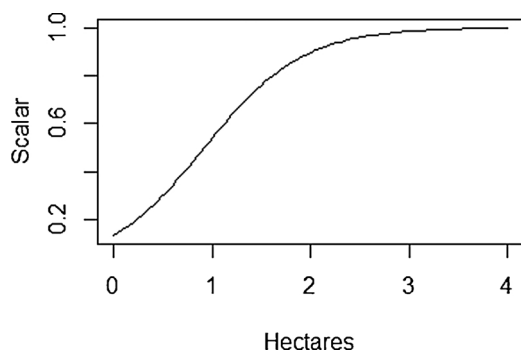

Fig. 4. Scalar for modifying attractiveness probability if a patch has been occupied in recent steps.

When the milkweed density parameter has been adjusted by area and memory to calculate the final attractiveness probability for each patch, the adjusted probabilities, which constitute a multinomial distribution, are normalized to sum to 1. A random number from 0 to 1 then determines which patch is chosen. When the patch is chosen, the model performs a query to determine the heading to the point of the patch nearest the monarch agent. The monarch then moves on that heading for the distance of one step length. If the monarch agent chooses the patch it currently occupies, it moves in a correlated random walk. After the monarch agent moves, the cumulative distance moved that day is updated. If the cumulative distance moved is ≥ the maximum daily distance, the monarch ends movement for that day.

2.8. Model calibration

Model parameterization and calibration involves optimizing parameters such that the model gives more realistic results (Thiele et al., 2014). In the case of monarch butterflies, our information is limited. Zalucki (1983) estimated that approximately 50% of potential eggs were laid each day, which was supported by limited field data. Therefore, we calibrated the milkweed density parameter to values that resulted in approximately half of available eggs being laid each day. Our original estimates of the relative egg densities elicited from our experts were scaled to be between 0 and 1. Calibration resulted in the original values being reduced by 90% (Table 1).

2.9. Computational resources

We ran simulations on the YETI computer cluster, operated by the Advanced Research Computing facility of the United States Geological Survey (Denver, CO), and on a 32-core machine on the Iowa State University campus. Each simulation takes from 0.25 to over 12 h
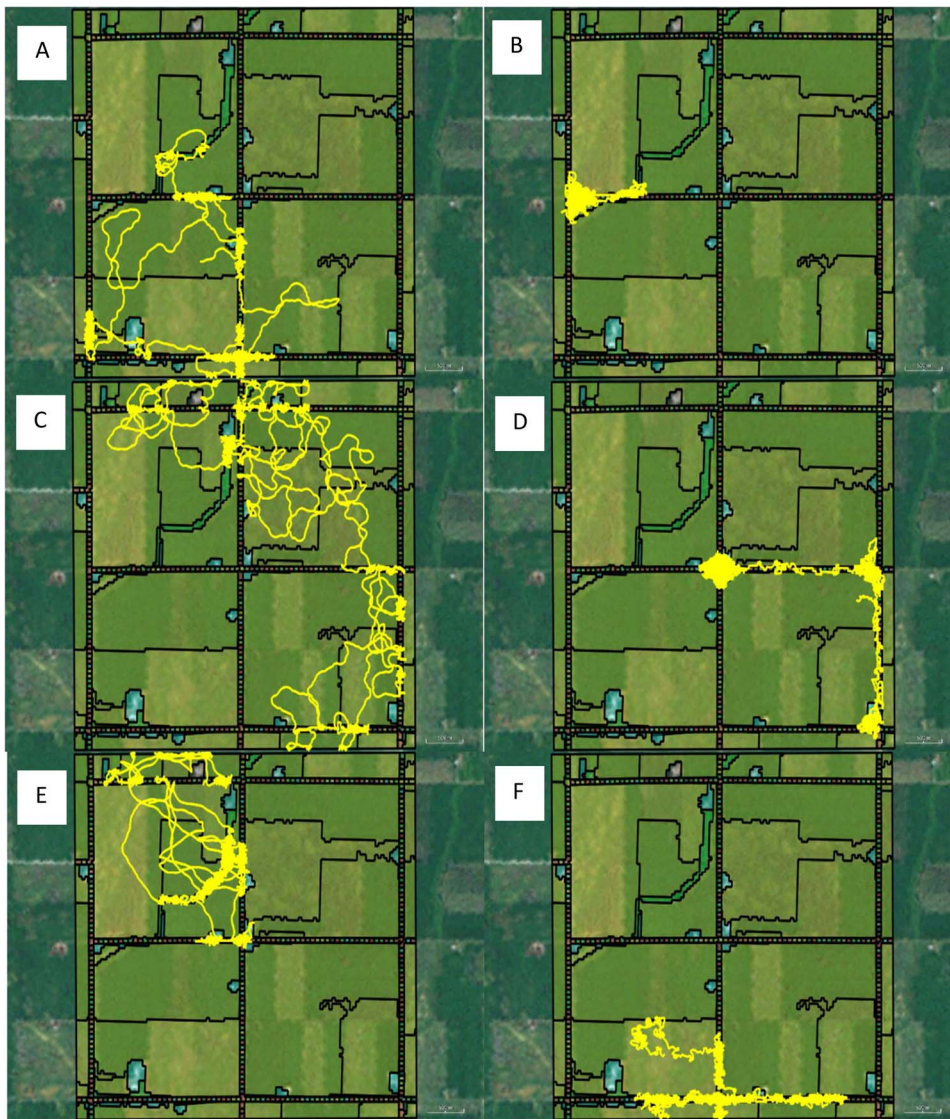
Fig. 5. Monarch agent movement paths under different parameter combinations. Each panel is the movement path for one monarch agent over ten days in a 1274 ha subset of Story County. Parameters are abbreviated as perceptual range = p, spatial memory = m, directionality = d, step length = s and units are as follows: perceptual range is meters, spatial memory is number of patches, directionality is categorical and has no units, and step length is meters. Panel A: p = 50, m = 10, d = 0.5–0.75, s = 30. Panel B: p = 400, m = 10, d = 0.5–0.75, s = 30. Panel C: p = 50, m = 100, d = 0.5–0.75, s = 30. Panel D: p = 400, m = 100, d = 0.5–0.75, s = 30. Panel E: p = 50, m = 10, d = 0.1–0.9, s = 30. Panel F: p = 50, m = 10, d = 0.1–0.2, s = 30 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

depending on the parameterization. This is largely due to the high resolution, large-scale spatial dataset used, and thus a large number of habitat patches iterated and stored in memory. Code profiling revealed that the most computationally-intensive operations were calculation of the area of overlap of the perceptual range buffer and the habitat patches.

2.10. Analysis

We begin with a comparison of graphical output of movement paths under a variety of parameterization scenarios. Visual inspection of model output is an important aspect of model evaluation (Bennett et al., 2013) and in our case provides important insight into movement patterns because observations of monarch flight at the spatial scales simulated in the model are not available in the scientific literature. We asked five experts in monarch butterfly behavior to independently evaluate the simulated movement patterns (see Acknowledgements). The experts provided opinions as to which panels in Fig. 5 best represent female monarch movement paths as well as the characteristics of the movement paths that formed the basis of their opinion.

Subsequently we estimated the egg density in habitat patches in a subset of Story County, including estimates of the proportion of eggs laid in each land-cover type. Because of the uncertainty in some parameters, we examine the distribution of the proportion of eggs laid in

each land-cover type across all 25 parameter combinations as described below.

Global uncertainty analysis (Marino et al., 2008; Thiele et al., 2014) was used to investigate responses of model outputs (utilization distribution; mean proportion of eggs laid per agent on day five; median egg density per grass/pasture patch; median egg density per road ROWs; total eggs laid in grass/pasture patches; total eggs laid in road ROWs, and total eggs laid in the study area) to uncertainty in four monarch parameters: perceptual range, spatial memory, directionality, and step length. This analysis provides insight into how these factors affect movement and egg-laying of monarch agents. Step length has important effects on model outputs. For example, the number of eggs laid per meter moved depends on step length because we kept the number of eggs laid per step constant (i.e., two eggs are laid at the end of each step, assuming the agent choses to lay eggs, regardless of step length). Consequently, smaller step lengths should result in a larger number of eggs laid per meter. Four values were evaluated per parameter (see Table 3), which results in 256 (4^4) possible parameter combinations for the uncertainty analysis. Twenty-five parameter combinations were selected using Latin Hypercube sampling (McKay and Beckman, 1979; R package *lhs*).

Perceptual range, spatial memory, and step length were treated as continuous variables. Directionality was treated as a categorical variable and considered in four scenarios. For each scenario, directionality
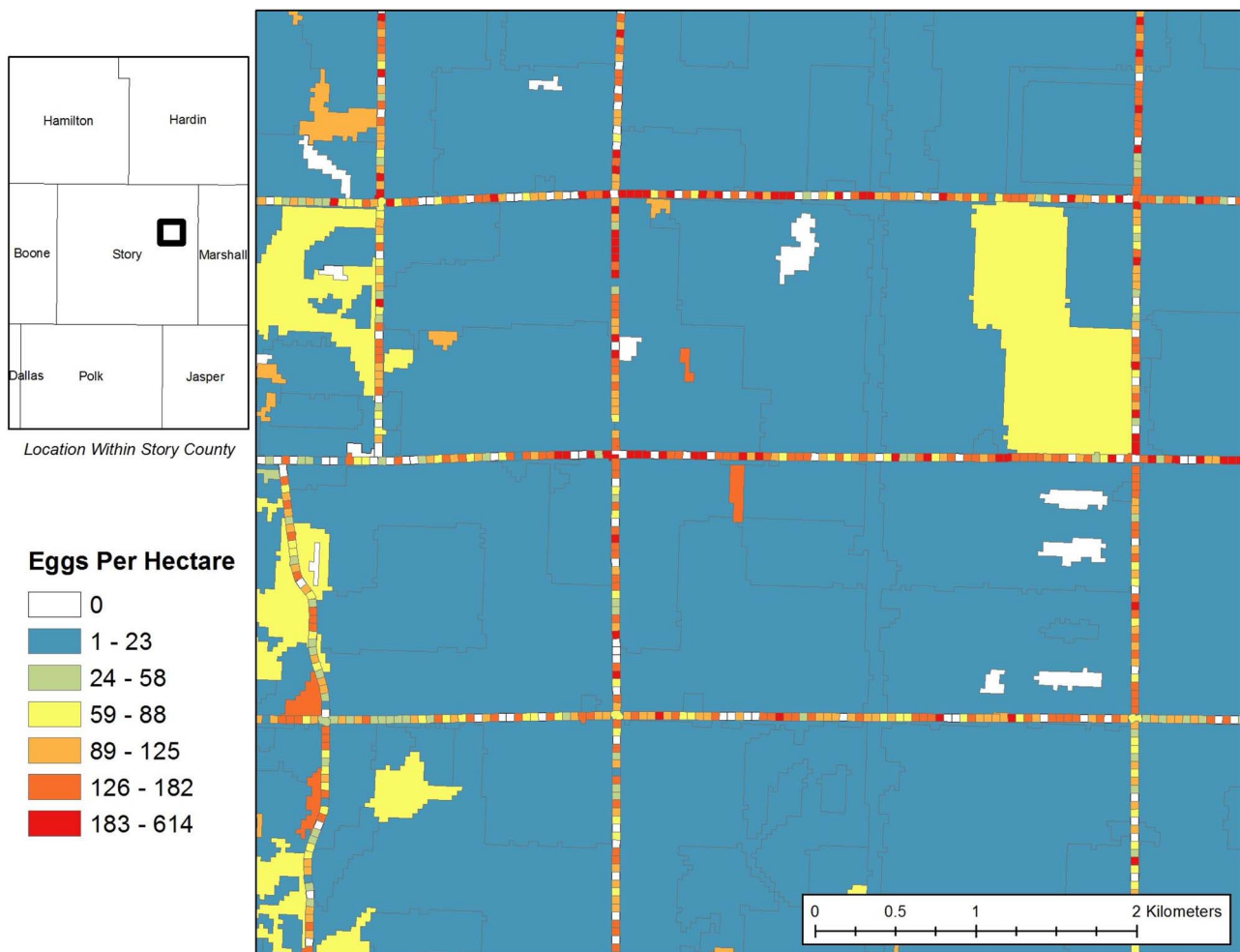
Fig. 6. Example egg density from a model simulation. Agricultural fields with glyphosate-resistant crops (blue) have very low egg density. Roadsides have variable density. Grass/pasture and non-glyphosate resistant agricultural fields have medium egg density (yellow or orange) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

varied from D_{min}, the minimum directionality that occurs in good habitat, to D_{max}, the maximum directionality that occurs in poor habitat. The four scenarios were: low directionality in good habitat ($D_{min} = 0.1$) and poor habitat ($D_{max} = 0.2$), low directionality in good habitat ($D_{min} = 0.1$) and high directionality in poor habitat ($D_{max} = 0.9$), an intermediate scenario ($D_{min} = 0.5$ and $D_{max} = 0.75$), and high directionality in good habitat ($D_{min} = 0.8$) and poor habitat ($D_{max} = 0.9$).

As discussed previously, the model incorporates a correlated random walk in patches outside the monarch agents' perceptual range and a decision-based movement algorithm when two or more different habitat patches are adjoined within the perceptual range. The outcome of the decision-based movement algorithm is dependent on assumptions of perceptual range and spatial memory. An uncertainty analysis including a null assumption that perceptual range is 0 m was not included given the literature (see 2.4.7) that documents monarchs do perceive milkweed and nectar sources through visual and olfactory cues. However a null assumption of no spatial memory was included in the uncertainty analysis, given the more tenuous nature of the best available experimental data.

Simulation results were analyzed using a linear multiple regression meta-model (Thiele et al. 2014). Exploratory analyses indicated that a multiple regression approach was sufficient because the relationships between model output variables and monarch parameters were generally linear; i.e., R^2 was above 0.7, which is the cutoff recommended by Saltelli et al. (2004, 2008). We report the amount of variation in the response variable explained by each parameter using a sensitivity index

(Saltelli et al., 2004, 2008). Sensitivity S_i, for parameter i, is calculated as:

$$S_i = \frac{SS_i}{SST} \tag{4}$$

Where *SST* is the total sum of squares and SS_i is the sum of squares for parameter i when it is first in the model. Regression coefficients and graphs of predicted response variables are provided in the Supplementary materials C. Because the parameters are non-orthogonal, the order of variables in the linear regression affects the direction of the regression coefficients. Consequently, the four predictor variables were added to the model using a stepwise algorithm (using package *stepAIC* in R, with lowest AIC variables added first).

3. Results

Simulated movement behavior of monarch butterflies are depicted in (Fig. 5) Under all 25 model parameter combinations, we found that the simulated monarch agents spent their time in areas with high milkweed density, such as road ROWs, with occasional forays into agricultural fields where milkweed was modelled as rare or non-existent. A correlated random walk alone, in which monarch agents do not respond to land cover types, would not replicate these movement paths. Four of the five expert panelists considered panel C to be the best representation of monarch movement paths, while one panelist considered panel A to be the best parameterization. All of our panelists

generally cited similar rationale for choosing C or A: female monarch butterflies move long distances across the landscape, do not stay in one habitat patch for long, and are a vagile species that disperses their eggs widely.

The amount of time monarch agents spent in agricultural fields and how far they moved across the landscape was affected by the parameter values (see Fig. 5A–F). With a long perceptual range (400 m) the monarch agent remained at the cluster of patches at a road intersection and failed to leave that cluster (Fig. 5B), whereas with a 50 m perceptual range the monarch agent moved more widely (Fig. 5B). Agents with longer term spatial memory (100 patches remembered) formed less dense clusters of movement in road ROWs (Fig. 5B) relative to those with fewer patches remembered (10 patches remembered, Fig. 5A). Longer-term spatial memory resulted in monarch agents more readily leaving a location and finding higher-quality habitat not previously visited. Although longer-term spatial memory (100 remembered patches) allows a monarch agent to occasionally leave clusters of patches at road intersections, large perceptual range (400 m) results in the agent utilizing much less of the landscape (Fig. 5D), as compared to an agent with a shorter perceptual range (50 m, Fig. 4A) (Fig. 5D). When directionality is high in poor habitat (0.9, Fig. 5E, the agent movement path is more linear as compared to tortuous movement paths with low directionality in poor habitat (0.02, Fig. 5F).

The land-cover types that accumulated the most eggs in the model, across all 25 parameter combinations, were road ROWs, grassland/pasture, and non-glyphosate resistant corn (Fig. 6, 7,). The proportion of eggs laid in ROWs (19%–49%) was highly variable across simulations, indicating that more precise values for perceptual range and spatial memory would reduce variability in quantifying use of ROWs. Grassland and pastures have the next highest accumulated eggs, varying from 24 to 42% of eggs laid. Non-glyphosate resistant corn constitutes 12% of the corn fields and is assumed to have relatively good higher milkweed density, consistent with 15–34% of eggs being laid in these patches. All other habitats accumulate relatively few eggs.

3.1. Effect of varying perceptual range on monarch movement and egg-laying

Perceptual range had an important effect on how monarch agents move and how eggs were distributed across the landscape (Table 4). Except for step length, which is a model construct, perceptual range explained more of the variance in utilization distribution, median egg density in road ROWs, and median egg density in grass/pasture, than spatial memory or directionality. Larger perceptual ranges resulted in monarch agents failing to move from groups of patches with high milkweed density, resulting in smaller utilization distributions (see Supplementary material B and C). A small perceptual range resulted in a higher median egg density in road ROWs as well as more evenly distributed eggs in these patches (Fig. 8). With a large perceptual range, median egg density was lower because eggs accumulated in a few patches, and many patches had few or no eggs (Fig. 8). Median egg density decreased in both road ROW and grass/pasture habitat as perceptual range increased, though more so in road ROWs (Supplementary material B and C). The proportion of eggs laid and total eggs laid in road ROWs, grass/pastures, and the full study area, were largely unaffected by changes in perceptual range, contrary to our hypothesis (Supplementary Material B and C). In summary, perceptual range affected where eggs were laid on the landscape, but not the cumulative total number of eggs.

3.2. Effect of varying the spatial memory on monarch movement and egg-laying

Spatial memory was the most important factor affecting the total eggs laid in road ROWs, other than step length (Table 4). Longer spatial memory decreased the total number of eggs laid in road ROWs, consistent with our hypothesis (see Supplementary Material B and C). Spatial memory explained 10–18% of variation in utilization distribution, proportion of eggs laid, median egg density in grass/pasture, and total eggs laid in the study area. Spatial memory explained very little of the variation in total eggs laid in grass/pasture. Increasing spatial memory increased the area of the utilization distribution, consistent with our hypothesis (Supplementary Material B and C). Longer term spatial memory also decreased the proportion of eggs laid, the total eggs laid in the study area, and the median egg density in grass/pasture (Supplementary material B and C).
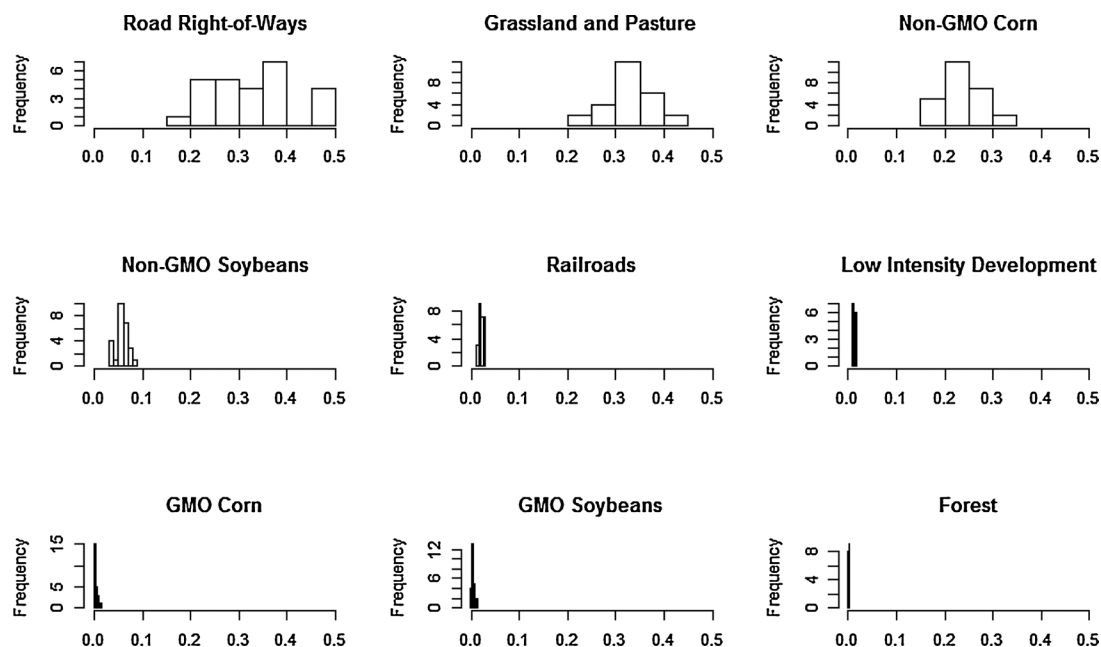

Fig. 7. Histograms of the proportion of eggs laid in each habitat type across all 25 parameter combinations. Road right-of-ways are combined for this figure. Other crops and wetlands had negligible proportions, similar to forest, and are not shown.

Table 4
Sensitivity indices for four parameters and six response variables, and R² statistics. Sensitivity indices were calculated as the Type I sum of squares for a parameter divided by the total sum of squares and range from 0, when a change in one unit of the parameter results in no change in the response variable, to 1, when a change in one unit of the parameter results in a change of 1 unit in the response variable.

Response Variable	Perceptual Range	Spatial Memory	Directionality	Step Length	R^2
Utilization Distribution	0.29	0.16	0.18	0.46	0.84
Proportion of Eggs Laid	0.02	0.12	0.40	0.89	0.95
Median Egg Density (Road ROWs)	0.57	0.18	0.13	0.02	0.84
Median Egg Density (Grass/Pasture)	0.37	0.10	0.26	0.21	0.76
Total Eggs Laid (Road ROWs)	0.03	0.25	0.08	0.59	0.71
Total Eggs Laid (Grass/Pasture)	0.01	0.05	0.44	0.72	0.84
Total Eggs Laid (Study Area)	0.02	0.12	0.40	0.89	0.95
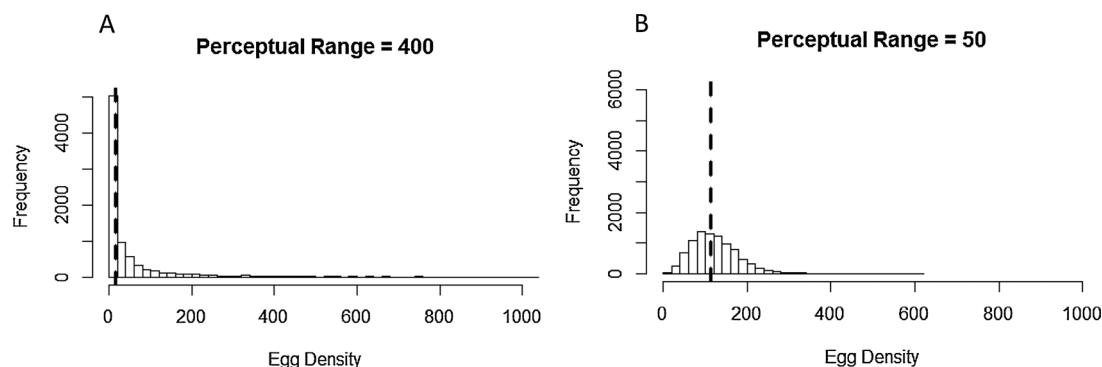
Fig. 8. Histogram of egg density (eggs/ha) among high density milkweed road ROW patches for a simulation where perceptual range = 400 m (A) and a simulation where perceptual range = 50 m (B). The vertical dotted line is at the median. The x-axis scale for A has been constrained to 0–1000 for comparison to B, though the range of egg density for A is 0–11,108.

3.3. Effect of varying directionality on monarch movement and egg-laying

Directionality explained 40–44% of variation in proportion of eggs laid, total eggs laid in grass/pasture, and total eggs laid in the study area (Table 4). When directionality was low (0.1) in good habitat, monarch agents stayed longer in grass/pasture habitat and laid more eggs, thus increasing the values of the above mentioned output parameters (Supplementary material B and C). Directionality explained 18% of the variation in utilization distribution area. High directionality in poor habitat increased the area of the utilization distribution as monarch agents moved farther from places they had been, especially those areas without milkweed such glyphosate-resistant corn and soybean fields (Supplementary material B and C). Directionality had the smallest effect on egg density in road ROWs and total eggs laid in road ROWs (Table 4). Higher directionality in good and poor habitat increased median egg density in road ROWs, and total eggs in road ROWs to some degree (Supplementary material B and C), likely because agents moving in straighter movement paths were more likely to find a road ROW.

3.4. Effect of varying step length on model output

Step length explained the largest proportion of variation in all response variables except median egg density in road ROWs and median egg density in grass/pasture (Table 4). Longer step lengths increased the area of the utilization distribution, but decreased all other response variables (Supplementary material B and C). Longer step lengths lead to farther movement, increasing the area of the utilization distribution, but longer step lengths meant fewer opportunities to lay eggs, decreasing all other response variables.

4. Discussion

Perceptual range is implicitly included in many individual-based models as the local area with which an agent may interact (Wallentin, 2017), but spatial heterogeneity of habitat within that perceptual range, as we have modelled here, has rarely been included in

individual-based models. Our results show that perceptual range and spatial memory can be critical input parameters. Lima and Zollner (1996) called for increased attention to the impacts of animal behavior at the landscape scale and Wallentin (2017) specifically called for more attention to spatial structure as a constraint on animal movement in spatial simulation studies. We found that perceptual range, in particular, has a dramatic effect on how monarch agents move and lay eggs on the landscape. Perceptual range in monarch butterflies, as with most phytophagous insects, is poorly understood (Garlick, 2007; Cardé and Willis, 2008), but has important implications for model behavior. When perceptual range was large, the model estimated that monarch agents have a much smaller utilization distribution and lay eggs in relatively few habitat patches. With a small perceptual range, eggs are more evenly distributed on the landscape. Monarch butterflies are a vagile species (Zalucki and Kitching, 1984; Ries and Debinski, 2001; Zalucki and Lammers, 2010) and our modelled movements with a smaller perceptual ranges are consistent with such behavior. Experimental determination of perceptual range up to several 100 m in free-ranging monarch butterflies will aid in refining this model input.

Increasing spatial memory can influence monarch agent movement, but the effect is most apparent at fine scales. The habitat in road ROWs is comprised of relatively small patches. As a result, monarch agents can avoid a patch visited in recent steps, which results in lowered egg densities in road ROWs as spatial memory increases (See Supplemental material B and C). In larger grass/pasture patches, which have an intermediate milkweed density value, and in which several steps can be required to leave a patch, there is no decline in total eggs in grass/pasture patches as spatial memory increases (see Supplemental material B and C) and a marginal trend of lower egg density (Supplemental material B and C). This response may reflect that while monarch agents 'remember' a large grassland/pasture patch visited in previous steps, once back in the patch it may take numerous steps before they depart a large area with a moderate milkweed density. Our model does not currently include spatially-explicit placement of 'high density' milkweed patches within the grass/pasture patches, because there is no systematically collected data available on milkweed patch sizes, stem

densities and spatial distributions for this land cover class. Collection of field survey data on milkweed patch characteristics within larger land cover classes, such as grass/pasture, would permit an evaluation of the extent to which estimated total eggs or egg density in a large patch is sensitive to spatial memory of explicitly located, high density milkweed patches.

Our results showed that different model parameterizations had little effect on the total number of eggs laid in Story County, even though the monarch agents exhibited a diversity of complex movements and associated egg density patterns in the landscape. The finding that total eggs laid did not significantly vary may be related to the observation that random walk models approximate a diffusion process at some scales and with large sample sizes (Turchin, 1998; Codling et al., 2008). While diffusion models can play an important role in quantitative movement analysis (Turchin, 1998), in our case a diffusion approximation would obscure movement and egg distribution patterns that have implications in predicting population responses. For example, higher rates of parasitism and predation likely occur in patches with high monarch and/or milkweed densities (Zalucki and Kitching, 1982c; Bartel et al., 2011; Stenoien et al., 2016). Thus, it is critical to predict where eggs will be laid in the landscape as well as how many eggs will be laid to fully inform conservation benefits and risks of different habitat restoration scenarios.

Directionality had the greatest effect on the mean proportion of eggs laid, the total eggs laid in the study area, and total eggs laid in grass/pasture. Less directionality in good habitat resulted in more eggs laid overall, likely because monarch agents executed more steps in grass/pasture patches and therefore laid more eggs. Field observations indicate that directionality is higher for monarchs in poor habitat (straighter flight patterns) and lower (more tortuous patterns) in good habitat (Zalucki and Kitching, 1982b; Zalucki, 1983).

Step length is a discrete representation of a continuous process (Turchin, 1998) and thus has an effect on model results. We found that step length affected the total eggs laid in grass/pastures, road ROWs, and the county because the egg-laying rate (number of eggs laid per m) was different with different step lengths. The sensitivity of the model to step length will be an important issue to address when attempting to estimate absolute numbers of eggs laid. Egg-laying rate can easily be fixed as a constant rate per m independent of step length, similar to the model of Parry et al. (2017), but empirical data is needed to determine monarch egg-laying rates in different land cover types. Nail et al. (2015) reported an average of 0.043 eggs per milkweed, or 1 egg per ~23 milkweed, in the sites they surveyed, but such data is not easily converted to an egg-laying rate. Additional empirical data is needed to reasonably estimate egg-laying rate in a variety of land cover types with different milkweed densities.

Regardless of egg-laying rate, step length also affected the utilization distribution. To control for the effect of step length on utilization distribution, future versions of the model could refine the movement algorithm. Movement decisions could be based on habitat evaluations that occur at a constant rate that is independent of the step length (currently decisions are made at the end of each step length). Alternatively, a variable step length could be drawn from a distribution derived from empirical observations of distances traveled in set time-periods. Zalucki and Kitching (1982b) found natural monarch step lengths to be auto-correlated, another consideration for precise modeling of step lengths. Systematic observational data of wild monarchs flight steps in a variety of Iowa and Midwestern landscapes would provide the information needed to ascertain the extent to which future model calibration or refinement is needed.

The landscape we evaluated has patches of vastly different sizes, which has implications for model behavior. For example, modeling monarch movement in the narrow but abundant road ROW habitat is critical. A correlated random walk would not capture monarch movement well in such a long, narrow habitat. Further, the road ROWs are quite heterogeneous in milkweed density, with patches of various sizes

scattered throughout (Hartzler, 2010; Kasten et al., 2016). Because of the long, narrow nature of the road ROW habitat, it was necessary to model this heterogeneity as a grid. Corn and soybean fields, on the other hand, are highly homogeneous habitat and a correlated random walk is likely adequate for modeling movement in these patches. Grassland and pastures have more heterogeneity than corn fields, but because they are typically in larger blocks a correlated random walk appears adequate to model movement. As discussed previously, empirical data is needed to better quantify and model heterogeneity within grass/pasture habitat.

Coordinating experimental studies with the development of mathematical models can provide an efficient means to advance knowledge (Restif et al., 2012). In this case, development of the model and evaluation of its outputs identified areas of additional research that would help reduce uncertainty in assigning attributes to monarch agents (i.e., perceptual range, spatial memory, step length), land cover patches (e.g., milkweed density in different land cover classes) and model outputs (e.g., egg densities in multiple habitat patches in adjoining land cover classes). For example, while Kasten et al. (2016) found increasing monarch egg density with increasing milkweed density in ROWs, consistent with model predictions, to more fully evaluate the model's predictions requires egg density data sets in adjoining land cover classes and at a spatial scale similar to that used in the model. Large scale monitoring programs for monarchs and milkweed, which are being designed and piloted (e.g., MJV 2016), may provide the needed information, in particular milkweed density and egg density estimates from a statistically rigorous sampling scheme for the land cover types in our model. Comparing experimental or field survey data to model outputs is, however, not the only approach to evaluate uncertainty in physical and mathematical models (Wallentin, 2017; Batty and Torrens, 2005). As noted previously, additional experimental research can advance fundamental understanding of monarch behavior and, in turn, advance the mechanistic basis of the model's movement algorithm. Our uncertainty analysis establishes high priority areas of additional research that include improved understanding of perceptual range and spatial memory.

The effect of landscape configuration on egg density in individual patches also needs to be evaluated in future modeling and empirical studies. Model results indicated some patches that have identical size, shape, and milkweed density have varying egg densities. This varying egg density is likely a function of the landscape configuration of surrounding patches. Various measures of landscape configuration and composition have been developed. Comprehensive modeling and field surveys are needed to identify factors that render some habitat patches better egg-laying sites than others. Model results to date inform several hypotheses about how landscape configuration factors might affect egg density. For example, the distance of a habitat patch to a road ROW seems likely to affect the ability of monarchs to find the patch. Employing a proximity index, i.e., the amount of habitat within a certain distance of a patch, may provide some insights (Gustafson and Parker, 1992). Because of the extensive pattern of corridors and isolation of individual patches that are not road ROWs, an analysis of connectivity may provide insights (Kindlmann and Burel, 2008). A sound understanding of the effect of landscape configuration will maximize habitat restoration effectiveness by providing the information necessary to create habitat patches that will attract high egg density.

Conservation planning is typically made in the face of uncertainty (Polasky et al., 2018). Formulation of habitat restoration options to support monarch butterfly conservation is no exception. Based on correlations of trends in estimated milkweed stems in the North Central U.S. to estimated annual overwintering monarch populations, habitat conservation goals expressed as the number of new milkweed stems have been proposed at the county level assuming a uniform distribution of stems in different land cover classes (Thogmartin et al., 2017; Rohweder and Thogmartin, 2015). Translating these goals into explicit landscapes with habitat patches of varying quality and in different

spatial patterns is needed to predict realized fecundity based on current and future conservation management practices. Our simulation of female monarch movement, which assumes spatial memory, and subsequent egg laying in a spatially-explicit agricultural landscape in the North Central U.S, suggests establishment of a relatively large number of small habitat patches dispersed at distances within the monarch's perceptual range will result in greater realized fecundity, and subsequent adult recruitment, rather than establishment of a smaller number of large habitat patches that are dispersed at distances beyond the perceptual range. The model presented here provides context to prioritize experimental studies to reduce uncertainty in monarch movement behavior and to formulate landscape-scale survey designs to assess monarch habitat utilization. The modeling framework can also contribute to decision-support tools needed by county, state or regional planning groups exploring the relative benefits of different conservation strategies for enhancing habitat in different land cover classes. Our model provides the foundation to help address challenging monarch butterfly conservation management issues by linking broad scale goals to fine scale spatial configuration of milkweed patches.

Acknowledgments

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.02.011.

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