### **RESEARCH ARTICLE**

# A priori assessment of reintroduction strategies for a native ungulate: using HexSim to guide release site selection

Patrick R. Huber · Steven E. Greco · Nathan H. Schumaker · Joe Hobbs

Received: 25 March 2013/Accepted: 14 February 2014/Published online: 4 March 2014 © Springer Science+Business Media Dordrecht 2014

Abstract Reintroduction of native species to unoccupied portions of their historical range is a common management strategy to enhance the future viability of animal populations. This approach has met with mixed success, due to unforeseen impacts caused by human or other factors. Some of these impacts could potentially be mitigated through the use of anticipatory modeling coupled with appropriate management strategies prior to release. As part of an ongoing restoration program, we evaluated a portion of the former range of the tule elk (Cervus elaphus nannodes) in the Central Valley of California for potential reintroduction of a free-ranging herd. We used a new spatially explicit population model (HexSim) to analyze four different elk release scenarios. Each scenario corresponded to a different release location, and the model was used to compare simulated elk

**Electronic supplementary material** The online version of this article (doi:10.1007/s10980-014-0006-2) contains supplementary material, which is available to authorized users.

P. R. Huber (⊠) · S. E. Greco University of California, Davis, One Shields Ave., Davis, CA 95616, USA e-mail: prhuber@ucdavis.edu

N. H. Schumaker U.S. EPA, 200 SW 35th St., Corvallis, OR 97333, USA

#### J. Hobbs

California Department of Fish and Wildlife, 1812 9th St., Sacramento, CA 95811, USA

movement and population dynamics 25 years into the future. We also used HexSim to identify likely locations of human–elk conflict. Population forecasts after the 25-year period were highest (mean female population size of 169.6 per iteration) and potentially harmful barrier interactions were lowest (mean 8.6 per iteration) at the East Bear Creek site. These results indicate the East Bear Creek site release scenario as the most likely to result in a successful elk reintroduction, producing the most elk and generating the fewest human conflicts. We found HexSim to be a useful tool for this type of reintroduction planning and believe that other reintroduction efforts could benefit from this type of anticipatory modeling.

**Keywords** SEPM · Population modeling · Tule elk · Human–wildlife conflict · Movement modeling · Grasslands Ecological Area

### Introduction

Globally, many animal species have been eliminated from portions of their historical range. One tool available to land managers to help remedy this problem is the reintroduction or translocation of animals that have either been bred in captivity or captured in remaining portions of the species' range (Morrison 2009). Some successful examples of reintroductions include black-footed ferrets (Biggins et al. 1998), gray wolves (Mao et al. 2005), and California condors (Ralls and Ballou 2004). However, not all reintroduction efforts succeed in re-establishing viable populations in historical ranges (e.g. Hedrick and Fredrickson 2008). There are many potential reasons that these efforts may fail, including: lack of suitable habitat, disease, human-caused mortality, competition with native and non-native species, and genetic concerns. Fortunately, some of these complications can be anticipated and addressed prior to reintroduction actions, in order to enhance the prospects of a successful recolonization event (Hopfensperger et al. 2007).

A number of issues that can significantly influence the probability of success of reintroduction efforts can be addressed using spatially explicit population models (SEPM). SEPMs have been used to explore patch occupancy (Rushton et al. 1997), source-sink dynamics (Wiegand et al. 1999), population viability (Alderman et al. 2005), invasive species (Almasi and Eldridge 2008), trophic interactions (Bianchi et al. 2007), future land use scenarios (Schumaker et al. 2004), and many other topics. These types of studies link demographic data with specific geographies to assess populations over time, and can be valuable tools for land planners and managers.

Many of the SEPMs used in these types of studies were developed specifically for use in a particular case. However, some SEPMs have been created for general use across species and locations. One of these that has been used a number of times over the past decade is PATCH (Schumaker 1998). This model has been used by various researchers to investigate future land use alternatives (Rustigian et al. 2003), habitat quality (Lawler and Schumaker 2004), resource selection functions (Carroll and Miquelle 2006), wolf reintroduction (Carroll et al. 2003), and habitat conservation opportunities (Spencer et al. 2011). PATCH is a stochastic model that couples spatial data with life history information to estimate population size, distribution, and viability.

In spite of its fairly wide application, the PATCH model was not flexible enough to simulate the complex life histories typical of many mammals, birds, amphibians, reptiles, and other taxa. In response, the PATCH model developers created HexSim (Schumaker 2010) to overcome these shortcomings. One of the features that distinguishes HexSim from its predecessor is the ability to model group, or herd, movement. This is accomplished through use of a "proto-disperser", an imaginary

individual that explores the landscape, finds resources, and then serves as a movement target for the other group members who converge on this target. This feature allows for modeling of both individuals and groups.

Another useful feature of HexSim is the barriers component. Multiple types of movement barriers can be included in the model, reflecting likely responses to various kinds of blockages to wildlife. Because many of these barriers tend to be human-related, this feature allows for assessing the potential impacts of multiple types of human infrastructure and landscape features on modeled species.

This paper examines several reintroduction scenarios for returning an endemic elk subspecies (tule elk; *Cervus elaphus nannodes*) to a portion of its native range in California, USA. We used data from other elk herds in California as well as expert knowledge of team members (where the data did not exist) to populate HexSim parameters. HexSim was then used to project future herd numbers and detrimental elkhuman interactions resulting from different potential release locations. Our results will be of use to land managers in their reintroduction efforts.

### Methods

### Tule elk

Tule elk is one of three subspecies of elk found in California. It is a California endemic subspecies originally found throughout the Central Valley and Central Coast regions of the state (McCullough 1969). The habitat preferences of tule elk are associated with the semi-arid climate of central California. They use open grasslands, freshwater wetlands (from which their common name is derived), and riparian areas to a much greater extent than do other elk subspecies (Huber et al. 2011). While tule elk no longer display distinct long-distance seasonal migration patterns, they have been observed to move regularly throughout an annual home range as a result of the effects of seasonal variation on forage and cover resources in a Mediterranean climate. While an estimated 500,000 tule elk inhabited California 200 years ago, their numbers rapidly declined with hunting and the largescale conversion of land to agriculture associated with the advent of the gold rush in the mid-nineteenth century. By the 1870s, the population had been reduced to less than ten and possibly as low as two individuals, all found on one ranch in the San Joaquin Valley (McCullough 1969; Williams et al. 2004). Beginning with these few individuals, captive breeding began and numerous re-introduction efforts (Koch 1987) have been undertaken over the past century, leading to the current population status of an estimated 3,900 individuals comprising 22 herds statewide (McCullough et al. 1996, Greco et al. 2009). Nearly all of the current herds are found in the Central Coast region and there are currently no free-ranging herds in the Central Valley portion of their former range.

### Study area

While the vast majority of the Central Valley in California has been converted to agricultural or urban land uses and thus rendered unusable for tule elk habitat, there are several remaining natural areas of size and quality sufficient to serve as tule elk habitat. One such block, the Grasslands Ecological Area (GEA), is located in the San Joaquin Valley. The GEA is approximately 90,000 ha located in central Merced County, on the floor of the Central Valley (Fig. 1). It consists of a mosaic of grasslands, freshwater wetlands, and riparian forest, embedded in an agricultural matrix. This landscape also includes highways (several of which bisect the GEA) and canals (including the concrete-lined San Luis Drain). Both of these features can be harmful to individual tule elk and, in the case of car-elk collisions on highways, to motorists as well.

Privately held land in the GEA is comprised mostly of agricultural fields, grazing land, or waterfowl hunting clubs. In addition, grazing is permitted on some of the public lands in the GEA because it can



Fig. 1 Study area—Grasslands Ecological Area and vicinity

help control some invasive weeds and can promote plant diversity. The hunting clubs consist mostly of seasonal wetlands managed for waterfowl production. These properties generally receive large amounts of human visitation.

# Re-introduction alternatives

This study assessed four possible reintroduction scenarios designed to establish a free-ranging, self-sustaining herd of tule elk to their native habitat in the GEA. We initially identified multiple candidate release sites based upon habitat quality (Huber et al. 2011). Then, the performance of each possible release site was evaluated using the simulation model. The candidate release sites (Fig. 2) were as follows:

• *Kesterson scenario* Tule elk released in this scenario would have access to all three major land cover types, including riparian forest in the San Joaquin River floodplain to the north of the release

site. The proximity of the concrete-lined San Luis Drain could potentially lead to detrimental effects on individual elk encountering this feature.

- Arena Plains scenario The land cover in the vicinity of the release site consists of grassland and freshwater wetland, but little riparian forest. This release site is situated on habitat of somewhat lesser quality than that of the other three modeled sites. However, it is further away from both California Highway 165 and San Luis Drain than are the other three scenarios.
- *San Luis scenario* This area, located in a mosaic of the three major natural land cover types, is near the center of the largest expanse of high quality habitat in the GEA (Huber et al. 2011). California Highway 165, a heavily traveled north–south corridor bisecting the GEA, is approximately 3 km to the west of the release site.
- *East Bear Creek scenario* Similar to the San Luis scenario, this release site is in the largest expanse of high quality habitat in the GEA. It too is



Fig. 2 A schematic of how the HexSim herd movement function works. A "protodisperser", "A", is created and allowed to move across the modeled landscape until suitable habitat is found. Then the modeled animals, "B", move toward A's stopping place following user-defined movement rules adjacent to the San Joaquin River levee, although east of the river rather than west. As such there is ready access to riparian forest, in addition to grassland and freshwater wetlands.

### HexSim inputs

HexSim is a simulation framework within which PVA and other models are constructed. HexSim simulations can range from simple and parsimonious, at one extreme, to complex, data intensive, and biologically realistic at the other. Our tule elk simulations were moderately complex, capturing major life history events such as survival, reproduction and movement, while ignoring other details such as impact of environmental stochasticity or the spread of diseases through the population. A full description of our tule elk model is provided in Appendix A in Supplementary Material.

All four modeled reintroduction scenarios were identical except for the initial population placement; therefore we used the same habitat data for all four scenarios. All scenarios were run for 100 replicate simulations, at 25 time steps (i.e. years) per replicate. We only considered female elk in the model. It is common to only females when modeling animal populations given that they often can be expected to have access to males and that female persistence is necessary (if not sufficient) for a release strategy to be considered successful.

#### **Populations**

Each scenario started with the release of four female elk at the reintroduction sites. No elk are currently found at these sites. We used an upper limit of 50 females in a herd; after this point the model forces individuals to split away and form a new herd.

The maximum space that an individual was allowed to occupy during any given event was set at 120 ha. This is approximately double the area used per individual as observed from the Cache Creek herd (O'Connor 1988) and was chosen to allow for use of larger areas of non-optimal habitat. Elk had access to all habitat types except urban land cover types.

Each individual requires access to minimum resources for survival. We set this resource target for adult elk equal to 10 ha of habitat with moderately high resource value. For comparison, tule elk at Grizzly Island NWR (a location with very high quality resources) use roughly 4 ha per individual. We chose to use the parameter inputs described above in order to take a more conservative approach in the ability of the GEA to provide necessary tule elk resources. We assumed that juvenile and adolescent tule elk would require half the resources of an adult.

We assumed that the four released individuals would be between 3 and 7 years of age, i.e. healthy adults. We set a maximum age for tule elk at 15. We established four age classes: juvenile (0-1 years old), adolescent (1-2), adult (2-11), and old (11-15). At the end of each time step, each individual ages 1 year.

#### Event (movement)

We established three movement events for the elk over the course of each time step: to their natal area, to resources, and to successful breeding areas. For all movement events, dispersal occurred first followed by exploration of the area to which the individuals dispersed

The mean dispersal distance for movement to resources was set at 20 hexagons (i.e. slightly greater than 2.1 km) while the maximum distance was set to 100 hexagons (i.e. slightly less than 11 km). These parameter values were chosen based on expert knowledge of typical dispersal patterns observed by California Department of Fish and Wildlife (DFW) biologists. Distances for movement events towards natal and successful breeding areas were set to smaller values (mean of 10 hexagons, maximum of 20 hexagons). These values were selected based on the belief that tule elk would range farther in the quest for necessary resources than to return to exact natal and breeding sites. While tule elk in general will move towards these areas that have been used in the past, it is not imperative that they make a full return to these sites.

The direction of dispersal for the resource-based movement event is set by a "proto-disperser", a temporary individual that moves across the landscape until it locates new suitable habitat (Fig. 2). True individual modeled elk will generally aim for the "proto-disperser" while being influenced in their movement by the habitat quality they encounter while doing so (i.e. avoiding less suitable habitat). Once the modeled elk have completed the movement event, the "proto-disperser" is removed from the model. We set auto-correlation to cause individuals to be repulsed by hexagons with resource scores of 0–10 and attracted by scores of at least 75 in the course of their movement towards the "proto-disperser". These auto-correlation values were used during natal and breeding movement events, only with destination targets set by past events rather than the "proto-disperser". Individuals dispersing towards resources would not necessarily arrive at the stopping place of the "proto-disperser"; they would stop if they experienced a mean resource score of 50 across a path length of ten hexagons. In essence, during this event, individuals move until they find a patch of relatively good habitat.

Once individuals are finished dispersing, they explore the immediate vicinity for resources to meet their resource targets. For resource movement events, maximum search area is set to 100 hexagons, while for the other two movement events a maximum of 50 is used (as the elk are moving back towards known habitat and not for the purpose of maximizing resources). All movement events require individuals to leave the herd (i.e. turn into "floaters"), so in order to re-form the herd while exploring, their goal (in addition to resource acquisition) is to re-join an existing herd if possible and if not, to start a new herd.

#### Event (reproduction)

Each female elk is capable of producing up to two female offspring each year. For each age class, we set the probability (based on DFW biologists' expert knowledge) for producing 0, 1, or 2 female offspring. We assumed that juvenile and old individuals would not reproduce. Adolescent reproduction is rare, so we set the probability of producing a single female calf at 5 % (i.e. a 10 % chance of having a calf of any gender). A high percentage of adult female tule elk successfully reproduce in the absence of natural predators. Thus, we set the chances of producing one female calf at 45 %, having female twins at 2 %, and either not reproducing at all or producing only male offspring at 53 %.

### Event (survival)

Survival rates among tule elk in the various California herds are quite high. There is currently little predation and currently few disease issues. We set survival, based on age classes, at the following rates: juveniles (75%), adolescents (80%), adults (95%), and senescent (60%). These rates are based on DFW biologists' and refuge manager's knowledge of patterns associated with other herds.

### Spatial data

We used three categories of spatial input (geographic data): range data, barriers, and initial population placements. Range data are spatial data that represent the habitat quality as experienced by the study organism. Individuals move across this landscape to procure resources. We used two different ranges to represent the capacity of tule elk to "learn" their environment over several years after release and to adapt their movements accordingly. Thus, to simulate this behavior, at the beginning of time step (year) three, the range changes from one based solely on habitat suitability ratings for tule elk based on individual land cover types (see Fig. 3a) to habitat suitability ratings modified by the configuration of habitat types and additional variables (see Figs. 3b; or 5 in Huber et al. 2011). This latter range consists not just of local land cover, but the interplay between the proximity of forage habitat to cover habitat, land cover heterogeneity, and human impacts. These range attributes are represented by 1 ha hexagonal polygons.

We identified three types of human-built barriers that impact the ability of tule elk to move across the landscape: highways, concrete-lined canals, and urban areas (Fig. 4). Canals represent a threat to elk because if elk enter the canal, there is a high probability of their drowning as they generally cannot climb the steep concrete sides to exit the canal. Both the highways and canals were represented as linear features, while the urban area barriers corresponded to the perimeter of polygons identified as'urban' in nature. Each of these three barrier types was given a probability of mortality, deflection, or transmission of tule elk attempting to cross (Table 1). These probabilities were determined in consultation with biologists with experience in tule elk interactions with these barrier types. During a movement event, if an individual encounters a barrier, the probabilities are used to determine whether the individual dies, deflects off the barrier, or successfully crosses to the other side. Barriers were included for all movement events.





Finally, a spatial dataset was created for each of the four scenarios depicting the potential reintroduction site. This dataset consists of a small number of 1 ha hexagons, each of which can hold one elk at the time of release. These serve as the starting location for the model runs.

#### Model outputs

For all four potential release scenarios, we calculated: mean final population (female only) after 25 time steps (Table 2), mean occupancy of individual 1 ha hexagons (Fig. 5), and sum total barrier



Fig. 4 Barrier types used in barrier impact assessment 1 highways; 2 concrete-lined canals; and 3 urban areas

 Table 1
 Probability of mortality, deflection, or transmission for each of the three barrier types

Barrier type	Mortality	Deflection	Transmission
Road	0.10	0.80	0.10
Canal	0.01	0.99	0.00
Urban	0.50	0.50	0.00

interactions across all time steps and replicates (Table 2).

### Results

### Kesterson scenario

The mean tule elk female population after 25 years under the Kesterson scenario was 84.2. The major

area of tule elk concentration was approximately 1.5 km southwest of the release site, near the lower end of the San Luis Drain. The mean number of barrier interactions per replicate was 2,837.5, the vast majority of which involved encounters with the San Luis Drain. Barrier interactions occurred to a lesser extent with both Highway 165 to the east of the release site and Highway 140 to the northwest. Additionally, there were a small number of interactions with three of the waterfowl hunting club headquarter areas to the southwest of the release site. There was little interaction with farmed lands under this scenario. The general pattern of herd dynamics across the replicates was a move from the release site to the major area of concentration over the first few time steps, followed by a gradual expansion of herd home range in an approximately concentric shape.

**Table 2** Mean female population and barrier interactions for all four release sites using three different maximum dispersal distances: *1* 20 hexagons (based on expert opinion); *2* 30 hexagons; and *3* 40 hexagons

Scenario	1	2	3
Kesterson			
Population	84.2	93.7	84.1
Barriers	2837.5	2978.3	2687.4
Arena Plain			
Population	122.0	124.6	106.8
Barriers	52.5	50.7	43.4
San Luis			
Population	159.3	155.2	149.9
Barriers	13.0	12.8	12.9
East Bear Creek			
Population	169.4	161.3	169.4
Barriers	8.6	5.8	6.4

### Arena Plains scenario

The mean tule elk female population after 25 years under the Arena Plains scenario was 122.0. The major area of tule elk concentration was  $\sim 1.0-1.5$  km southwest of the release site in the vicinity of the East Side Canal. The mean number of barrier interactions per replicate was 52.5, most of which involved the poultry farms approximately 1.5 km north of the release site. There were a small number of additional barrier interactions at Highway 140 north of the release site. Agricultural land that elk occupied under this scenario included grain crops east of the release site and several areas of pasture to the south and southwest of the release site. The general direction of herd expansion was to the southwest, including a number of replicates in which herd members occupied East Bear Creek Unit and the San Joaquin River riparian corridor.

#### San Luis scenario

The mean tule elk female population after 25 years under the San Luis scenario was 159.3. The major area of tule elk concentration was immediately adjacent to the release site. The mean number of barrier interactions per replicate was 13.0, most of which were



Fig. 5 Results of the four modeled release site scenarios. Elk were modeled within the *black outlines*. Mean occupancy of hexagons within these *outlines* is shown

concentrated on Highway 165 between Salt Slough and the San Luis Drain. Several individuals that successfully crossed Highway 165 (either across the road or through one of several existing undercrossings) encountered the San Luis Drain as well. Most replicates modeled the tule elk as expanding roughly concentrically from the release site. Several of the replicates however had small sub-herds venturing northeast of the release site towards the Arena Plains Unit. Aside from several parcels of pasture, there was little interaction with farm lands under this scenario.

# East Bear Creek scenario

The mean tule elk female population after 25 years under the East Bear Creek scenario was 169.6, the most of any of the four scenarios. The major area of tule elk concentration was immediately adjacent to the release site. The mean number of barrier interactions per replicate was 8.6, fewest among the four scenarios. These interactions were concentrated on Highway 165 between Salt Slough and the San Luis Drain as well as at the San Luis Drain, both across Highway 165 from the release site and along the segment of the canal paralleling Highway 165 southwest of the release site. Most replicates modeled the tule elk as expanding roughly concentrically from the release site. Several of the replicates however had small sub-herds venturing northeast of the release site towards the Arena Plains Unit. Aside from several parcels of pasture, there was little interaction with farmlands under this scenario.

# Dispersal distance

The effect of changing the maximum dispersal distance was minimal across all four release site scenarios. This was true for both mean population size after 25 years and barrier interactions.

# Discussion

There has been a great increase in peer-reviewed publications on reintroductions over the past two decades (Seddon et al. 2007). Many of these have been descriptions of efforts or evaluations of the results of monitoring. In response, Armstrong and Seddon (2008) have proposed a set of ten questions that should lead to a more strategic and comprehensive approach to reintroduction planning. While HexSim could potentially be used to address aspects of all ten questions, the analysis presented here touches on two of them:

- What is the optimal allocation of translocated individuals among sites?
- How are post-release survival and dispersal affected by pre- and post-release management?

The four release site alternatives explored here speak to the first, while the barriers assessment at least serves as a prelude to the second

# Alternatives comparison

Based on the final population size and barrier interactions (Table 1), the scenario most likely to lead to a viable free-roaming tule elk herd in Grasslands Ecological Area is the East Bear Creek scenario. This scenario resulted in both the highest mean population of female elk and the lowest incidence of harmful barrier interactions. Further, model results show little interaction between tule elk and agricultural areas, excluding scattered pasture surrounded by grassland located northeast of this release site. Model results for the San Luis scenario showed similar population numbers and barrier interactions, although slightly worse than those under the East Bear Creek scenario. The spatial location of the tule elk between these scenarios was relatively identical.

Both the Kesterson and Arena Plains scenarios provided more problematic results. At Kesterson, the San Luis Drain proved to be a detrimental landscape feature located at the heart of suitable tule elk habitat. There was a much higher incidence of interaction with this barrier than with any other barrier included in the four scenarios. If this scenario were to be selected for implementation of a reintroduction program, measures such as construction of extensive elk-proof fencing would need to be taken to ensure safety of the tule elk in this area. Further, there is potential for encounters between tule elk and waterfowl hunting clubs under this scenario. Finally the barrier interactions with Highway 140 suggest that under this scenario tule elk individuals might move towards and across the border of GEA, likely increasing the probability of detrimental tule elk-human interactions.

The Arena Plains scenario also resulted in increased potential for negative interactions between tule elk and

human landscape features. The poultry farms to the north of the release site and grain fields to the east could prove to be areas of conflict between tule elk and land owners. Movement of tule elk north of the release site to Highway 140 could also lead to conflict between tule elk and motorists.

### Management suggestions

For this project, perhaps the most important HexSim component was the integration of barrier interactions. Natural elk predators have largely been removed from this landscape and hunting will not be permitted until a herd has successfully established. This coupled with the relatively large amount of high quality habitat means that interaction with human infrastructure will in all likelihood largely shape the population levels of any reintroduced herd. Therefore it is crucial to assess the impacts of this infrastructure under the reintroduction scenarios. We were surprised to see the moderate effects of the highway in comparison with the vastly more impactful canal.

The use of HexSim in pre-release modeling can help identify management actions that could potentially lead to a greater chance of a successful reintroduction. For example, under both San Luis and East Bear Creek scenarios, one of the most likely locations of tule elk-human conflict is Highway 165. While tule elk generally tend to refrain from crossing paved roads, as elk numbers increase there will be a greater likelihood of individuals crossing this highway. There are several culverts along this stretch of road that might be large enough to accommodate tule elk movement, however, even taking into account the existence of these culverts there is undoubtedly the potential for elk crossing the road surface itself. HexSim results can be used to target locations along the highway for specific actions designed to reduce auto-elk collisions.

Another potential source of conflict identified by the HexSim model is the San Luis Drain. If the Kesterson scenario were chosen as the release alternative, fencing or other management actions could be undertaken to reduce the threat to the elk in the problematic locations. Finally, potential impacts to agricultural fields can be identified and appropriate fencing or other actions could be undertaken to reduce threats to farming losses.

### Herd movement

One way in which HexSim differs from previous SEPMs is in its inclusion of a herd movement component. This feature was critical in modeling tule elk locations, herd size, and barrier interactions. The ability to both model herds and individuals within herds is a more sophisticated and realistic depiction of the autecology of species such as elk. While models such as PATCH (Carroll and Miquelle 2006), which treats herds as a single entity, can work well at larger spatial scales, fine scaled analyses such as this are likely more effective if individuals can be tracked.

#### Parameter selection

While it was beyond the scope of the project to extensively test the resilience of the model to changes in the parameter inputs, there was very little change in the results when we used different maximum dispersal distances. A likely explanation for this is that there is enough high quality habitat in the GEA to make long distance movement events in search of resources unlikely to occur. This being said, future uses of HexSim in tule elk modeling should focus on testing some of the other parameters used in the model.

### Caveats

The accuracy of predictions produced by SEPMs is directly related to the quality of the data used to parameterize the models. For many species, these data do not exist or are incomplete. While a number of tule elk herds in California have been subject to years of study (e.g. O'Connor 1988; Howell et al. 2002), input data for HexSim are still unclear for elk in the Central Valley because it is a much different environment than locations where herds currently exist. It is likely that tule elk will use the GEA in ways different than either coastal mountains or arid scrub land. Therefore care should be taken in the interpretation of the results presented here. While we believe that they are likely to be relatively accurate in the ranking of the scenarios, we are less certain that either actual population levels or barrier interactions will hew closely to the model outputs. This being said, once elk are reintroduced in GEA, monitoring of the new population can be used to better estimate parameters for future reintroduction modeling efforts.

The model tracks tule elk populations 25 years into the future from time of release. Potential impacts are based on tule elk populations and locations at the end of this time period. If the herd is allowed to continue its growth patterns, the range is very likely to expand as well, leading to potentially negative interactions in more locations than are noted here. For example, under the East Bear Creek or San Luis scenarios, field crops to the south and southeast of the release sites could be impacted by tule elk foraging. The modeled scenarios only show a limited spatial impact; additional impacts will need to be assessed at a later date. Because natural tule elk predators have been extirpated from the region, hunting will likely need to be used as a population management tool at some future date as determined by herd evaluation by management agency personnel.

### Conclusion

This study provides a modeled comparison of reintroduction scenarios for tule elk in its historical range. Results such as these can be used by managers to increase the likelihood of successful reintroduction efforts and to anticipate potential management issues. Use of the HexSim SEPM allows for the assessment of systematic and key questions inherent in reintroductions (Hopfensperger et al. 2007; Armstrong and Seddon 2008; Morrison 2009). Monitoring of a reintroduced herd of elk can lead to more accurate parameterization of the model for future efforts as restoration of tule elk to the Central Valley continues (Huber et al. 2011). We believe that greater use of HexSim or similar SEPMs will increase the success rate of future reintroductions of many species in many locations.

Acknowledgments We wish to thank the Rocky Mountain Elk Foundation and U.S. Fish and Wildlife Service for their generous financial support of this project. We also wish to thank the California Department of Fish and Wildlife for their support and valuable expertise. The information in this document has been funded wholly (or in part) by the U.S. Environmental Protection Agency. It has been subjected to review by the National Health and Environmental Effects Research Laboratory's Western Ecology Division and approved for publication. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names commercial products constitute endorsement or or recommendation for use.

### References

- Alderman J, McCollin D, Hinsley SA, Bellamy PE, Picton P, Crockett R (2005) Modelling the effects of dispersal and landscape configuration on population distribution and viability in fragmented habitat. Landscape Ecol 20:857–870
- Almasi KN, Eldridge PM (2008) A dynamic model of an estuarine invasion by a non-native seagrass. Estuar Coast 31:164–176
- Armstrong DP, Seddon PJ (2008) Directions in reintroduction biology. Trends Ecol Evol 23:20–25
- Bianchi FJJA, Honěk A, van der Werf W (2007) Changes in agricultural land use can explain population decline in a ladybeetle species in the Czech Republic: evidence from a process-based spatially explicit model. Landscape Ecol 22:1541–1554
- Biggins DE, Godbey JL, Hanebury LR, Luce B, Marinari PE, Matchett MR, Vargas A (1998) The effect of rearing methods on survival of reintroduced black-footed ferrets. J Wildl Manag 62:643–653
- Carroll C, Miquelle DG (2006) Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. J Appl Ecol 43:1056–1068
- Carroll C, Phillips MK, Schumaker NH, Smith DW (2003) Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Conserv Biol 17:536–548
- Greco SE, Huber PR, Hobbs J, Garcia J, Stromayer K, Parris R (2009) Grasslands Ecological Area tule elk reintroduction feasibility study (Year 1 final report). Rocky Mountain Elk Foundation, Missoula
- Hedrick PW, Fredrickson RJ (2008) Captive breeding and the reintroduction of Mexican and red wolves. Mol Ecol 17:344–350
- Hopfensperger KN, Engelhardt KAM, Seagle SW (2007) Ecological feasibility studies in restoration decision making. Environ Manag 39:843–852
- Howell JA, Brooks GC, Semenoff-Irving M, Greene C (2002) Population dynamics of tule elk at Point Reyes National Seashore, California. J Wildl Manag 66:478–490
- Huber PR, Greco SE, Hobbs J (2011) Assessment of habitat for the potential reintroduction of tule elk to the San Joaquin Valley, California. Calif Fish Game 97:117–129
- Koch DB (1987) Tule elk management: problems encountered with a successful wildlife management program. T West Sect Wildl Soc 23:1–3
- Lawler JJ, Schumaker NH (2004) Evaluating habitat as a surrogate for population viability using a spatially explicit population model. Environ Monit Assess 94:85–100
- Mao JS, Boyce MS, Smith DW, Singer FJ, Vales DJ, Vore JM, Merrill EH (2005) Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. J Wildlife Manag 69:1691–1707
- McCullough DR (1969) The tule elk: its history, behavior, and ecology. U Calif Publ Zool 88:1–209
- McCullough DR, Fischer JK, Ballou JD (1996) From bottleneck to metapopulation: recovery of tule elk in California. In:

McCullough DR (ed) Metapopulations and wildlife conservation. Island Press, Washington, DC, pp 375–403

- Morrison ML (2009) Restoring wildlife: ecological concepts and practical applications. Island Press, Washington, DC
- O'Connor PM (1988) Home range and habitat use by tule elk at Cache Creek, California. Master's thesis, Humboldt State University, Arcata
- Ralls K, Ballou JD (2004) Genetic status and management of California Condors. Condor 106:215–228
- Rushton SP, Lurz PWW, Fuller R, Garson PJ (1997) Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. J Appl Ecol 34:1137–1154
- Rustigian HL, Santelmann MV, Schumaker NH (2003) Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landscape Ecol 18:65–81
- Schumaker NH (1998) A user's guide to the PATCH model. EPA/600/R-98-135. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis
- Schumaker NH (2010) HexSim (Version 1.5.1.14). US Environmental Protection Agency, Environmental Research

Laboratory, Corvallis, OR. Retrieved February 27, 2010 from http://www.epa.gov/hexsim

- Schumaker NH, Ernst T, White D, Baker J, Haggerty P (2004) Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. Ecol Appl 14:381–400
- Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. Conserv Biol 21: 303–312
- Spencer W, Rustigian-Romsos H, Strittholt J, Scheller R (2011) Using occupancy and population models to assess habitat conservation opportunities for an isolated carnivore population. Biol Conserv 144:788–803
- Wiegand T, Moloney KA, Naves J, Knauer F (1999) Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. Am Nat 154:605–627
- Williams CL, Lundrigan B, Rhodes OE Jr (2004) Microsatellite DNA variation in tule elk. J Wildl Manag 68:109–119