

A Strategy for Prioritizing Threats and Recovery Actions for At-Risk Species

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Abstract Ensuring the persistence of at-risk species depends on implementing conservation actions that ameliorate threats. We developed and implemented a method to quantify the relative importance of threats and to prioritize recovery actions based on their potential to affect risk to Mojave desert tortoises (*Gopherus agassizii*). We used assessments of threat importance and elasticities of demographic rates from population matrix models to estimate the relative contributions of threats to overall increase in risk to the population. We found that urbanization, human access, military operations, disease, and illegal use of off highway vehicles are the most serious threats to the desert tortoise range-wide. These results suggest that, overall, recovery actions that decrease habitat loss, predation, and crushing will be most effective for recovery; specifically, we found that habitat restoration, topic-specific environmental education, and land acquisition are most likely to result in the greatest decrease in risk to the desert tortoise across its range. In addition, we have developed an application that manages the conceptual

model and all supporting information and calculates threat severity and potential effectiveness of recovery actions. Our analytical approach provides an objective process for quantifying threats, prioritizing recovery actions, and developing monitoring metrics for those actions for adaptive management of any at-risk species.

Keywords Threats assessment · Conservation planning · Species recovery · Endangered species · Adaptive management · Mojave desert tortoise

Introduction

Effective conservation of at-risk species requires identifying and alleviating the threats to their existence. Most at-risk species for which conservation efforts have been successful were in decline primarily because of easily identifiable and remediable threats, such as the effect of DDT on bald eagles (*Haliaeetus leucocephalus*) (Abbitt and Scott 2001; Doremus and Pagel 2001). In contrast, species that face multiple, interacting threats (e.g., threats related to habitat loss and degradation) present greater challenges for recovery (Doremus and Pagel 2001; Scott and others 2006). Quantifying risks posed by threats to these species and prioritizing recovery actions can be difficult and ineffective because of lack of knowledge regarding relative importance of threats and inadequate information about potential effectiveness of conservation actions (Clark and others 2002; Scott and others 2006, 2010). The complexities of quantifying effects of multiple, interacting threats to a species often contribute to the arbitrariness and failure of conservation efforts (Lawler and others 2002).

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Efforts to address the complexity of assessing multiple threats and prioritizing conservation actions include the development of a standard lexicon (IUCN 2005; Salafsky and others 2008, 2009; Balmford and others 2009) and use of conceptual modeling to transparently describe the paths from threats to targets to broad strategies for conservation (TNC 2000; Salafsky and others 2002; CMP 2003; Margoluis and others 2009). These methods, however, do not provide a quantitative ranking of threats and actions at the species-effect scale that is needed for endangered species recovery planning (NMFS 2007). Methods for quantifying multiple threats to endangered species have recently been developed (Bolten and others 2011; Donlan and others 2010), but do not evaluate indirect effects of threats nor do they explicitly prioritize recovery actions based on relative importance of threats facing a species.

Here, we describe a strategy to (a) identify and quantify direct and indirect effects of threats to a species across its range, (b) prioritize recovery actions based on this systematic threats assessment, and (c) identify monitoring metrics to assess the effectiveness of recovery actions and test model assumptions in an adaptive management framework (Runge 2011). We build a conceptual model to capture all threats affecting at-risk populations and to explicitly identify causal relationships among these threats, the mechanisms (stresses) through which the threats affect populations, and which of these linkages are susceptible to specific recovery actions, so that negative impacts on at-risk species are reduced. We quantify the strength of these relationships using expert opinion and elasticities from a matrix population model to rank threats and prioritize recovery actions based on changes in risk to the population, where risk refers to overall population change. We use sensitivity analyses to test the stability of our results to perturbations in the model. Our approach creates a well-chronicled assessment of the relative severity of each potential threat and identifies specific parameters to monitor for evaluation of recovery actions effectiveness.

We developed this approach to help plan and implement a recovery strategy for the Mojave desert tortoise (*Gopherus agassizii*) (Cooper 1863; Murphy and others 2011), which is listed as threatened under the U.S. Endangered Species Act (USFWS 1990). Its decline is thought to be a result of a complex interaction of threats, including loss of habitat to development, reduced habitat quality due to alteration of plant species presence and abundance, increased predation, deliberate killing by humans, and increased disease prevalence. The effects of threats vary spatially and temporally across the tortoise's range (USFWS 2010), which includes more than 2.4 million ha of designated critical habitat (USFWS 1994).

Because there are few data available to quantify the absolute effects of different threats on desert tortoise populations (Boarman 2002; USFWS 2011), our approach estimates the relative importance of each threat and prioritizes recovery actions based on their predicted effect on risk to the population (Boarman and Kristan 2006).

A Conceptual Model for Describing Relationships Among Threats, Recovery Actions, and Population Effects

Conceptual models represent complex processes and articulate assumptions and expected outcomes; they are often used in biological conservation applications (Margoluis and others 2009). Here, we used a conceptual model to organize interacting threats, develop pathways through which threats affect overall population change for an at-risk species, and associate each potential recovery action with pathways they can interrupt. We used a standard lexicon for biodiversity conservation (Salafsky and others 2008), which defines and provides a list of potential threats, stresses, and conservation actions. This lexicon provides common elements that can be linked in a causal chain that represents a hypothesis about how actions are expected to bring about desired outcomes. For each threat, we create an individual sub-model, then connect the set of sub-models so that the direct and indirect effects of all threats to a species are captured in a single network. Linkages in the network indicate relationships that can potentially be affected by application of recovery actions. We provide details on each step below; a glossary of terms is provided in Table 1. An interactive version of the complete desert tortoise model is available online (<http://www.spatial.redlands.edu/dtro/modelexplorer/>).

Identify Threats that Affect the Species

Identifying the specific threats to at-risk species can be challenging, but is necessary to define causal relationships and to identify the most important conservation needs (Efroymson and others 2009). Therefore, we began with a comprehensive list of threats to biodiversity, which is designed to be applicable to any species (Salafsky and others 2008). We then identified and defined the subset of threats that are relevant to Mojave desert tortoises as described in scientific publications and government agency reports (e.g., USFWS 1990, 1994, 2010, 2011). For example, the proliferation of non-native plant species (i.e., invasive plants) in desert tortoise habitat has been identified as a threat to the species. More than 100 nonnative plant species have been documented in the Mojave and Sonoran deserts (Brooks and Esque 2002); many have

Table 1 Definition of terms used to quantify the effects of threats and to rank recovery actions for at-risk species

Term	Definition
Conceptual model	A representation of the set of causal relationships between factors that are believed to affect an at-risk species
Conservation action	Interventions undertaken to reach conservation goals and objectives (Salafsky and others 2008)
Direct effects of a threat	Pathways from threats to stresses to associated population effects on population risk
Generations of indirect effects	First generation: effects of threats that proximately result from the focal threat. Second generation: effects of threats that result from generation 1 threats are second-generation indirect effects, etc.
Indirect effects of a threat	Pathways to population risk that lead from a threat through resulting threats rather than directly through stresses
Population effect	Change in mortality, reproductive output, or immigration or emigration in a population
Recovery	The process by which the decline of an at-risk species is arrested or reversed so that its long-term survival in nature can be ensured
Recovery action	Conservation actions that are designed specifically to contribute to the recovery of at-risk species
Risk to the population	The contribution of threats, stresses, and demographic rates to the overall change in population that is occurring; for the desert tortoise, the absolute magnitude of that decline is unknown.
Stress	Degraded conditions or “symptoms” of the species that result from a threat (Salafsky and others 2008)
Threat	Proximate human activities that have caused, are causing, or may cause the destruction, degradation, or impairment of species (Salafsky and others 2008)
Threats assessment	A systematic approach to assessing the relative importance of each threat to a species’ status

become common to abundant in desert tortoise habitats due to historic and ongoing land disturbances (Brooks 2009).

Determine Relationships Among Threats

Each relevant threat can have direct and indirect effects to consider (Fig. 1). The direct effects of a threat result in stresses (threat-stress [T–S] relationships), which we identify in the next step (Fig. 1, point 2). A threat can also impact a species indirectly by initiating related threats (threat-threat [T–T] relationships). These related threats can have direct and indirect effects as well, creating a cascade of sub-models stemming from the original threat of interest (Fig. 1). We identified all related threats as indirect effects of one another where appropriate. For example, an increase in fire frequency is an indirect effect of proliferation of nonnative plant species. The invasive plants provide fuel to carry fires, especially in the inter-shrub spaces that are mostly naturally devoid of native vegetation (Brown and Minnich 1986; Brooks 1998; Brooks and Esque 2002) (Fig. 2). In any system with multiple interacting threats, the only way to quantify each threat’s total contribution to increase in risk to the population is to also quantify the indirect effects of that threat. Describing the relative impact of invasive species without the contribution to increasing fire potential would underestimate the risk posed by this threat to the Mojave desert tortoise.

Additionally, threats that arise from an originating threat may have cascading indirect effects of their own; therefore, we introduce the concept of “generations” of indirect effects. Threats that proximately result from the focal threat are the first-generation indirect effects of that focal

threat. Threats that enter the individual threat model through sub-models of the first-generation threats are the second-generation of indirect effects, and so on. For example, in the individual model for invasive plants, fire is a first-generation threat that leads to some of the second-generation indirect effects of invasive plants.

Identify Stresses and Population Effects that Result from Threats

Threats directly impact populations through stresses. Stresses are degraded characteristics of the recovery target (here, the Mojave desert tortoise and the ecosystem upon which it depends) that reflect the impacts of threats (Salafsky and others 2008) (Table 1). Habitat loss, disease, and death by crushing are stresses to the tortoise that can result from different threats and will be reflected in decreased dispersal, recruitment, or survivorship; they are the mechanisms through which threats cause population effects. Identifying stresses that result from each threat (threat-stress [T–S] relationships) clearly specifies the paths by which individual threats directly affect the population as opposed to indirectly through other threats. For every stress, we indicated the life stages and mechanisms of population change that would be affected by that stress (Fig. 1, S–PE relationships). We evaluated two life-stages, reproductive (adults) and non-reproductive (juveniles), because available data do not support further demographic distinctions and it is likely that threats and recovery actions do not act differently on more finely subdivided life stages of desert tortoises (Reed and others 2009). Stresses affecting mortality or immigration/emigration could impact

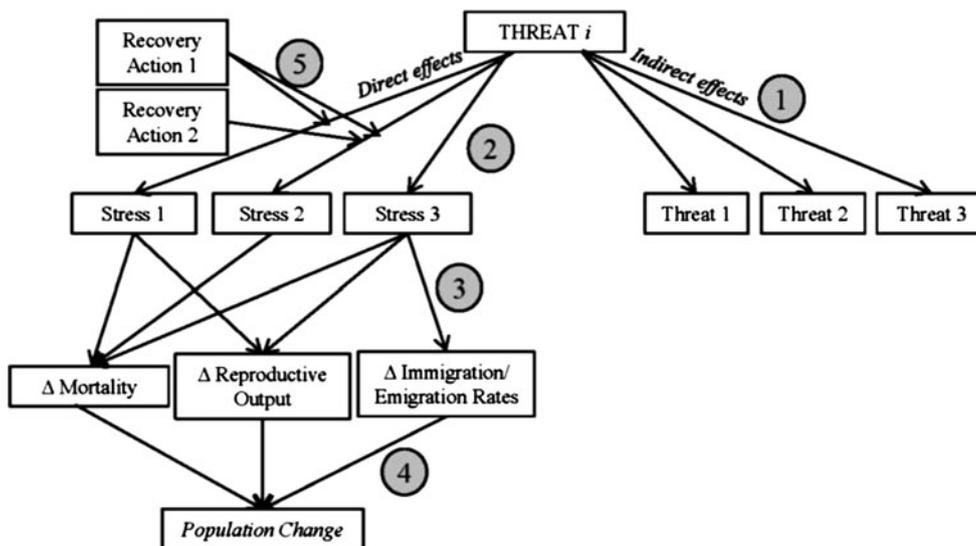


Fig. 1 Structure for assessing the effects of a single threat to an at-risk species and the effects of the recovery actions relevant to that threat. This sub-model is constructed for every potential threat. The numbers in the figure indicate individual steps in the strategy for each threat. 1 Threat-to-threat (T–T) relationships: threats that result from the focal threat, the effects of which are the indirect effects of the focal threat, 2 threat-to-stress (T–S) relationships: stresses that result

directly from the focal threat, 3 stress-to-population effect (S–PE) relationships: effects of each stress on population effects, 4 population effect-to-population change (PE–PC): contribution of changes in population effects to population change, 5 recovery action to T–S relationships: recovery actions that alleviate stresses as caused by the focal threat

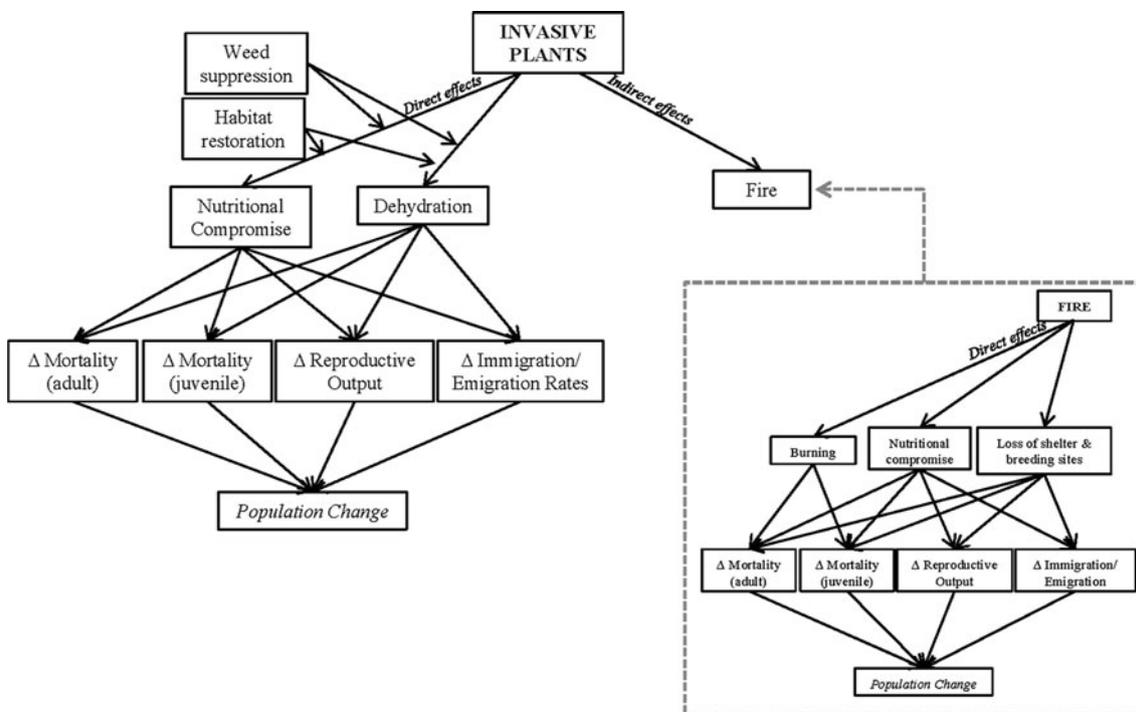


Fig. 2 An example sub-model for the effects of invasive plants on the rate of population change for the Mojave desert tortoise. Fire is identified as an indirect effect of an increase in invasive plants (the

threat fire has its own indirect effects and recovery actions which are not shown in the inset). In the same way, invasive plants can be an indirect effect of another threat (e.g., unpaved roads)

both adults and juveniles; stresses affecting reproductive output could only affect adults. Continuing our example, proliferation of nonnative plants has contributed to at least

one stress in Mojave desert tortoises, nutritional compromise (Fig. 2). Nonnative annual grasses have lower nutritional value than native forbs (Nagy and others 1998), so

the effects of increasing presence and use of these annual grasses by tortoises include reduced growth rates and survivorship in juveniles (e.g., Medica and others 1975; Oftedal 2002; Oftedal and others 2002; Tracy and others 2006) and decreased female reproductive output (e.g., Turner and others 1986).

Identify Recovery Actions to Alleviate Threat-to-Stress Relationships

Recovery actions can be applied to threats, stresses, or the at-risk species itself, but the ultimate intent of these actions is to minimize negative changes to the population by intervening to address the stress caused by a particular threat, such as nutritional compromise caused by nonnative plants or mortality caused by a predator. The ultimate goal is to see eventual population increases. Therefore, recovery actions in our conceptual model target the stresses caused by each threat, rather than the threats themselves (Fig. 1, RA to T–S relationships). We incorporated into our model the 28 recovery actions recommended in the recovery plan for the Mojave desert tortoise (USFWS 2011). For example, weed suppression/eradication and habitat restoration through revegetation/seeding with native food plants are recovery actions that can reduce the stresses of nutritional compromise and dehydration caused by establishment of nonnative plants (Fig. 2). When lacking a pre-existing list of recovery actions, the comprehensive list of general conservation actions in Salafsky and others (2008) provides options to consider.

Targeting stresses with recovery actions is useful for identifying expected outcomes. In many cases, it is not the threat *per se* that can be ameliorated with a conservation action; rather, it is the stress caused by the threat. For example, tortoises are crushed by cars on paved roads. The threat is the cars; the effect of that threat, the stress, is tortoises being crushed. The recovery action of installing tortoise-exclusion fencing along the road does not reduce the threat (i.e., car traffic), but it does reduce the effect of the threat (i.e., tortoises being crushed by cars on the road). By identifying the exact stress caused by a particular threat that we expect to reduce with a particular recovery action, we explicitly define our expected outcomes. For example, where tortoise-exclusion fencing is installed and maintained along a road, we assume that we will see (1) a decrease in tortoises crushed by cars on the road, which should result in (2) increased survival of reproductive and non-reproductive life stages, and, eventually, (3) an increase in the tortoise population. Directed monitoring of expected outcomes will allow for adjustment of models and on-the-ground actions as learning occurs and lays the foundation for adaptive management (see below).

Quantifying Relationships Among Threats, Recovery Actions, and Population Effects

Our conceptual model captures the most current and plausible hypotheses about the ways in which the complex network of threats, stresses, and recovery actions affect tortoise populations. However, as a qualitative description, it does not establish the relative severity of each threat to the species or prioritize recovery actions in terms of their predicted effect on risk to the population. Quantitative estimates of threat severity, or even the relative magnitude, do not exist for many at-risk species, including the Mojave desert tortoise (Boarman 2002). We therefore used expert assessment and an existing population matrix model for Mojave desert tortoises (Doak and others 1994) to weight the strength of linkages in our conceptual model. Expert assessment is used frequently in conservation planning and is particularly useful in data-poor and contentious situations (Aipanjugul and others 2003; Halpern and others 2007; Donlan and others 2010; Martin and others 2012). We characterized the relative contribution of each threat to a stress with a single weight. Assuming our model includes all threats to desert tortoises, the weights of all threats contributing directly to an individual stress sum to 100 %. We also assumed that we had captured all relationships among threats, all stresses contributing to each population effect, and all population effects contributing to overall population change. Due to the comprehensive nature of the conceptual model, linkage weights from one level of the model describe proportional contributions to the next level of mechanisms; they are not simply relative ranks of importance. The addition of proportional relative weights to each linkage in the conceptual model allows comparison of the relative strength of complete pathways from each threat and recovery action to overall population change, or risk. All weights are included in the online version of the model (<http://www.spatial.redlands.edu/dtro/modeexplorer/>).

Relative Contributions of Threats to Increase in Risk to the Population

The relative contributions of each threat to an increase in risk were calculated through a combination of the contributions of that threat to other threats, through direct and indirect contributions to stresses, stresses to population effects, and population effects to overall population change at the range-wide scale. Twelve desert tortoise biologists estimated the relative contribution of an increase in severity of a particular threat by 10 % over 10 years on the severity of other threats (Fig. 1, T–T relationships). Tortoise biologists who participated in the T–T assessment were experts chosen based on their experience applying regulations to address how threats (like urbanization, solar

energy development, or roads) contribute to other threats (like invasive weeds, ravens, or human access). We used an ordinal scale (Malczewski 1999) for estimated contributions (Negligible Contributor, Small Contributor, Contributor, Major Contributor, Dominant Contributor), corresponding to weights of 0, 0.25, 0.5, 0.75, and 1.0, respectively. We provided an online interface that guided the expert through each threat and provided general context and definitions for terms. We aggregated the responses from all biologists by removing the highest and lowest estimates and averaging the remaining 10 values for each threat. Next, these average weights were normalized so that weights of contributions of all other threats to each individual threat summed to one. The context and results of the expert assessments are available online (<http://www.decisionharvest.com/dhroot/dhowners/fw/DTRepsAnon/>).

A separate group of 12 experts used a similar interface to evaluate the relative contribution of threats to each stress (Fig. 1, T–S relationships). These experts were active Mojave desert tortoise biologists with experience and awareness of current research on mechanisms by which threats degrade conditions such as nutritional quality, extent of habitat loss, or predation rates specific to tortoises. We applied the same scaling and aggregation procedures as above. Four of the authors acted as a third independent assessment group and determined the relative contributions of individual stresses to each population effect (Fig. 1, S–PE relationships) by consensus. These biologists were also authors on the revised recovery plan for Mojave desert tortoises (USFWS 2011) and are regularly involved in evaluating and summarizing the state of knowledge about how human activities can incrementally depress survival and reproductive rates. Immigration/emigration rates are not meaningful at the scale of the entire (range-wide) species, so we did not incorporate them in this iteration of the model.

To quantify the weights for the relationships between population effects and overall population change, we used elasticity values from an existing population viability analysis for desert tortoises (Doak and others 1994) that was adjusted to reflect one reproductive and one non-reproductive life stages. If a population dynamic model had not been available, experts could also have been used to develop relative weights for the contribution of each population effect to population change.

Elasticities are traditionally used to indicate which demographic rates in the model have the greatest effect on population growth rate and persistence (Burgman and others 1993). To modify the original population viability analysis based on eight size classes, we calculated survival rates for juvenile and adult stages as the geometric mean of survival rates of the five smallest and three largest stages, respectively, to reflect the multiplicative aggregate

probability of survival through the consecutive classes. Our approach treats tortoises with a midline carapace length up to 180 mm as non-reproductive. We calculated fertility rates as the arithmetic mean of the number of yearlings produced per female in the three largest stages. We conducted new population viability analyses based on demographic rates from the reduced number of stages using the “medium–low” and “medium–high” reproduction levels defined by Doak and others (1994) and averaged elasticities across reproduction levels to generate weights for adult and juvenile demographic rates. The average values were 0.87 and 0.12 for adult and juvenile survival, respectively, and 0.02 for fertility.

Effectiveness of Recovery Actions

We estimated effectiveness of recovery actions on a 5-point scale, where 5 indicated the recovery action would fully ameliorate the stress caused by a threat and 0 meant the recovery action would have no effect. The effectiveness of recovery actions for the desert tortoise remains largely unknown (GAO 2002; Boarman and Kristan 2006; USFWS 2011). Therefore, we estimated the predicted effectiveness of recovery actions at reducing each stress caused by a particular threat under two recovery action scenarios: best-case effectiveness (high-end) and worst-case effectiveness (low-end). We then calculated the average of these two values, and divided by 5 to express it as a percentage of the highest possible effectiveness score, which represents the overall recovery action effectiveness at reducing the effects of that threat. For example, an action with a high-end score of 5 and a low-end score of 2 would be given a predicted recovery action effectiveness score of $(3.5/5) \times 100 = 70\%$ effectiveness at reducing the particular effects of the threat. Other pathways from this threat that increase risk will not be affected. Although these values have been reviewed by the authors of this paper, they represent coarse expert opinion due to the lack of research results characterizing the effectiveness of recovery actions for desert tortoises. We incorporated the average recovery effectiveness scores, and also the high- and low-end scenario estimates to help reflect the uncertainty in our results. These three scenarios were all subsequently incorporated into the sensitivity analyses described later in conjunction with ranking the importance of possible recovery actions. Modeling in the face of such uncertainty can improve transparency, while directing strategic data collection and monitoring as part of the adaptive management cycle (Starfield 1997). Ideally, as we implement recovery actions and evaluate their effectiveness, the range of values currently in the model can be narrowed based on the results of effectiveness monitoring.

Estimating the Relative Severity of Threats to Rates of Population Change

Each threat contributes to an increase in risk to the population directly through stresses that arise from it, as well as indirectly via its contribution to other threats. Thus, the contribution of a threat to overall increase in risk is the sum of the contributions of both direct and indirect effects (Figs. 3, 4). Direct effects of each threat were calculated as the product of the contribution of that threat to each stress (T–S relationships), the contribution of each stress to each population effect (S–PE relationships), and by the contribution of that population effect to overall population change (PE–PC relationship). For each threat, we summed these products across all stress-to-population-change paths in our conceptual model (Figs. 3, 4). This approach does not estimate the absolute change in population, but rather the relative contribution of threats to whatever population change is occurring and thus the contribution to an increase in risk to the population (Fig. 4).

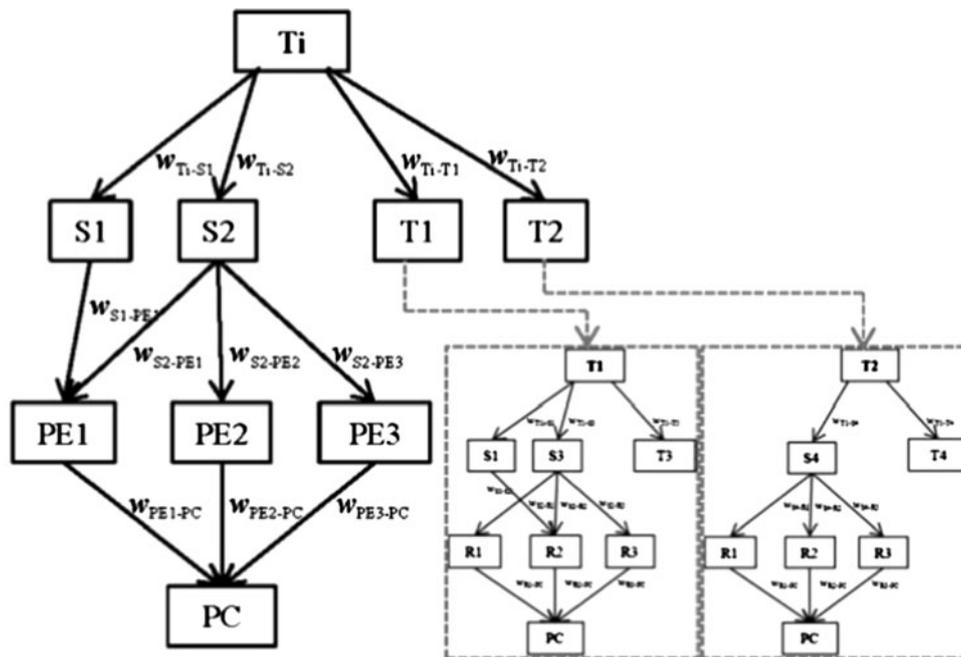
The indirect effects of a threat were estimated using a similar calculation for each of the resulting threats (Fig. 3).

Because all linkage weights are < 1, products describe a proportionally smaller indirect effect as subsequent generations of effects are examined (Fig. 4). We continued adding generations of indirect effects until either (a) all indirect effects that result from a threat were included, or (b) the inclusion of an additional generation of indirect effects resulted in a contribution ≤ 0.01 % of the threat (usually < 5 generations).

We similarly quantified the contribution of stresses to population effects and, therefore, to overall population change. To determine the relative importance of each stress, we used the same calculations as above, starting from stresses instead of threats and summing the products of pathway linkages from that stress through all population effects to overall population change.

Estimating the Relative Contribution of Recovery Actions to Reducing Risk

Recovery actions can be prioritized based on their predicted decrease in risk to the population. Our threats

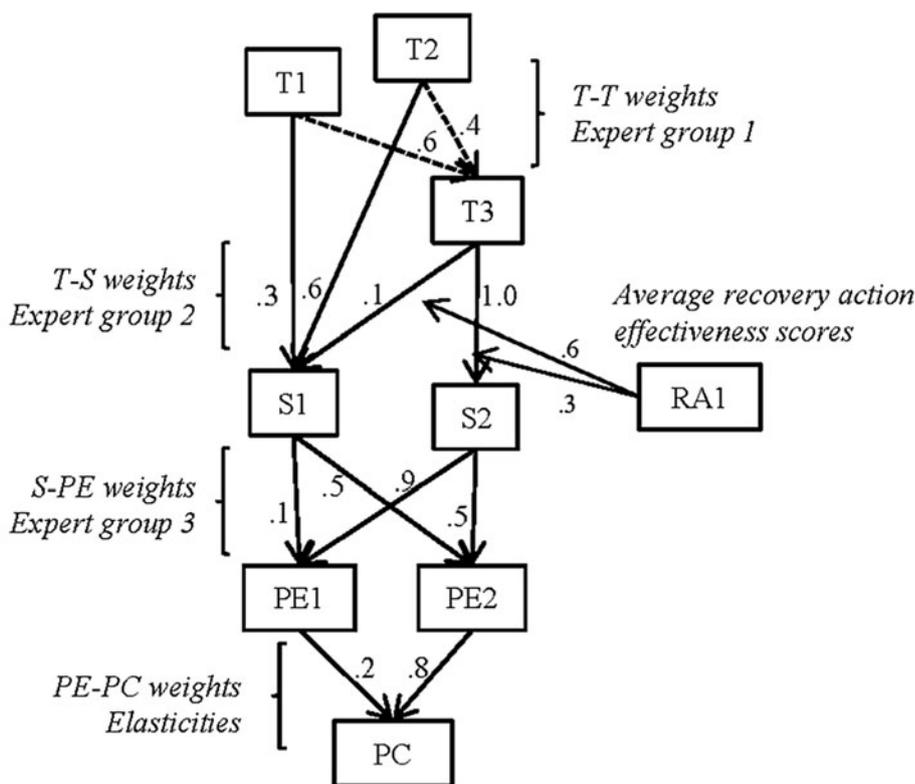


Contribution of T_i to increase in risk to the population = (Direct effects of T_i) + (Indirect effects of T_i)

$$= [w_{T_i-S1}w_{S1-PE1}w_{PE1-PC}] + w_{T_i-S2} [(w_{S2-PE1}w_{PE1-PC})+(w_{S2-PE2}w_{PE2-PC})+(w_{S2-PE3}w_{PE3-PC})] + [(w_{T_i-T1} * \text{Contribution of } T1-PC)+(w_{T_i-T2} * \text{Contribution of } T2-PC)]$$

Fig. 3 Threat i (T_i) contributes to an increase in risk to the population as the sum of its direct contribution to population change (PC) and indirect contribution through the effects of other threats, Threat1 (T_1) and Threat2 (T_2). To calculate the contribution (effect) of T_i to PC, we multiplied the contribution (w) of T_i to each population stress (S1 and S2) by the contribution of stress to a population effect (PE1, PE2, and PE3) by the contribution of that rate to PC. We then sum these products across all S to PC relationships

that result from the threat T_i . The direct contributions of threats T_1 and T_2 to population change are calculated the same way. The contribution of these indirect effects to the overall contribution of T_i , is obtained by multiplying the direct contributions of T_1 and T_2 by the contribution of T_i to T_1 and T_i to T_2 , respectively. The effects of T_1 and T_2 on PC account for the first generation of indirect effects of T_i



Total Risk to the Population with only 3 Threats = {Direct effects of T1} + {Direct effects of T2} + {Direct effects of T3} = 100%
 = $\{(.3)[(.1)(.2)+(.5)(.8)]\} + \{(.6)[(.1)(.2)+(.5)(.8)]\} + \{(.1)[(.1)(.2)+(.5)(.8)] + (1.0)[(.9)(.2)+(.5)(.8)]\} = 1.0$
 Contribution of T1 to increase in risk to the population = $\{(.3)[(.1)(.2)+(.5)(.8)]\} + \{Indirect\ effects: [(.6)(Direct\ effects\ of\ T3)]\} = .499$
 Contribution of T2 to increase in risk to the population = $\{(.6)[(.1)(.2)+(.5)(.8)]\} + \{Indirect\ effects: [(.4)(Direct\ effects\ of\ T3)]\} = .501$
 Contribution of T3 to increase in risk to the population = $\{(.1)[(.1)(.2)+(.5)(.8)] + (1.0)[(.9)(.2)+(.5)(.8)]\} = 0.622$
% Reduction in Total Risk to the Population from RA1 = $\{(.6)(.1)[(.1)(.2)+(.5)(.8)]\} + \{(.3)(1.0)[(.9)(.2)+(.5)(.8)]\} = 0.199$

Fig. 4 A hypothetical, complete network in which only three threats affect a population and only one recovery action is proposed. This network captures the direct and indirect effects of the three hypothetical threats (T1, T2, and T3), which affect population change (PC) through two stresses (S1 and S2) and two population effects (PE1 and PE2). Each weight is the average across the group of experts, normalized so the contributions into each “box” sum to 1, reflecting the fact that the full set of contributions to each S, PE, and

to PC have been accounted for. The average recovery action effectiveness score come from the average of the high and low-end effectiveness values. To estimate the % reduction in total risk to the population from RA1, we multiplied the overall recovery action effectiveness score by the contribution to increase in risk of each affected T–S relationship, then summed across all T–S relationships reduced by that recovery action

assessment estimates the relative contribution to increased risk rather than to existing risk to the population, so our recovery action calculations are targeted at reduction in future risk (Fig. 4). Every recovery action has an effectiveness score for each T–S linkage. To arrive at a single, overall measure of each recovery action’s effectiveness at reducing population risk, we summed the products of T–S risk pathways by their specific T–S effectiveness score (Fig. 4). We also investigated the extent to which uncertainty in recovery action effectiveness scores might affect rankings; we calculated the contribution of each recovery action using the high- and low-end estimates, as well as the average overall effectiveness score.

Sensitivity of Rankings to Uncertainty in Weights

The stability of recovery action rankings can be estimated through the sensitivity of those rankings to weights in the model. We investigated the sensitivity of the recovery action ranking to changes in weights of stresses to population effects and changes in the weights of population effects to overall population change using two methods: varying the weights themselves and varying the model structure.

First, we individually varied each of the 49 weights by an absolute increase of 25 % of its maximum value, and renormalized the associated weight set to sum to 1, before re-ranking the recovery actions. We chose 25 % to reflect

one increment in the five-step ordinal scale for estimated contributions. We then recorded the number of recovery actions originally ranked in the top 10 that remained in the top 10 under that weight variation. Second, we conducted a structural sensitivity analysis in which we removed each stress in turn from the model, effectively setting all weights from that stress to 0 and renormalizing the associated weight set to sum to 1. We again recorded the number of actions originally ranked in the top 10 that remained in the top 10 under that weight variation.

Results

Identifying the Importance of Each Threat

Generally, we found that each individual threat has a relatively small contribution to increase in risk. The five most important threats were urbanization (direct contribution: 3.1 %, indirect contribution: 19.7 %), human access (2.4, 15.8 %), military operations (2.8, 7.0 %), disease (8.6, 0 %), and illegal off-highway vehicle use (2.6, 4.9 %) (Fig. 5). For urbanization, human access, and military operations, the contributions of their indirect effects are 2.5–6.6 times greater than the contributions of direct effects. For example, direct effects of urbanization are largely a result of habitat loss, but urbanization also indirectly affects tortoise populations through increasing other threats, including roads, traffic, pollution, human-subsidized predators, and human access. In contrast, disease only contributes to increase in risk through direct impacts; no additional indirect threats are identified in the literature. The three most important stresses to the Mojave desert tortoise are habitat loss, predation, and crushing, which accounted for 45.6 % of the total risk to the population (Table 2).

Prioritizing Recovery Actions

Using the overall, average effectiveness score of each recovery action, we found that habitat restoration (9.4 % decrease in risk to the population), environmental education (5.9 %), land acquisition (5.5 %), installing/maintaining tortoise-exclusion fencing (5.3 %), and reducing predator access to human subsidies (3.6 %) to be the five top-ranked, range-wide recovery actions in terms of their ability to reduce risk to the population (Fig. 6).

Sensitivity Analysis

We found the top 10 recovery actions to be robust to changes in weights considered. The results of varying each stress weight by 25 % indicated that of the 10 actions that

were ranked from 1 to 10 under the original set of weights, 1 through 9 remained in the top 10 under at least 46 of the 49 (92 %) variations in weights. The tenth-ranked action, sign and fence protected areas, fell out of the top 10 in over 30 % of the variations. On the other hand, the eleventh-ranked action, remove grazing, was elevated into the top 10 for only 30 % of the weight variances. All recovery actions with ranks 12 and larger were elevated for less than 15 % of the variations, with nine of the lowest ranked actions never reaching the top 10.

The results of the structural sensitivity analysis indicate that of the 10 recovery actions that were ranked from 1 to 10 under the original model structure, 1 through 9 remained in the top 10 under 17 out of 18 variations (94 %). The tenth-ranked action fell out of the top 10 in only 4 of the 18 variations (72 %). Similarly to the 25 % weight variation results, the eleventh and twelfth ranked actions were elevated to the top for only 4 out of the 18 variations in structure. The lowest 12 ranked recovery actions never reached the top 10. The stability in rankings seen in both sensitivity analyses suggests that managers can be confident in investing their resources in the top ranked recovery actions proposed by the model.

Discussion

The explicit modeling framework described here addresses shortcomings in how recovery efforts have been approached for the Mojave desert tortoise in the past (Averill-Murray and others 2012). The nature of threats to the desert tortoise is such that many can never be eliminated entirely, but will require ongoing management attention (i.e., the Mojave desert tortoise is a “conservation-reliant” species; Scott and others 2005, 2010). We developed a systematic strategy for quantifying threats and prioritizing recovery actions in terms of their relative, predicted impact on risk to a population. This strategy will facilitate the ongoing assessment of threats, prioritization and evaluation of conservation actions, and adjustments to the recovery program over time.

Although we developed this approach to prioritize recovery actions for the threatened Mojave desert tortoise, it is a process that can be valuable for threats assessment and recovery planning for other at-risk species, and it can be readily employed even in situations for which very little data exist on the effects of threats on a species. In addition, by testing our approach with a complicated and large-scale case study (e.g., for a conservation-reliant species with > 40 identified threats and over 2.4 million ha of critical habitat) we can be fairly certain that this strategy would be useful for most threatened and endangered species. As a result of the complexity and geographic scope of the Mojave desert tortoise recovery program, we developed our initial

Fig. 5 The range-wide contribution of direct and indirect effects of each potential threat to an increase in risk to the Mojave desert tortoise

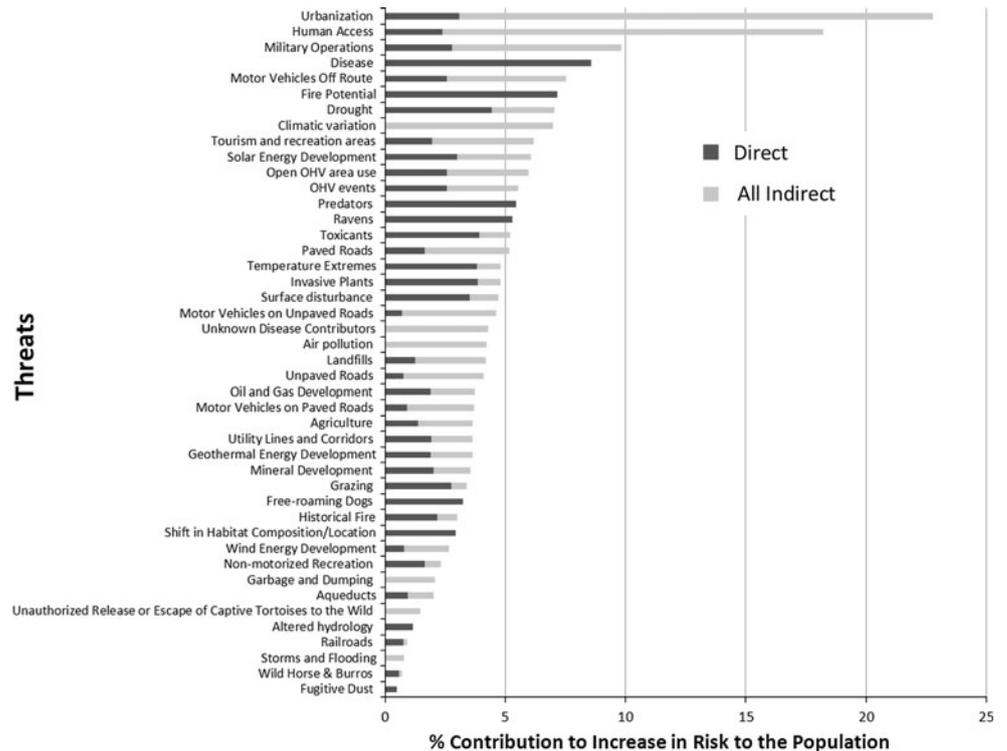


Table 2 Range-wide percentage contribution of stresses to an increase in risk to the population in the Mojave desert tortoise

Stress	Increase in mortality (adult)	Decrease in reproductive output	Increase in mortality (juvenile)	Total % contribution to increase in risk
Habitat loss	15.8	0.4	2.2	18.4
Predation	11.7	–	2.2	13.9
Crushing	11.7	–	1.6	13.3
Nutritional compromise	7.8	0.4	1.6	9.8
Dehydration	7.8	0.4	1.6	9.8
Loss of shelter and breeding sites	7.8	0.2	0.5	8.5
Disease	7.8	0.2	0.5	8.5
Burning or smoke inhalation	3.9	–	1.3	5.2
Entrapment/burial	3.9	–	0.5	4.4
Collection	3.9	–	0	3.9
Toxicosis	3.9	–	0	3.9
Small population and stochastic effects	0	0.2	–	0.2
Injury	–	0.1	–	0.1
Altered behavior	–	0.1	–	0.1
Deliberate maiming or killing	0	–	0	0
Altered hatching success or sex ratios	–	0	–	0
Genetic contamination	0	0	–	0
Total % contribution to increase in risk	86	2	12	100

framework by eliciting expert input from small groups in order to produce a prototype model. The prototype can now be applied to a broader participatory process in which additional stakeholders provide input on model structure through a “recovery implementation team” process

(Averill-Murray and others 2012). Greater stakeholder participation could be incorporated initially for a smaller model for less challenging species. In either case, our approach is dynamic and transparent, and the threats assessment and recovery action prioritization can be easily updated in an

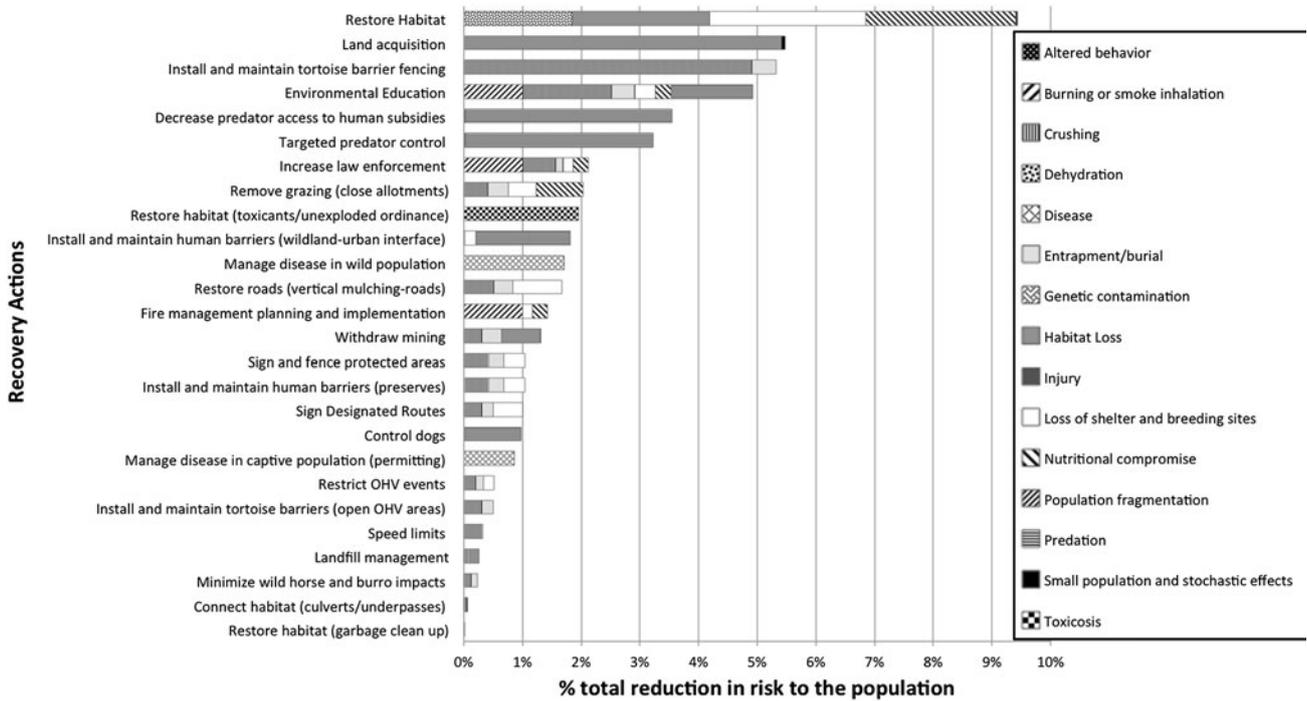
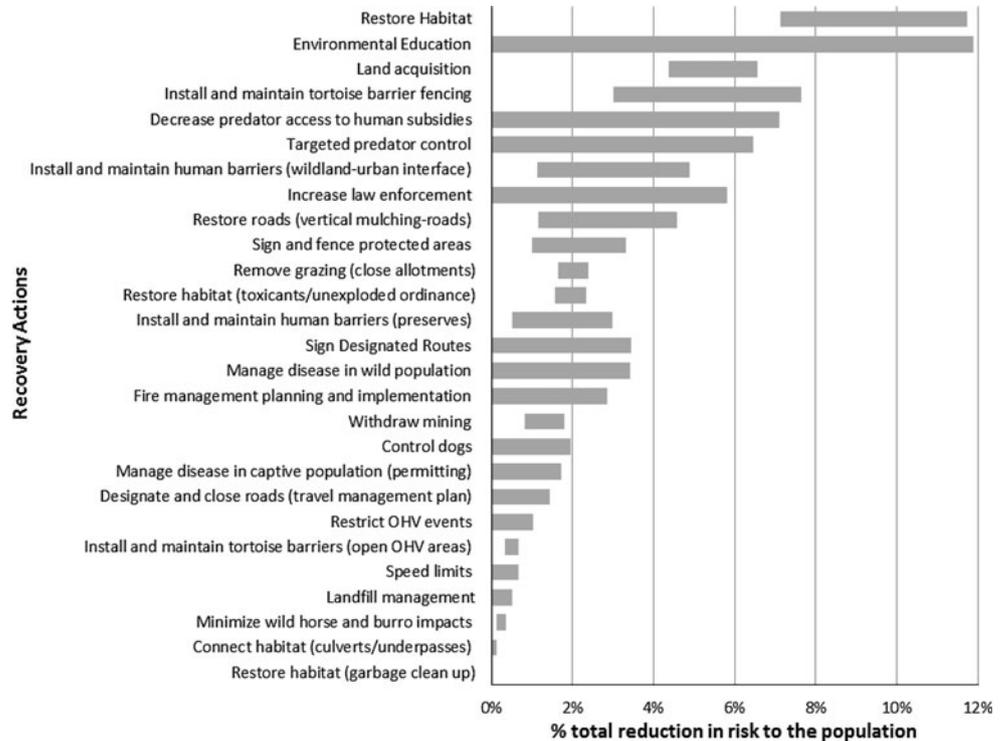


Fig. 6 The decrease in risk to the Mojave desert tortoise for each recovery action type implemented across the range based on the mean recovery action effectiveness score, shown as the sum of the decreases in all stresses affected by that action

Fig. 7 The range in predicted decrease in risk to the Mojave desert tortoise generated by the potential high and low estimates of the effectiveness scores of each recovery action



adaptive management framework as new information becomes available.

While we demonstrated the ranking of recovery actions on a range-wide scale, implementation typically occurs in

smaller areas for the Mojave desert tortoise. Nevertheless, this ranking provides an important evaluation of the types of actions that should be considered for implementation at smaller scales. The importance of counteracting habitat

loss (Table 2) is reflected in the high rankings of recovery actions for habitat restoration and land acquisition (Fig. 6). Tortoise-exclusion fencing and, to some extent, environmental education achieve relatively high priority by preventing crushing of tortoises (Fig. 6). The contribution of predation to risk (Table 2) results in relatively high priorities for decreasing predator subsidies and targeted predator control (Fig. 6). Lower-priority actions range-wide may still be effective and important at local scales (e.g., garbage clean-up and installation of culverts and underpasses).

In addition, uncertainty associated with the potential effectiveness of each recovery action may be useful when prioritizing actions for implementation (Fig. 6). For example, high variation in potential effectiveness of environmental education suggests that it may be prudent not to invest too heavily in this action relative to others, such as habitat restoration, until the effectiveness of specific educational tools can be clarified or targeted to have a high probability of effecting the desired change in human behavior. Evaluation of high-end and low-end effectiveness scenarios indicates that, in general, the range of potential effects of a given recovery action decreases as the actions address more localized or less severe stresses (Fig. 7).

Our strategy differs from other recent efforts for quantifying multiple threats to endangered species (Bolten and others 2011; Donlan and others 2010) in three important ways. First, we used an established lexicon for conservation planning (Salafsky and others 2008). A standard terminology for describing and organizing threats and their effects is important for communicating and working with numerous stakeholders across a large geographic area and for dealing with complex ecological systems in which threats vary spatially and temporally and operate at different scales. Our experience in the early stages of soliciting input from diverse stakeholders in the development of this model revealed that many people interpreted previously undefined terms differently, which resulted in differences in perceived relationships between threats, which compromised the ability to develop consistent conceptual models.

Second, we explicitly address both direct and indirect effects of threats, capturing each threat's total contribution to increase in risk to the population. Threats that act indirectly can pose great danger to a species (Fig. 5), yet they are often ignored or insufficiently considered because of the difficulty in understanding the complex relationships that can result from multiple, interacting threats. By identifying explicitly the interrelationships of indirect effects, we can begin to predict the cumulative effect of each threat, as well as understand the effects of recovery actions on a suite of threats when the effect of a single threat is changed.

Third, we quantify the effects of recovery actions on decreasing risk to the population, which is the first step towards prioritizing recovery actions and developing

appropriate monitoring metrics for each action. Identifying the stresses and their originating threats that will be affected by a particular action clarifies our expected outcomes of each recovery action and indicates what should be measured to test these assumptions and evaluate success. As we collect information through monitoring and validation, we can re-run our models and modify on-the-ground actions as outcomes and other events become better understood (i.e., adaptive management; Runge 2011).

Finally, our ranking of recovery actions by predicted effectiveness at decreasing risk to the population is the first step towards a multicriteria decision analysis (MCDA) approach in which additional criteria, such as costs, funding sources, and level of public support, can also be incorporated into the prioritization (Kiker and others 2005). Given the four-state landscape encompassed in the range of the Mojave desert tortoise, no single MCDA model will fit the heterogeneous management context. Thus, we decided to first focus on creating science-based quantitative estimates based solely on decreasing risk to the population. Integrating the estimates of risk to the species described in this paper into a broader management MCDA model by jurisdiction would be an appropriate next step for managers.

Assumptions

We have adopted an iterative approach to quantifying the importance of threats and ranking recovery actions for at-risk species. At each new iteration, we attempt to use what has been learned in the previous iteration to better address key assumptions in our model. The key assumptions in this iteration include assumed linearity and model completeness, no inclusion of time lags, that experts are experts range-wide, and that the species can be recovered by incremental reduction in stresses.

First, the changes in threats, stresses, and population are modeled as linear responses to either increases in threats or the implementation of recovery actions. While this approach allows for cumulative effects analyses, it does not model for thresholds in population responses or habitat degradation. Also, the effects of threats and stresses are considered independent. Our current approach does not adequately account for feedback loops in the immediate habitat (e.g., invasive species and fire). As such, we may be underestimating the speed at which local conditions can change. Second, the contributions of threats to threats, threats to stresses, and stresses to population effects are assumed to be complete—all relative weights of all contributing entities adds to 1. This assumes, supported by third party expert opinion and/or the literature, that factors not included are not significant. This is unlikely to be true throughout the model network, and we are likely overweighting the known contributors in some parts of the

model. Third, population responses are treated as instantaneous, even for the indirect effects. This assumption means the current approach likely over-emphasizes immediate effects and fails to distinguish between responses that are deterministic and downstream indirect responses for which there is greater uncertainty. Fourth, we assume that our experts are range-wide experts, across all threat relationships; though we strove to choose experts appropriate to each level in the model, the large range of the desert tortoise means that individual expert knowledge may be deep, but localized. Finally, we make an assumption that the species can be recovered by incremental reduction in stresses to the population, in particular, that the cumulative reduction in stresses from recovery actions is not overwhelmed by catastrophic events. If there is a high likelihood of a catastrophic event, more radical recovery actions should be prioritized. We look to address many of these assumptions in a new round of work that is underway.

Accounting for Spatial Heterogeneity in Threats and Populations

Our threat assessment process treats the effects of threats and recovery actions as being uniform across the range of a species (i.e., the effects are aspatial). For narrowly distributed species for which the spatial variation in risk is relatively homogeneous, this aspatial approach to threats assessment and recovery action ranking is likely to be adequate. For wide-ranging species such as the Mojave desert tortoise, however, the array of threats varies both spatially and temporally across its range (USFWS 2011). Accurate ranking of threats and prioritization of recovery actions at regional and local scales requires accounting for spatial heterogeneity in threats and population distribution. Therefore, the aspatial approach we have described in this paper was the first step of the necessary spatially explicit approach that allows us to incorporate spatial variation in threat severity and to identify and apply the suite of recovery actions predicted to provide the greatest benefits to the species in each region.

The Conceptual Model Manager

To organize the model and perform analyses described in this paper, we developed an application called the Conceptual Model Manager. The Conceptual Model Manager has a graphical display showing threats, stresses, population effects, and recovery actions as labeled boxes, connected by lines where a relationship exists. Each box and line is fully annotated with name, definition, and supporting citations. The weights for those relationships are also displayed, described, and annotated. The data and relationships are fully editable, and all information is stored in a database that can be a local file or accessed as web

service. An interactive version of the model is available online (<http://www.spatial.redlands.edu/dtro/modeexplorer/>).

The Conceptual Model Manager combines the different kinds of relationships described in Fig. 1 into a fully connected network for all direct and indirect effects of threats to a species. By determining weights and implementing the calculations described above for ranking threats and prioritizing recovery actions, we have made the complex conceptual model computational, which allows users to extract rankings useful for conservation and recovery planning efforts. Additionally, using the Conceptual Model Manager, we can integrate the conceptual model directly with a spatial decision support engine, so the same rankings can be calculated when spatial variation in threats and populations is incorporated. The Conceptual Model Manager tool is available via <http://www.spatial.redlands.edu/cmm/>.

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