Contributed Paper

Calculating Biologically Accurate Mitigation Credits: Insights from the California Tiger Salamander

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Abstract: *Current conservation mitigation plans often fail to ensure full in-kind habitat replacement for endangered species, which suggests the need for improved methods for calculating mitigation credits. A simple, yet biologically meaningful method for calculating mitigation credits would be to let the number of mitigation credits assigned to a parcel of land scale with the reproductive value of the individuals occupying that parcel. This can be accomplished by dividing the population into 2 or more subdivisions with different reproductive values, calculating the densities of these subdivisions as a function of one or more habitat parameters, and then forming a weighted sum of these densities such that each density distribution is weighted by the reproductive value of its respective subdivision of the population. This weighted sum is the density distribution of reproductive value, and by integrating it over a particular parcel, one can determine the mitigation value of that parcel. We carried out this procedure for a population of California tiger salamanders (*Ambystoma californiense*), with distance from breeding site as our habitat parameter and the 3 visually identifiable age classes (adults, juveniles, and metamorphs) as our population subdivisions. This led to a density distribution of reproductive value that decreased exponentially with increasing distance from a breeding site. Mitigation strategies derived from this function will be more likely to ensure the persistence of California tiger salamander populations than current approaches, which assign all land within 1.6 km of a breeding site the same mitigation value. Use of the density distribution of reproductive value as a basis for mitigation plans is a procedure that can be applied to all endangered species, and it should improve the quality of mitigation decisions.*

Keywords: *Ambystoma californiense*, California tiger salamander, density distribution, mitigation credit, pond-breeding amphibian, reproductive value, survivorship value

Cálculo de Créditos de Mitigación Biológicamente Precisos: Perspectivas para la Salamandra Tigre de California

Resumen: *Los planes actuales de mitigación de la conservación a menudo no aseguran el reemplazo total del hábitat de especies en peligro, lo que sugiere la necesidad de mejores métodos para calcular los créditos de mitigación. Un método simple, pero biológicamente significativo, para calcular créditos de mitigación sería dejar que el número de créditos de mitigación asignadas a una parcela de tierra escalen con el valor reproductivo de los individuos que ocupan esa parcela. Esto se puede lograr dividiendo a la población en 2 o más subdivisiones con valores reproductivos diferentes, calculando las densidades de estas subdivisiones como una función de uno o más parámetros del hábitat y luego formado una suma ponderada de estas densidades de tal modo que cada distribución de densidad está ponderada por el valor reproductivo de su respectiva subdivisión de la población. Esta suma ponderada es la distribución de la densidad de valor reproductivo, y al integrarlo en una parcela particular, se puede determinar el valor de mitigación de esa parcela. Llevamos este procedimiento a cabo con una población de salamandras tigre de California (*Ambystoma californiense*), con la distancia al sitio de reproducción como nuestro parámetro de hábitat y las 3 clases de edad identificables visualmente (adultos, juveniles y metamorfos) como nuestras subdivisiones de la población. Esto llevó a una distribución de la densidad de valor reproductivo que decreció exponencialmente con el incremento*

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de la distancia al sitio de reproducción. Las estrategias de mitigación derivadas de esta función tendrán más probabilidad de asegurar la persistencia de las poblaciones de salamandra tigre de California que los enfoques actuales, que asignan el mismo valor de mitigación a todo el terreno dentro de un radio de 1.6 km del sitio de reproducción. El uso de la distribución de la densidad del valor reproductivo como la base para planes de mitigación es un procedimiento que puede ser aplicado a todas las especies en peligro, y debería mejorar la calidad de las decisiones de mitigación.

Palabras Clave: *Ambystoma californiense*, anfibio reproductor en charcas, crédito de mitigación, distribución de la densidad, salamandra tigre de California, valor reproductivo, valor de supervivencia

Introduction

The idea of mitigation was introduced by the Fish and Wildlife Coordination Act of 1958 (Blomberg 1987). The basic concept is simple and pragmatic. Although harming or harassing endangered species is a violation of the U.S. Endangered Species Act, there are times when such "take" inevitably occurs. In such cases an incidental take permit is issued, which allows the take of a certain number of individuals of an endangered species. In return, mitigation is required that compensates for the take to the greatest extent practicable and ensures that no appreciable reduction in the likelihood of species survival results (Stanford Environmental Law Society 2001). The issue then becomes deciding how much mitigation is required to ensure no appreciable reduction in the likelihood of species survival.

When the disturbance involves destruction of the habitat of an endangered species, a certain number of mitigation credits are assigned to the destroyed habitat, and the responsible party must protect or enhance other habitat to compensate for the loss. Depending on the credit ratio, they may have to protect or enhance habitat containing an equal number of mitigation credits (1:1 credit ratio) or habitat containing much greater mitigation credits than the destroyed habitat (e.g., 3:1 credit ratio). The protected land can be either other land belonging to the party creating the disturbance (project-proponent mitigation) or land purchased from a conservation bank. Ninety-one percent of the time, conservation-bank managers use the simplest possible metric to assign mitigation credits to their land: the area of the habitat protected (Fox & Nino-Murcia 2005). That is, a constant conversion ratio is established that equates a certain area of habitat with a certain number of credits. For example, 1 ha could be equal to one credit. Although such a simple metric is easy to quantify and apply, it ignores the existing or potential functions of a particular piece of habitat (Institute of Water Resources 1994). Obviously, some habitat is of higher quality than other habitat (i.e., habitat that is more important to the survival of the endangered population is of higher quality). Quantifying habitat quality for a target species, however, has proven difficult. The simplest method for determining habitat quality is to use "best professional judgment." Problems with this method include its uncertainty, potential irreproducibility, and subjective nature (Stein et al. 2000). The challenge then is to establish a method of assigning mitigation credits that is accurate, repeatable, and objective.

Several new methods for objectively assigning mitigation credits have been developed. Some assign credits on the basis of ecosystem function (Rheinhardt et al. 1997), spatial structure (Bruggeman et al. 2005), or probability of habitat establishment (Robb 2002). Some (e.g., Robb 2002) provide only a coarse measurement of habitat quality, whereas others require extensive measurements of habitat parameters (Rheinhardt et al. 1997) or future projections of habitat quality (Bruggeman et al. 2005). The U.S. Fish and Wildlife Service (2003*b*) suggests using the number of nest sites or family groups as a quantifiable metric that works well with species whose nest sites and family groups are easily counted. Nevertheless, this cannot be used with solitary or cryptic species, such as species of pond-breeding amphibians. For these taxa we propose following Van Horne (1983), who suggests that habitat quality may be quantified as "the product of density, mean individual survival probability, and mean expectation of future offspring." This strategy assigns value to habitat according to the density of individuals weighted by their reproductive value, or what we call the density of reproductive value. The essential reason for assigning mitigation credits on the basis of density of reproductive value is that it is both biologically accurate and general enough to apply to any target species. We advocate using this metric to calculate mitigation credits associated with both the land being altered and with the land being protected to mitigate for the alteration. This will be effective with both project-proponent mitigation and mitigation with conservation banks.

To illustrate how this approach can be applied, we used data from the California tiger salamander (*Ambystoma californiense*), which is protected under the U.S. Endangered Species Act as a series of 3 distinct population segments (U.S. Fish and Wildlife Service 2000, 2003*a*, 2004). We chose this species for 3 reasons. First, over the past decade, the California tiger salamander has emerged as one of the most intensively studied species of declining amphibians in North America. We now understand a great deal about California tiger salamander life history, demography, ecology, and genetics (e.g., Austin & Shaffer 1992; Trenham 2001; Shaffer et al. 2004). Second, most California tiger salamander habitat lies in California's Central Valley, which is the site of the most rapid urbanization in the United States (U.S. Census Bureau 2005). Rapid urbanization makes land development and mitigation issues of primary concern in the region. Third, spatial analysis of California tiger salamander declines indicates that habitat loss is a primary threat to the species (Davidson et al. 2002), suggesting that mitigation will continue to play an important role in future species management.

Methods

Application to the California Tiger Salamander System

To apply Van Horne's definition of habitat quality to California tiger salamanders, we first assumed that all adults have the same expectation of future reproduction. Then what remained for us to do was measure the density of California tiger salamanders across the relevant landscape and determine their probability of surviving to adulthood. In ecological studies of pond-breeding amphibians, the most important and easily measured metric of terrestrial habitat quality is distance from the breeding site (e.g., Semlitsch 1998; Johnson & Semlitsch 2003; Semlitsch & Bodie 2003); thus, we used this metric in our model. To measure survival probabilities, we separated individuals into 3 visually identifiable age classes: metamorphs, juveniles, and adults. By determining the density distributions of these 3 age classes and multiplying them by their respective survival probabilities, we derived an accurate measure of habitat quality, and thus an appropriate mitigation value, as a function of distance from the breeding site.

Study System

We conducted our research at the Jepson Prairie Preserve, Solano County, California, building on the work of Trenham and Shaffer (2005). The preserve covers 625 ha and is dominated by Olcott Lake, a playa vernal pool that reaches a maximum size of 36 ha during the height of the wet season. The site represents optimal breeding habitat for California tiger salamanders because of the large size of Olcott Lake, the protection granted to the land by the preserve, and the high level of pocket gopher (*Thomomys bottae*) activity. California tiger salamanders use pocket gopher and California ground squirrel (*Spermophilus beecheyi*) burrows during their terrestrial phase, and the abundance of salamanders is correlated with the abundance of burrows (Loredo et al. 1996; Trenham et al. 2001; Trenham & Shaffer 2005).

Experimental Procedure

To quantify California tiger salamander landscape use as a function of distance from the shoreline of Olcott Lake, we set up a drift-fence array parallel to the shoreline. We constructed the drift fences and pitfall traps as in Trenham and Shaffer (2005), with a few minor alterations. The drift fences in our array were shorter (0.3 m rather than 0.9 m tall). In addition, we used paired pitfall traps, rather than use a single divided pitfall trap (Trenham & Shaffer 2005), at each end of the fences.

The array of pitfall traps consisted of 10 lines of fences placed at increasing distances from the shoreline of Olcott Lake. Each line covered an arc along the northeast side of Olcott Lake, and we placed the lines at 10, 100, 200, 300, 400, 500, 600, 700, 850, and 1000 m from the lake shoreline. The line of fences at 10 m from the shoreline was continuous, such that the only spacing between the fences was the width of one bucket, where a pitfall trap was placed. The other lines of fences consisted of 10-m fences with 90 m between them, providing 10% coverage of each arc (Trenham & Shaffer 2005). There were 136 fences in total.

We opened the traps during most rainy nights and nights subsequent to a rainy night from 27 October 2005 until 2 March 2006, which encompassed the entire winter breeding and activity season (Shaffer & Trenham 2005). We also opened the traps for 49 of the 53 nights between 20 May 2006 and 11 July 2006, which encompassed the majority of spring metamorph emergence (Petranka 1998). Given our past experience with California tiger salamander movements, we were confident that the traps were open on essentially all nights that had significant terrestrial salamander movement and that our data set accounted for any temporal variation in salamander movement across a full year of activity.

We checked the traps every morning starting immediately before sunrise. For each California tiger salamander captured, we recorded the location of the trap in which it was found and its life stage. We calculated the density of each life stage (adult, juvenile, metamorph) at each distance from Olcott Lake as the number of California tiger salamanders caught at the fence line over the course of the entire field season divided by the number of 10-m fences in that line. We identified adults by their keeled tails, swollen vents (males), and obvious gravid condition (prebreeding females). In addition, we categorized animals that were over 18.5 g (the largest confirmed weight for a juvenile) that did not have a keeled tail or swollen vent as adult females. We identified metamorphs by their poorly defined spotting pattern and juveniles on the basis of their adult color pattern, lack of other adult characteristics, and small size.

Analyses

The probability of each salamander age class reaching maturity was calculated on the basis of survivorship values taken from Trenham et al. (2000), who found that metamorphs have a 0.3 probability of surviving their first summer and that all older age classes of salamanders have a 0.63 probability of surviving to the following year. On the basis of these probabilities and an average age at maturity of 4 years (Trenham et al. 2000), metamorphs had a 0.08 probability of reaching maturity, whereas juveniles had a 0.37 probability of reaching maturity. When calculating the density distribution of reproductive value, the metamorph density distribution was therefore weighted by 0.08, the juvenile density distribution by 0.37, and the adult density distribution by 1.0. We fit 5 different regression lines to the density distribution of reproductive value (exponential, linear, logarithmic, power, and quadratic) and compared goodness of fit with R^2 values.

Results

We captured 5582 California tiger salamanders, including 608 adults, 1828 juveniles, and 3146 metamorphs. The density distributions of the 3 age classes (Fig. 1a) were weighted by the probabilities of their respective age classes reaching maturity and were then summed to give a density distribution of reproductive value for the entire salamander population (Fig. 1b). The exponential regression provided the best fit to these data ($y = 21.883e^{-0.0019x}$, where x is distance from the shoreline of the pond and y is reproductive value; $R^2 = 0.9243$). Using this exponential function as the model for the density distribution of reproductive value, we developed another function that related mitigation ratio to distance from breeding site (Fig. 1c). The mitigation ratio and reproductive value functions had the same shape, ensuring that the cost of mitigation scales with the relative biological value of habitat to the salamander population. The magnitude of the mitigation-ratio function was such that if one were to mitigate for all of the land within 1.6 km of a California tiger salamander breeding site (all of the land considered potential California tiger salamander habitat under current regulatory practice), one would incur the same total cost as under a constant 1:1 mitigation ratio. Thus, our new mitigation-ratio function did not change the total cost of mitigation; it only redistributed that cost across the landscape such that biologically more important land required a higher mitigation ratio and less important land a much lower ratio. We based these calculations on a breeding pond with a radius of 17 m, which was the average size of 10 California tiger salamander breeding

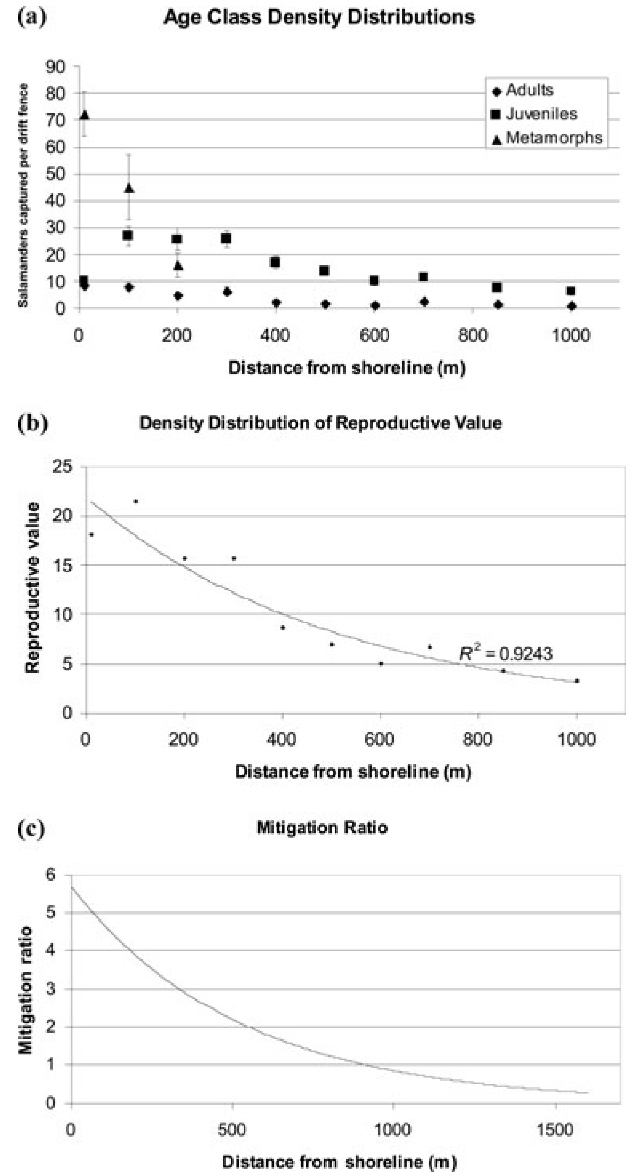

Figure 1. Calculation of the mitigation-ratio function on the basis of (a) the density distributions of the 3 age classes (metamorphs, juveniles, and adults) of 5582 individuals captured at Olcott Lake, (b) the density distributions weighted relative to probabilities of their respective age classes reaching maturity (metamorph weight = 0.08, juvenile weight = 0.37, adult weight = 1) and added together to give the density distribution of reproductive value, and (c) a mitigation-ratio function that ensures that land at the shoreline has the same relative increase in mitigation value as it does in value to the salamander population.

ponds studied across an intact landscape in Monterey County, California (Trenham et al. 2001). This yielded a final equation for the mitigation-ratio function of $y = 5.683e^{-0.0019x}$.

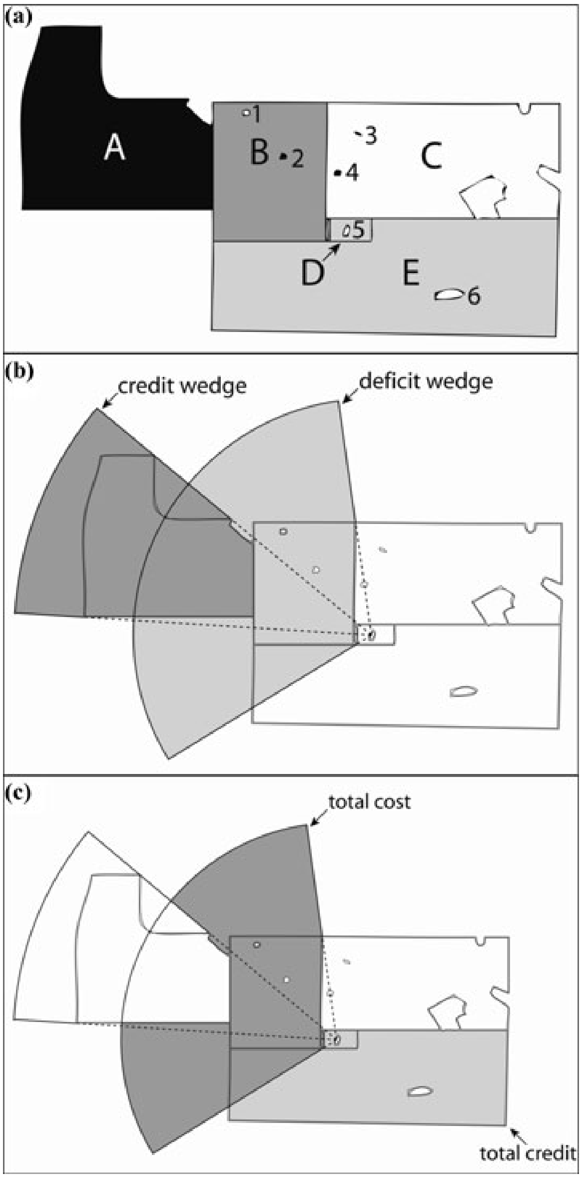

Figure 2. Map of (a) Potrero Hills Landfill expansion (parcel A, existing landfill; parcel B proposed expansion; parcels D and E proposed for protection as part of the mitigation plan; parcel C belongs to the landfill, but is not part of the mitigation plan; numbers are the 6 ponds supporting salamander populations); (b) deficit and credit wedges for pond 5 (deficit wedge is created by projecting from the center of the pond past the corners of the proposed landfill expansion [parcel B] for 1.6 km; credit wedge is created by projecting from the center of the pond past the corners of the existing landfill [parcel A] for 1.6 km, although here it is projected for more than 1.6 km for the purpose of illustration; and (c) area of total mitigation cost (deficit wedge, credit wedge) and total mitigation credit (summation of parcels to be placed under protection that are accessible to salamanders on the landscape).

Case Study: Potrero Hills Landfill Project

To illustrate how our mitigation-ratio function can be applied in accordance with existing U.S. Fish and Wildlife Service standards, we examined a mitigation effort for a proposed development project in Solano County, California (Fig. 2a). The Potrero Hills Landfill project is typical in that there is a currently existing land use that seeks to expand onto prime California tiger salamander habitat and to mitigate for the proposed expansion. The landfill currently occupies parcel A, and expansion into parcel B is proposed. Parcel B includes 2 California tiger salamander breeding sites, and there are 4 more salamander breeding sites on the landfill's property that are within 1.6 km of parcel B. One of the suggested mitigation plans developed by the landfill managers is to place parcels D and E under protection. A simple area metric yielded an overall mitigation ratio of 2.33:1 for this plan because the area of parcel B is 79 ha and the combined area of parcels D and E is 184 ha. By incorporating more biological detail into the analysis, our new approach can be used to determine whether this mitigation plan is sufficient to offset the lost reproductive value to California tiger salamanders incurred by the proposed expansion.

When making calculations of the land required to compensate for the lost biological value of parcel B, we treated each breeding pond separately and then added together the land required to mitigate for all of the ponds. The first step was to determine a separate mitigation-ratio function for each pond. The magnitude of this curve will vary slightly with pond size because larger ponds have more area within 1.6 km of their shoreline.

The second step was to integrate that function over the affected region for each pond. We refer to this region as the *deficit wedge* for a pond because it includes the loss of habitat incurred by rendering parcel B both uninhabitable and impassible to terrestrial salamanders. We calculated the deficit wedge for each pond as all land within 1.6 km of the shoreline of that breeding pond that was either contained in parcel B or rendered inaccessible to a salamander migrating in a straight line away from the center of the pond by parcel B (Fig. 2b). We based this calculation on the reasonable assumption that California tiger salamanders migrate to and from breeding ponds in a straight line and thus any land that does not have straight-line access to a breeding pond becomes unsuitable salamander habitat. The deficit wedge will be different for each pond because from each pond's perspective a different parcel of land is hidden in the "shadow" of the projected expansion. For the special case of ponds 1 and 2, which will actually be destroyed by the landfill expansion (Fig. 2a), the deficit wedge included all the area within a 1.6-km radius of the ponds.

The third step was to subtract from the deficit wedge any land already unsuitable for the salamander on the basis of either natural conditions or preexisting

Table 1. Calculated mitigation costs of a planned landfill expansion and calculated mitigation credits of the proposed mitigation plan.

Pond	Mitigation-ratio function	Mitigation cost (ha)		
		*subdivision**		*total*
1	$y = 5.651e^{(-0.0019x)}$	deficit wedge	836.495	668.575
		credit wedge	167.920	
2	$y = 5.667e^{(-0.0019x)}$	deficit wedge	834.337	738.023
		credit wedge	96.314	
3	$y = 5.683e^{(-0.0019x)}$	deficit wedge	232.126	208.919
		credit wedge	23.207	
4	$y = 5.667e^{(-0.0019x)}$	deficit wedge	362.758	332.947
		credit wedge	29.811	
5	$y = 5.615e^{(-0.0019x)}$	deficit wedge	239.155	221.223
		credit wedge	17.932	
6	$y = 5.464e^{(-0.0019x)}$	deficit wedge	13.344	13.344
5	$y = 5.615e^{(-0.0019x)}$	mitigation credit	286.62	286.62
6	$y = 5.464e^{(-0.0019x)}$	mitigation credit	414.509	414.509
			Total credit	2183.031
			Total credit	701.129
			Grand total	1481.902

**Deficit wedge refers to the mitigation cost of a developed parcel with respect to a given pond due to the land directly affected by the parcel and the land in the "shadow" of the parcel. Credit wedge refers to the land within the deficit wedge that is already unsuitable habitat prior to the proposed development plan, and is thus not counted against the proposed development project. Mitigation credit refers to the mitigation value of the parcels that are going to be protected as a result of the proposed mitigation plan.*

development. In the case of the Potrero Hills Landfill, this would be any land within the preexisting landfill (parcel A) or in the shadow of the existing landfill. We refer to this land as the *credit wedge* (Fig. 2b), and the mitigation-ratio function of each pond must be integrated over its respective credit wedge as well.

The final step was to sum all deficit-wedge values and subtract from that sum all credit-wedge values to determine the total cost of mitigation for the biological impacts of parcel B (shown for pond 5 in Fig. 2c). The cost for the Potrero Hills Landfill was 2183 ha (Table 1). This was the cost under the assumption of an overall 1:1 credit ratio. Under an overall 2:1 or 3:1 credit ratio, the cost would be 2 (4366 ha) or 3 (6549 ha) times greater, respectively.

We applied similar logic to determine whether the proposed mitigation plan (protection of parcels D and E) generates enough credits to equal this cost. According to U.S. Fish and Wildlife Service standards, mitigation credits are given for any parcel that is slated for protection and contains, or is connected with other protected parcels containing, a California tiger salamander breeding site. In the case of the Potrero Hills Landfill, both parcels D and E qualify because they will receive protection and contain breeding ponds 5 and 6 (Fig. 2c). When calculating the mitigation values of parcels D and E, one should only include the sections of those parcels from which a salamander can reach the center of the pond without passing through unprotected land. For pond 5, a section of parcel E is within the shadow of the landfill expansion and thus should not count as mitigation credit for that pond (Fig. 2c). After the mitigation credits are calculated for each pond, they can be summed to yield a total credit value (shown for pond 5 in Fig. 2c). The plan to protect parcels D and E had a total credit value of 701 ha (Table 1). This is 1482 ha less than the total cost of the project, implying that the proposed mitigation plan is insufficient for California tiger salamanders, even under an overall 1:1 credit ratio. Under an overall 2:1 or 3:1 credit ratio, it would fall even further below parity (3665 ha or 5848 ha, respectively).

Discussion

Lessons from the Case Study

Our analysis of the Potrero Hills mitigation plan demonstrates the magnitude of changes that may result from incorporating biological detail into mitigation assessments. With a simple area metric, the Potrero Hills mitigation plan had an overall mitigation ratio of 2.33:1, whereas with our more biologically informed approach, it had an overall mitigation ratio of only 0.32:1 (a greater than 7-fold difference). This change came from incorporating details of species density and reproductive potential into the calculation of mitigation credits, both of which are key components of species persistence. Incorporation of these biologically relevant parameters into mitigation calculations is relatively simple to perform, provided the relevant data concerning species demography and habitat use are available. In the case of species for which such data are not available, the key information to be generated by future studies is a density distribution of the species across a landscape.

Why does such a conceptually simple procedure lead to such drastic changes in the assignment of mitigation costs? Our new mitigation procedure changed the total area that needed to be mitigated and how this area was valued on the basis of its physical placement with respect to biologically important landscape features. The total area changed because we accounted for the migratory behavior of California tiger salamanders. This meant that habitat loss affected both the area actually affected and the land that became isolated from a given breeding pond as a consequence of the impact (Fig. 2c). The relative importance of the altered area and the land isolated as a result of the alteration varied with the particular configuration of the affected landscape. The larger and closer the affected area was to the breeding ponds, the more it dominated the mitigation calculations with respect to the smaller, more distant parcel that was isolated behind it. Critically, our approach also changed the way land was valued because it assigned value on a more biological basis. The density distributions of adult and juvenile salamanders decreased exponentially as a function of distance from the breeding site, similar to results found in other species of pond-breeding amphibians (Rittenhouse & Semlitsch 2007). This implies that it is critically important to protect land near the edge of a breeding site. In our example, much of the land in parcel B was situated near breeding sites, which explained why it was so costly to develop. On the other hand, much of the land in parcel E was distant from all of the breeding sites, resulting in a relatively low mitigation value for this parcel. Thus, one lesson from our worked example is that it is important to protect centrally located land that lies near a number of breeding sites. In doing so, the protected land gains value from each of the ponds it borders, and preserving it will keep the entire metapopulation of ponds intact.

The Broader Picture

The need for a shift in mitigation procedures is clear, given the current record of mitigation efforts within the United States. A survey of 45 mitigation wetlands across the country revealed that only 49% have been successful at in-kind habitat replacement on the basis of a series of vegetation criteria (Spieles 2005). This national situation is mirrored in the San Francisco Bay delta region of northern California, where we conducted our study. Thirty wetland creation projects in the region were scored from 0 to 10 on their ability to replace in-kind habitat, and the average score was only 4.66 (DeWesse 1994). Failure to replace in-kind habitat can have an extremely detrimental impact on most organisms, including amphibians. For example, salamanders and wood frogs are almost entirely absent from wetlands constructed for mitigation purposes in Ohio. This absence apparently reflects the way mitigation has been accomplished in the region; although forested habitat constitutes a substantial portion of affected wetlands in Ohio, over 85% of mitigation wetlands in that state have <25% forest cover (Porej 2003). Clearly, it is important to develop a better system for ensuring that mitigation projects are replacing an acceptable amount of biologically appropriate in-kind habitat.

An important early attempt to scale mitigation ratios to the biological value of habitat has been implemented in Sonoma County, California, where there is an endangered distinct population segment of California tiger salamanders (U.S. Fish and Wildlife Service 2003*a*). The current mitigation plan stipulates a 1:1 mitigation ratio for land between 671 m and 2.1 km of a breeding site, a 2:1 mitigation ratio for projects between 152 and 671 m of a breeding site, and a 3:1 mitigation ratio for projects within 152 m of a breeding site (U.S. Fish and Wildlife Service 2005). Like our method, this encourages development in the biologically least valuable habitat, and thus this is a move in the right direction. Nevertheless, the step-function approach is somewhat arbitrary because its basis is subjectively chosen distance cutoffs, rather than field-measured density distributions. Given that biological usage by salamanders appears to be a continuous function, rather than a step-function, we recommend using land valuation and mitigation procedures that accurately reflect the continuous distribution of land value to a species.

Aspects of the Model

The mitigation scheme we propose here has 2 other attractive features. First, it incurs no increase in total mitigation costs. That is, if one was to mitigate for all of the land within 1.6 km of a breeding site, it would cost the same amount in terms of mitigation credit-acres as under the currently accepted strategy. Instead of increasing total costs, our approach simply redistributes those costs in a biologically relevant manner. In terms of particular projects, some will require more mitigation than under the current strategy (as with the Potrero Landfill example) and others less, depending on the details of the project. Second, our approach provides developers with an economic incentive to avoid the biologically most important habitat. Because land at the shoreline of a breeding site is now approximately 21 times as valuable (in terms of mitigation) as land 1.6 km from the shoreline, developers may choose to avoid land in the vicinity of breeding sites entirely. Thus, the new mitigation system not only requires biologically accurate mitigation but also provides strong economic incentives to encourage less-severe impacts.

Future Directions

The mitigation system we propose only makes credit evaluation more accurate in terms of a single parameter—distance from the shoreline. There are obviously other parameters that could be used to measure habitat quality.

Semlitsch (1998) suggests topography and vegetation as possible parameters affecting amphibian habitat use, and vegetation type influences the habitat use of many amphibian species (e.g., Findlay & Houlihan 1997; Mitchell et al. 1997; Guerry & Hunter 2002). Another parameter that could influence salamander density is proximity to additional breeding sites. Our model treats each pond independently, but in an intact landscape with a network of breeding sites, ponds may well operate non-additively. For example, eastern tiger salamanders (*A. tigrinum tigrinum*) have a higher population density in the vicinity of a network of ponds (Porej et al. 2004). Yet another class of parameters that could influence amphibian density is the presence and density of strongly interacting species. This could include both positive density covariances with mutualist species such as pocket gophers (Trenham et al. 2001) and negative density covariance with native (Resetarits 2005) and non-native (Fisher & Shaffer 1996) predator species. In principle, these and other biologically relevant factors could be included in mitigation calculations for individual species and landscapes.

Because we based our proposed mitigation system on survivorship values and density distributions, it is important to consider how these values influence our calculations. The survivorship values we used were taken from a study in Monterey County, California (Trenham et al. 2000), whereas the density distributions were derived from our drift-fence array at Olcott Lake some 225 km distant. It would be more satisfying if the survivorship values and density distributions were derived from the same population, and we are currently collecting survivorship data from the Olcott Lake site. Our current model also assumes that all adults have the same reproductive expectation, which is almost certainly an oversimplification. This assumption will not affect the calculations of the model, unless an individual's future reproduction is correlated with distance of that individual from the shoreline. Although this has never been examined in an amphibian system to our knowledge, such a relationship between reproductive output and position on the landscape seems plausible given the recent observation that male spotted salamanders (*A. maculatum*) living closer to their breeding pond have greater mass than those living further away (Regosin et al. 2003). If adults living near the breeding site have a higher reproductive expectation, then land at the shoreline should be given an even greater relative mitigation value.

Implementation of our method of calculating mitigation credits on the basis of density of reproductive value will not remove the necessity of individually negotiating each mitigation plan. Such direct oversight and flexibility is necessary to deal with the complexities of mitigation decisions. For instance, our method does not address minimum viable population sizes. How should a project that destroys enough habitat to bring a population below its minimum viable size be assessed for this impact that extends beyond the habitat that it is actually affecting? Dealing with this and similar complexities will continue to be the purview of experts at the U.S. Fish and Wildlife Service. Nevertheless, if the mitigation function in Fig. 1 is used to calculate mitigation impacts and credits, rather than the static ratio-based approach currently in use, it should help remedy the most egregious failing of current mitigation plans—inability to measure and ensure in-kind habitat replacement.

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