Rethinking a rare-species conservation strategy in an urban landscape: The case of the valley elderberry longhorn beetle

Theresa Sinicrope Talley[a,*], *Erica Fleishman*[b,1], *Marcel Holyoak*[a], *Dennis D. Murphy*[c], *Adam Ballard*[d]

[a]*Department of Environmental Science and Policy, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA*
[b]*Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA*
[c]*Department of Biology, University of Nevada, Reno, NV 89557, USA*
[d]*ECORP Consulting, Inc., 2525 Warren Drive, Rocklin, CA 95677, USA*

ARTICLE INFO

ABSTRACT

Reflecting the lack of critical information for most protected species, recovery plans for organisms listed as threatened or endangered under the U.S. Endangered Species Act tend to oversimplify habitat descriptions. Here we present our approach for improving the definition of habitat for rare and patchily distributed listed species. The valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*) occurs in riparian and scrub communities in California's Central Valley. Habitat quality for the species currently is defined essentially exclusively in terms of presence and abundance of its larval host plant, elderberry (*Sambucus* spp.). Using detailed measures of physical and biological attributes at diverse sites occupied by the beetle, we characterized and defined habitat quality on the basis of not only host plants, but on an array of biotic and abiotic environmental characteristics. We identified four geomorphically distinct habitat associations: alluvial plain, narrow riparian corridor, upper riparian plain, and non-riparian scrub. Depending on habitat type, the environmental characteristics most strongly associated with beetle presence were host plant availability, topography and proximity to habitat edge. Increased local population size of beetles was associated with higher elderberry density and the presence of larger, more mature plants. Stochasticity in site occupancy over space and time confounds our ability to identify sites that are most able to contribute to long-term beetle survival, while underscoring the importance of unoccupied habitat to the beetle. Adopting a multivariate definition of habitat may facilitate more effective identification of locations critical to the recovery of the valley elderberry longhorn beetle, and prioritization of those management actions that can contribute effectively to meeting conservation goals for the species.

---

* Corresponding author: Tel.: +1 530 752 0676; fax: +1 530 752 3350.
  E-mail addresses: tstalley@ucdavis.edu (T.S. Talley), fleishman@nceas.ucsb.edu (E. Fleishman), maholyoak@ucdavis.edu (M. Holyoak), ddmurphy@biodiversity.unr.edu (D.D. Murphy), aballard@ecorpconsulting.com (A. Ballard).
  1 Present address: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA.

1. Introduction

Habitat loss undeniably has been the primary cause of the decline of most species designated as endangered or threatened under the U.S. Endangered Species Act (Wilcove et al., 1998). For species that historically occupied California's vast Central Valley bottomlands, the magnitude of habitat loss over the past 150 years has been extreme. An estimated 90% of riparian woodlands and an even greater percentage of native grasslands have been replaced by agricultural and urban development (Katibah et al., 1984). As a result, many plants, such as vernal pool and grassland herbs and grasses, have declined to the brink of extinction (USFWS, 1997, 1998), and woodland-dependent vertebrates, such as the yellow-billed cuckoo (*Coccyzus americanus*) and the riparian brush rabbit (*Sylvilagus bachmani riparius*) have been nearly lost across much of their former ranges (USFWS, 2000, 2001, 2004). Habitat loss in the Central Valley is so pervasive that it jeopardizes the viability of a number of terrestrial invertebrates despite their extensive geographic ranges and relatively limited habitat area requirements (USFWS, 1976, 1980a,b). The extent of land cover change has led conservation planners to ask whether it is possible to compensate to some extent for lost habitat by enhancing quality of remaining habitat, and to use information on habitat quality to identify realistic goals and strategies for achieving sustainable populations and ecosystems (e.g., Aronson et al., 1995). Unfortunately, few data on habitat quality exist for the majority of the valley's imperiled species.

When a species is listed under the federal Endangered Species Act, the U.S. Fish and Wildlife Service or National Marine Fisheries Service are generally required to develop a recovery plan that describes the status of the species, threats to its persistence, strategies for its recovery, and criteria that must be met for its delisting. Subsequently, habitat conservation planning efforts, whether single-species and local or multiple-species and regional in scale, generally draw from those recovery plans. A review of recovery plans for 181 species found that single-species plans tend to emphasize population number size as the target metric of recovery, rather infrequently including other demographic or ecological relationships with habitat features or with other species (Campbell et al., 2002). Furthermore, single-species recovery plans typically define habitat in terms of a very limited number of environmental attributes that relate to the most basic requirements of the species, such as geographic location, land cover type, or vegetation structure (USFWS, 1984; Campbell et al., 2002). Recovery plans so constrained usually present recovery criteria that are too simplistic to be biologically meaningful or to guide effectively management efforts intended to contribute to the persistence of the species (Tear et al., 1993; Scott et al., 1995; Wilcove et al., 1998; Campbell et al., 2002; Gerber and Hatch, 2002).

Our focal species, the valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*), was federally listed as threatened in 1980 in response to the then few known populations and extensive historical loss of the "riparian environments" in the Central Valley that were thought to support the species (USFWS, 1980b). Regulations resulting from listing defined habitat for the beetle merely in terms of presence of its larval host plant, elderberry (*Sambucus mexicana* and, to a lesser extent, *S. racemosa*), shrubs that are widespread, often abundant and, importantly, exist in many locations without resident populations of the beetle. In part because beetle larvae and adults are extraordinarily cryptic – so much so that populations cannot be surveyed or censused directly – local abundance of shrubs has served as a surrogate metric for assessment of both habitat loss and compensation for incidental take, that is, harm to the species from otherwise legal activities (USFWS, 1984, 1999). The importance attributed to this simplified identification of habitat reflected a general lack of information about use of elderberry and other potential resource requirements of the beetle at the time of listing.

Implications of this habitat definition to conservation planning have been substantial. All landscapes that support elderberry shrubs have been treated as habitat for the beetle, without effective differentiation with respect to habitat quality. Take of elderberry shrubs is assumed to result in take of beetles, although most plants and many patches of plants do not support beetles at any given time. Accordingly, certain landowners may be subjected to regulatory actions and mitigation costs inappropriately. In addition, there can be costs to the species. The assumption of general occupancy of elderberry can lead to the identification of lesser quality sites as targets for mitigation or other conservation activities. The threats to the species listed in the beetle's recovery plan (USFWS, 1984) mostly focus on actions that could possibly cause harm to the beetle through losses of and negative impacts to individual elderberry shrubs. Mitigation requirements for landowners seeking incidental take permits are based on number of elderberry shrubs that are disturbed or destroyed, with no explicit consideration of the ability of individual host plants or presumptive habitat to sustain the valley elderberry longhorn beetle.

For regulatory purposes, there is a clear need for improved, empirically validated predictors of beetle occupancy that can be used to define and assess habitat quality. Listing under the federal Endangered Species Act may have slowed or halted the decline of the beetle by protecting substantial portions of its remaining habitat. After 25 years, however, recovery seems to have stalled, with no demonstrable increase in the distribution or abundance of the beetle. Surveys conducted throughout the range of the valley elderberry longhorn beetle in 1991 and 1997 indicated that only 25% of apparently suitable sites were inhabited (Barr, 1991; Collinge et al., 2001), strongly suggesting that factors beyond host plant abundance influence site occupancy.

In this paper, we define habitat and habitat quality for the valley elderberry longhorn beetle on the basis of multiple variables that operate and interact across different spatial and temporal resolutions. We describe four distinct types of habitat for the beetle, and explore the spatial structure and mechanisms of the association between the beetle and its host plant. In so defining habitat we believe recovery planning better can be focused for the valley elderberry longhorn beetle and its associated ecological communities throughout the American River basin and ultimately in other watersheds in California. Our data also provide a benchmark of environmental conditions and distribution of populations against

which future assessments of status and recovery can be made.

2. Methods

2.1. Study sites

The American River basin (Sacramento County, California, USA) contains critical habitat for the valley elderberry longhorn beetle (USFWS, 1980b), yet urbanization near Sacramento is leading to direct loss and reduction in quality of habitat. We conducted surveys along 24 km of the 37-km American River Parkway, a riparian corridor that borders both sides of the American River (Fig. 1). This stretch of river spans three major geomorphological zones: a 760 ha alluvial floodplain from the mouth of the river to 11 km upstream; a steep, 300 ha basin with a narrow river and riparian corridor that continues for another 10 km upstream; and a 425 ha, 3-km long upper riparian terrace. We also conducted surveys across a fourth geomorphological zone, a privately owned, 3700 ha area of non-riparian scrub located 1–4 km to the south of the American River (Fig. 1).

The alluvial plain, riparian corridor, and upper riparian terrace were surveyed between June 2002 and September 2004, whereas the non-riparian scrub was surveyed between March and July 2004. Coordinates of every elderberry shrub encountered along the 24 km stretch of alluvial plain, riparian corridor, and upper riparian terrace were recorded using global positioning systems (GPS). The extent of the non-riparian scrub rendered mapping of all shrubs prohibitive. Instead, we established six 1-km² blocks distributed across the property that collectively represented the gradient of shrub densities, soil types, and microtopographic features. Within each block, we delineated 5–7 circles with 50 m radius that collectively represented the variation in density of elderberry shrubs within the block. Outside the blocks, we delineated and surveyed an additional 25 circles. Coordinates of all elderberry shrubs within each circle were recorded with GPS.

2.2. Data collection

At each elderberry shrub, we recorded measures of shrub size, shrub condition, and associated vegetation. Elderberry can reproduce vegetatively, and shrubs often have multiple main basal stems. Measures of elderberry size included maximum basal stem diameter, maximum height (midpoint of one of six height classes: 1–2, >2–4, >4–6, >6–8, >8–10, >10 m), and the number of main stems within each of four diameter classes (2–7, >7–12, >12–20, >20 cm). Height classes were used because the study area was large and abundance of shrubs was high. Stem diameter classes were similar to those used in USFWS guidelines (USFWS, 1999), and height classes were above the height of most seedlings. We calculated perimeter to area ratios for each shrub. For shrubs with a canopy diameter $\geqslant 5$ m, area and perimeter were measured by delineating a polygon around the drip line of the shrub. We then conducted a linear regression in which we regressed number of
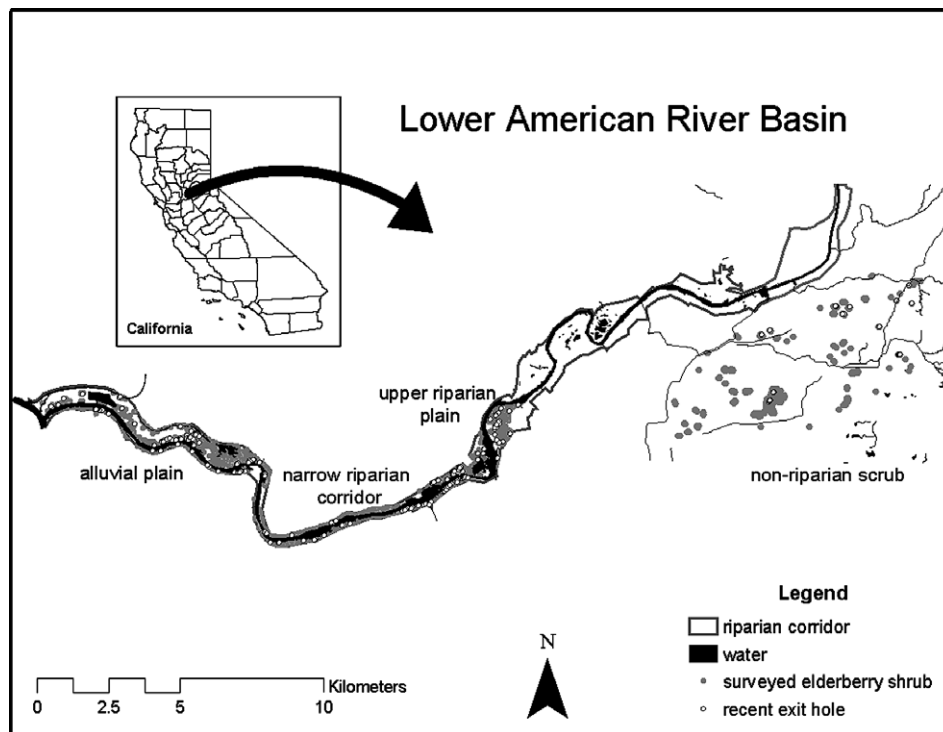

Fig. 1 – Locations of the valley elderberry longhorn beetle (*Desmocerus californicus dimorphus*) and its host plant, black elderberry (*Sambucus mexicana*), within the American River valley, Sacramento County, California, USA. Areas surveyed are speckled with gray dots (elderberry shrubs).

stems per shrub (canopy diameter $\geqslant 5$ m) against area and perimeter. That regression was used to estimate the area and perimeter of shrubs with canopy diameter <5 m based on number of stems. A subsample of the area and perimeter estimates made using this regression function was validated successfully in the field.

We estimated elderberry condition on the basis of percent dead stems (0–25, >25–50, >50–75, >75–100) and apparent presence or absence of past burns. Similarly, we recorded the identity and percent cover class (0, 1–25, >25–50, >50–75, >75–100) of plants growing over a given elderberry shrub (canopy cover), within the shrub (shrub cover), or under the dripline of the shrub (ground cover).

We searched each shrub for evidence of beetle occupancy using the methods of Barr (1991) and Collinge et al. (2001). Although adult beetles live for only a few weeks in the spring, during which they feed on elderberry leaves, the larvae develop for 1–2 years, feeding on pith at the center of stems (Linsley and Chemsak, 1972). Fifth instar larvae create exit holes in the stems, then plug the holes and remain in the stems through pupation. Adults emerge in the spring through the distinctive exit holes. Because the beetles are rare in space and time, whereas exit holes are present for at least several years, exit holes are used to estimate population size (Barr, 1991). We estimated the age of each hole as recent ($\leqslant 1$ year) or old, and recorded both height off the ground and diameter of the stem or branch containing the hole. Unlike Barr (1991) and Collinge et al. (2001) who performed analyses using counts of current year (new) and old holes, only recent holes (new and 1-year-old holes) were included in our analyses; old holes were used solely to calculate occupancy patterns over time. Recent holes had crisp margins, minimal evidence of healing, light gray wood color, and, in some cases, contained frass (wood shavings and droppings). Old holes were characterized by faded margins, clear evidence of healing, and dark gray to black wood color.

2.3. Spatial analyses

We examined relationships between beetle occurrences and environmental variables using both data from this project and existing data for the American River Parkway and California (CaSIL, 2000). The shortest distances from each elderberry shrub to (1) the nearest road or trail, (2) the upland riparian edge (for riparian areas only; usually associated with flood control levees beyond which urban development dominates), (3) the nearest source of surface water (usually a stream), (4) the nearest neighboring elderberry shrub, and (5) the nearest recent exit hole were calculated using the Nearest Features script available for ArcView 3.2 (Jenness, 2004). ArcGIS 9 was used for all other calculations and analyses. Digital elevation models (30 m resolution) were used to calculate elevation, slope and aspect for this region, which has relatively little elevational variation (range of 2–18 m for the Parkway). The weak but significant relationships between beetle occupancy and topography indicate that fine-scale topographic changes may be important to beetle occupancy and should be explored further.

Relationships between occurrence of the beetle and abundance of elderberry for distances $\leqslant 100$ m were explored by calculating the density of shrubs and density of main stems over several spatial extents. Shrub densities along the American River Parkway were estimated within discrete circles with radii of 25, 50, and 100 m. The number of main stems within 625 m^2 was calculated at each point (shrub) in order to standardize the quantity of elderberry available to the beetle at fine resolution while removing the bias associated with distinguishing individual shrubs.

2.4. Statistical analyses

We explored differences in environmental characteristics and beetle occurrence among the four habitat types with Pearson's contingency tests (ordinal data) and Kruskal–Wallis rank sum analyses (continuous data) (JMP(R), 2005). Due to the large number of comparisons, we adjusted α for all analyses within or among habitat types using the sequential Bonferroni technique. Relationships between the predictor variables were explored where necessary using simple regressions in JMP®.

The spatial population structure of the beetle along the Parkway was investigated in ArcGIS 9 using Moran's I test for spatial autocorrelation calculated across distance intervals of 0–10, >10–25, >25–50, >50–75, >75–100 m. Moran's I statistic ranges from about -1 to 1. Values ca. 1 indicate positive spatial autocorrelation (clustering), those ca. -1 indicate even distributions, and values of 0 indicate no discrete pattern.

To identify factors most strongly associated with variation in occurrence of recent beetle holes, we used hierarchical partitioning (Chevan and Sutherland, 1991; Walsh and Mac Nally, 2004) in the R computing environment (R Development Core Team, 2004). Hierarchical partitioning is designed to alleviate problems of multicollinearity among predictor variables. The increase in model fit associated with each predictor variable is estimated by averaging its additional explanatory power in all models (i.e., all possible combinations of the independent variables) in which that variable appears (Mac Nally, 2000). For each predictor variable, explanatory power is segregated into independent effects (I) – effects asserted to be associated with that variable independently of other predictor variables – and joint effects (J), which are effects that are attributable to the joint action of the variable with other predictor variables. Log-likelihood goodness-of-fit measures were used for binomial data, so explanatory power was given in terms of χ^2 [χ^2 = log-likelihood of the full model – log-likelihood of null model (e.g., Tabachnik and Fidell, 2004)]. Because log-likelihood does not provide an R^2 statistic to assess fit, values were converted to an analogous goodness of fit measure, R^2_{LL} (Darlington, 1990). The whole independent model (total independent contributions) was considered strong if $R^2_{LL} \geqslant 0.10$ and individual variables were considered to have a substantial independent effect on the response variable if $R^2_{LL} \geqslant 0.03$.

Because the hierarchical analysis software accepts a maximum of 12 predictor variables, we reduced our initial list of ~ 60 predictor variables to the 12 or fewer variables that made considerable ecological sense a priori or appeared to have the greatest explanatory power ($p \leqslant 0.05$, $R^2 \geqslant 0.03$) on beetle presence or abundance in exploratory logistic and linear

regression analyses performed within each geomorphic region (Table 1).

All values presented in the text are means ± 1 SD unless otherwise noted.

3. Results

3.1. Differences among habitat types

Shrub occupancy by the beetle was highest (11.2%) in the lower alluvial plain of the American River. This area is generally flat, with the lowest elevation and closest proximity to groundwater of the four habitat types (Fig. 2), and is relatively open, with little canopy cover and ground cover. Shrubs and overgrowth were more commonly associated with elderberry in the alluvial plain than in other habitat types, but average cover still was low (Fig. 2). Cover included shade intolerant species such as willow (*Salix* spp.), box elder (*Acer negundo*), grape (*Vitis californica*) and blackberry (*Rubus discolor, R. ursinus*). Mean area of individual elderberry shrubs was 200–800% greater, perimeter of shrubs 200–900% greater, and density of stems 120–140% greater on the lower alluvial plain than in the other geomorphic zones (Fig. 2).

Table 1 – Explanatory variables included in the hierarchical partitioning analysis

Explanatory variable	Definition
Elderberry size	
Maximum height (m)	Maximum height of each elderberry shrub visually estimated as 1–2, >2–4, >4–6, >6–8, >8–10, >10 m. Maximum height was positively correlated with maximum stem diameter (linear regression $F_{1,855} = 715$, $R^2 = 0.28$, $p < 0.0001$)
Stem size proportions	The first principal component axis (67% of total variance) collapsing the proportion of stems falling into each of 4 size classes (2.7, >7–12, >12–20, >20 cm). This axis is positively associated with the ⩾7 cm classes
Stem density (number per 625 m^{-2})	The sum of main stems occurring in a 25 × 25 m area around the centroid of each shrub
Shrub area (m^2)	The area of each shrub measured by creating a polygon around the dripline of shrubs with canopies ⩾5 m in diameter. Area for shrubs <5 m were estimated using a regression function (see text)
Shrub perimeter (m)	The perimeter of each shrub measured by creating a polygon around the dripline of shrubs with canopy ⩾5 m in diameter. Perimeter for shrubs <5 m were estimated using a regression function (see text)
Elderberry condition	
Dead stems per shrub (%)	The percent of dead stems and branches on each shrub visually estimated as 0–25%, >25–50%, >50–75%, >75–99%
Burned	A binomial measure of whether there was evidence of fire (e.g., charred wood) on the shrub
Topography	
Elevation of shrub (m)	Elevation above mean sea level, calculated from a 30 m resolution digital elevation model
Slope (°)	The slope of the ground on which each elderberry shrub grows, calculated from a 30 m resolution digital elevation model
Aspect (°)	The aspect of the ground on which each elderberry shrub grows, calculated from a 30 m resolution digital elevation model
Northing and easting (m)	The coordinates of each shrub
Habitat edge	
Riparian width (m)	The width of the riparian corridor at the point at which each elderberry shrub occurs, calculated as a sum of the minimum distances between the shrub and both the river and the upland riparian edge. No value for the non-riparian scrub
Distance to upper edge (m)	The minimum distance of each elderberry shrub to the upland riparian edge. No value was available for the non-riparian scrub
Distance to road (m)	The minimum distance from each elderberry shrub to the closest road or major trail
Distance to river (m)	The minimum distance from each elderberry shrub to the nearest open water source
Associated vegetation	
Canopy cover (%)	The percent of elderberry shrub canopy covered by overstory visually estimated as 0%, 1–25%, >25–50%, >50–75%, >75–100%
Shrub cover (%)	The percent of elderberry shrub canopy and stems intertwined with other freestanding plants visually estimated as 0%, 1–25%, >25–50%, >50–75%, >75–100%
Ground cover (%)	The percent of the ground beneath the elderberry shrub dripline that was covered by vegetation, visually estimated as 0%, 1–25%, >25–50%, >50–75%, >75–100%
Robinia cover (%)	The percent of elderberry shrub canopy both covered by and intertwined with black locust (*Robinia pseudoacacia*) visually estimated as 0%, 1–25%, >25–50%, >50–75%, >75–100%
Native perennial (%)	The percent of the ground beneath the elderberry shrub dripline that was covered with native perennial plants, visually estimated as 0%, 1–25%, >25–50%, >50–75%, >75–100%

Different variables (maximum 12) were included in analyses for different habitat types and for the system as a whole.
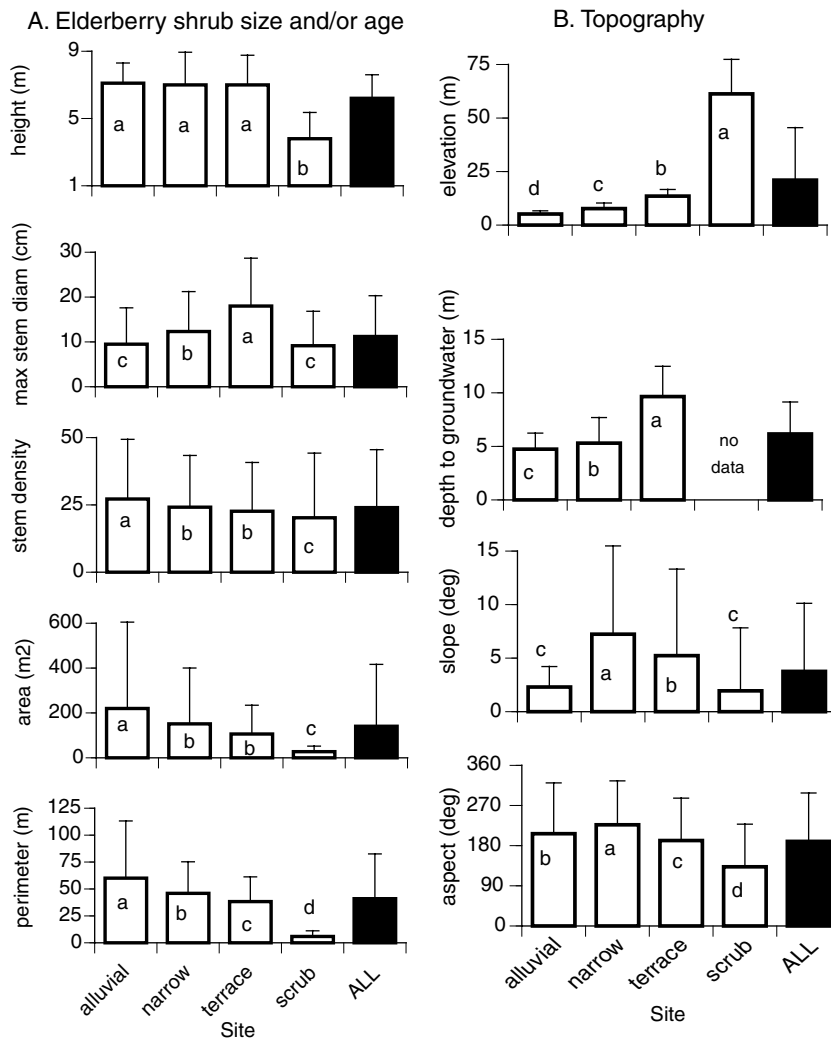
Fig. 2 – Environmental attributes of the three riparian and one non-riparian habitat types. Data are means ± 1 SD. Different letters indicate significance at $p \leqslant 0.002$ based on a sequential Bonferroni adjusted α of 0.05.

Shrub-level occupancy by the beetle in the mid-elevation riparian corridor was 10.5%. The corridor was 400–600% narrower than in the alluvial plain or upper riparian terrace. Consequently, elderberry shrubs generally were located 400–600% closer to the river and to the upland riparian edge, and twice as close to the nearest road, than in the alluvial plain or upper riparian terrace (Fig. 2). This riparian corridor contained the greatest structural complexity of the four habitat types, with elderberry found on the steepest slopes, beneath the densest canopy cover, and among the highest ground cover (Fig. 2). Plants commonly associated with elderberry included cottonwood (*Populus fremontii*), valley oak (*Quercus lobata*), exotic annual grasses and forbs, grape, blackberry, and wild rose (*Rosa californica*).

Occupancy of shrubs in the upper riparian terrace was 8.7%. Elevation and depth to groundwater were greater in this area than in the alluvial plain or riparian corridor (Fig. 2). The riparian area was widest in this geomorphic zone, with elderberry occurring farther from both the river and the upland riparian edge than in the alluvial plain or riparian corridor. The degree of topographic heterogeneity (variation in slope

and aspect) in the upper riparian terrace was intermediate between the riparian corridor and the alluvial plain. Shrub and canopy cover in the upper terrace also was intermediate. Dominant canopy species included valley oak, upland species such as walnut (*Juglans hindsii*), live oak (*Q. wislizenii*), and buckeye (*Aesculus californica*), as well as two non-natives, tree of heaven (*Ailanthus altissima*) and fig (*Ficus carica*). Cover of native perennial herbaceous species was greater than in the alluvial plain or riparian corridor, whereas overgrowth of vines was lower. Cover of shade tolerant vines, such as Dutchman's pipevine (*Aristolochia tomentosa*) and wild cucumber (*Marah fabaceus*), however, was higher in the upper riparian than in the other three habitat types (Pearson's contingency test, $\chi^2 \geqslant 32$, $p \leqslant 0.001$, $n = 4387$). Compared with the other three geomorphic zones, elderberry shrubs on the upper terrace were the second most stressed (as measured by dead stems) and appeared to be the oldest, with the greatest proportion of large main stems (Fig. 2).

Occupancy rates were lowest (2.9%) in the non-riparian scrub. This area had an open canopy (Fig. 2) with a mix of non-native annual grasses and herbaceous ground cover, as
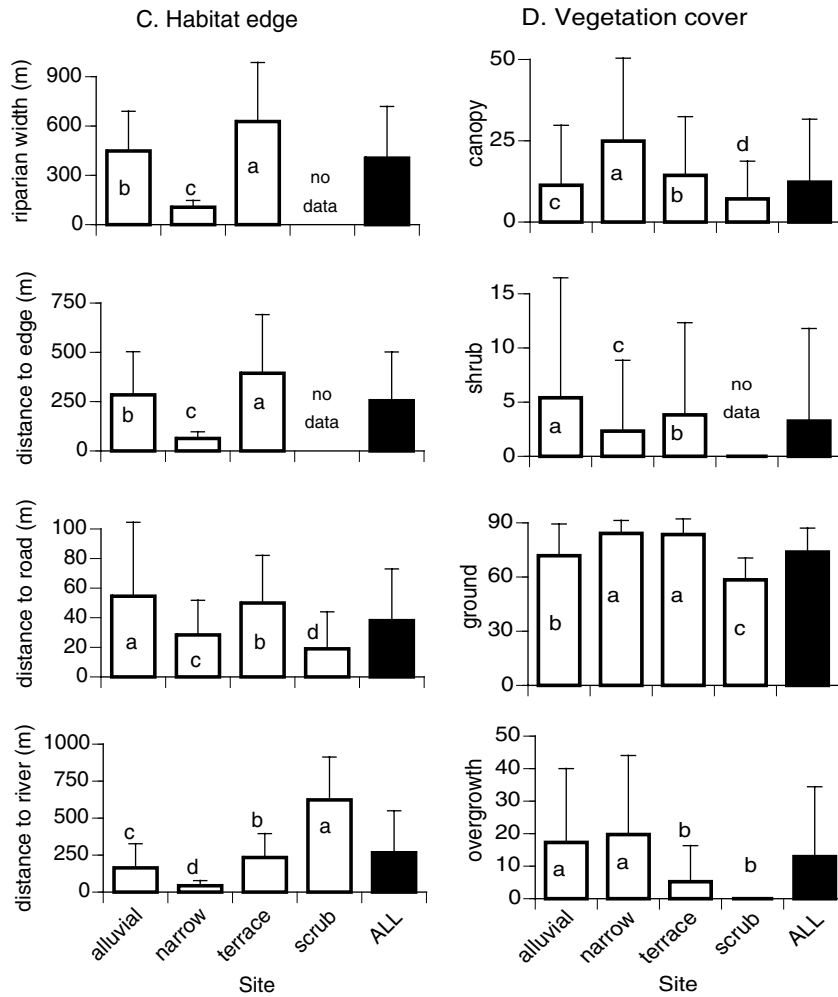
C. Habitat edge   D. Vegetation cover

Fig. 2 – continued

well as coyote brush (*Baccharis pilularis*) and poison oak (*Toxicodendron diversilobum*). Elderberry grew on gentle slopes with a more easterly exposure than along the American River (Fig. 3). Elevation of the non-riparian scrub was 5–12 times higher than the other habitats and elderberry shrubs grew 3–15 times farther from surface water than shrubs along the
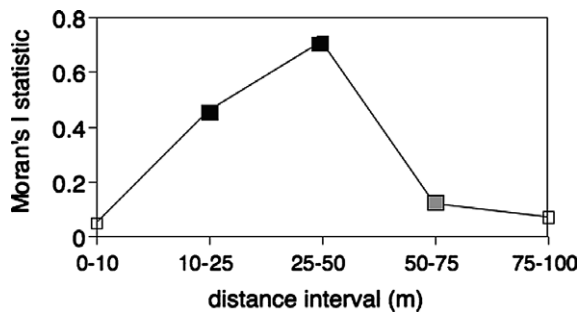

Fig. 3 – Correlogram of the abundance of recent valley elderberry longhorn beetle exit holes along the American River Parkway. Solid symbols = significant at $p \leqslant 0.01$, gray = $p = 0.10$, no fill = $p > 0.10$.

American River (Fig. 2). Elderberry shrubs in this area appeared to be the most stressed, with 32 ± 9% (mean ± SE) dead stems per shrub (Pearson's contingency test, $\chi^2 = 4127$, $p < 0.0001$, $n = 4478$). Whether due to stress, age, or both, shrub area and perimeter were 10–15% of values along the American River Parkway. Shrubs also were small in terms of height, average maximum stem diameter, and density of stems (Fig. 2).

Although occupancy varied among habitat types, the average number of beetle holes per occupied shrub did not (Table 2). The density of holes (number of holes per 100 m^2 of elderberry shrub canopy), however, was more than twice as high in the non-riparian scrub than in other habitat types.

3.2. Environmental influences on beetle presence and abundance

When both independent and joint contributions were considered (whole model), the environmental variables found to be important within each habitat type collectively explained an additional 33% of the variance in beetle presence in the alluvial plain, 25% of the variance in the narrow riparian corridor, 158% in the upper riparian terrace, 12% in the non-riparian

Table 2 – Density of valley elderberry longhorn beetle exit holes within each of the four habitat types

Habitat type	Holes per shrub mean ± SD	Holes per 100 m² shrub area mean ± SD
Lower alluvial plain	2.7 ± 3.2	2.5 ± 3.4[b]
Narrow riparian corridor	2.2 ± 2.2	2.0 ± 2.3[b]
Upper riparian terrace	2.9 ± 3.5	2.5 ± 2.9[b]
Non-riparian scrub	1.6 ± 1.1	5.3 ± 5.8[a]
p	0.17	0.03
$\chi^2_{df=3}$	5.1	8.9

Values are Kruskal–Wallis rank sums. Different letters indicate significance at $p \leqslant 0.05$.

scrub, and 27% across the entire system (Table 3). Although the theoretical maximum is 100% additional variance explained, values exceeding 100% are possible and indicate high amounts of colinearity among predictor variables. When only the independent contributions were considered, contributions of the environmental variables to explaining beetle occupancy ranged from 7% to 30%. This suggests colinearity and potential interactions among some of the variables. No individual variable (e.g., maximum plant height) independently contributed >5%. The four categories of variables (e.g., all metrics of elderberry size or all metrics of topography, see Table 4) accounted for an additional 0–12% of variance in occupancy. Although weak, these associations were statistically significant ($p \leqslant 0.0001$; Table 4).

Variables reflecting the availability of elderberry over small spatial scales (tens of meters) collectively accounted for 6–7% of the variance in beetle occupancy in three of the four habitat types (Table 3). No individual shrub variable accounted for more than 3% of the variance, but those that collectively contributed to the explained variance in occupancy included shrub area, perimeter, height, and stem diameter (Tables 3, 4). Shrub condition, expressed as percent of dead stems per shrub and evidence of past fire (>5 year), contributed ⩽2% to explained variance in occupancy.

Variables reflecting topographic characteristics within each habitat type collectively explained an additional 12% of the variance in beetle occupancy in the upper riparian terrace and 1–4% in the other habitat types (Table 3). Elevation, slope, and aspect each contributed ⩽3% to explained variance in each habitat type. Latitude was important to beetle occupancy (an additional 5% of variance) in the upper riparian terrace, where occupancy increased toward the south of the site (Table 4).

Measures of distance from shrubs to continuous openings or transitions in land cover (e.g, roads and trails, boundary between habitat and urban development, river edge) collectively accounted for an additional 8–12% of explained variance in beetle occupancy in the alluvial plain and upper terrace and 1% in the narrow corridor and non-riparian scrub (Table 3). Variance in occupancy was influenced by proximity to roads or trails, the river, and the upland riparian edge, as well as the width of the riparian corridor. Riparian width had the greatest influence on occupancy (5% of additional variance) in the wide, upper riparian terrace (Table 4).

There were no substantial effects (>3% of variance explained) of plant cover on beetle occupancy (Tables 3, 4).

None of the measured environmental variables explained sufficient variance in beetle abundance to meet our criteria for inclusion in hierarchical partitioning analysis.

3.3. Fine-resolution beetle distributions

The abundance of exit holes in the alluvial plain, riparian corridor, and upper riparian terrace was spatially autocorrelated over distances of 10–50 m (Fig. 3). This pattern corresponded with the average nearest neighbor distances of 43 ± 44 m between recent exit holes. In the non-riparian scrub, nearest neighbor distances between recent exit holes averaged 25 ± 16 m. These data suggest that the dispersal distances of adult beetles from the sites at which they emerge typically are ⩽50 m.

Within all four habitat types, the presence of recent exit holes in a given shrub was correlated with previous occupancy (Pearson's contingency, $U = 0.28$, $p < 0.0001$, $\chi^2 = 1010$, $n = 4424$); 73% of shrubs with recent holes also had old holes.

Table 3 – Results of hierarchical partition showing collective and individual contributions of environmental variables that explained an additional ⩾5% of variance of presence of the valley elderberry longhorn beetle

	Alluvial plain	Narrow riparian corridor	Upper riparian terrace	Non-riparian scrub	All habitat types
R^2_{LL} whole model	0.33	0.25	1.5	0.12	0.27
R^2_{LL} independent model	0.21	0.09	0.30	0.11	0.07
Environmental variable class	Independent contribution of individual variables (R^2_{LL})				
Elderberry size	0.06	–	0.07	0.06	–
Elderberry condition	–	–	–	–	–
Topography	–	–	0.13	–	–
Habitat edge	0.08	–	0.13	–	–
Associated vegetation	–	–	–	–	–
Number of shrubs	1622	888	874	846	4230

Table 4 – Environmental variables associated with the presence of the valley elderberry longhorn beetle in one or more habitat types in the lower American River basin

	Alluvial plain		Narrow riparian corridor		Upper riparian terrace		Non-riparian scrub	
	Occupied Average ± SD	Unoccupied Average ± SD	Occupied Average ± SD	Unoccupied Average ± SD	Occupied Average ± SD	Unoccupied Average ± SD	Occupied Average ± SD	Unoccupied Average ± SD
Elderberry								
Maximum height (m)	8.0 ± 1.0	7.0 ± 1.3	7.4 ± 0.9	7.0 ± 1.0	7.5 ± 0.7	7.0 ± 0.9	4.5 ± 0.5	3.8 ± 0.8
Proportion $\geqslant$ 12 cm stems	17 ± 24	13 ± 24	28 ± 27	15 ± 23	21 ± 21	17 ± 29	19 ± 34	12 ± 27
Stem density (no. 625 m^{-2})	35.9 ± 29.5	26.1 ± 20.8	34.6 ± 26.8	22.9 ± 17.7	40.4 ± 32.4	21.0 ± 15.1	20.0 ± 14.9	23.3 ± 27.9
Shrub area (m^2)	225 ± 305	219 ± 395	203 ± 227	145 ± 251	194 ± 248	98 ± 106	96 ± 104	36 ± 46
Shrub perimeter (m)	63 ± 38	60 ± 55	56 ± 38	45 ± 28	51 ± 34	37 ± 21	21 ± 22	8 ± 10
Dead stems per shrub (%)	25 ± 9	22 ± 10	16 ± 5	18 ± 7	22 ± 7	27 ± 10	28 ± 5	33 ± 9
Topography								
Elevation (m MSL)	5.2 ± 1.7	5.2 ± 1.4	8.9 ± 3.0	7.6 ± 2.5	10.8 ± 2.5	13.8 ± 3.0	68.6 ± 16.1	61.1 ± 16.1
Slope (°)	3.0 ± 2.1	2.2 ± 1.9	10.5 ± 10.2	6.9 ± 7.9	12.8 ± 9.9	4.5 ± 7.5	1.3 ± 0.5	2.0 ± 5.9
Aspect (°)	236 ± 114	203 ± 113	210 ± 101	229 ± 98	141 ± 53	196 ± 97	172 ± 78	132 ± 96
Easting (10^4 m)	204.8 ± 0.21	204.8 ± 0.21	205.4 ± 0.22	205.3 ± 0.20	205.7 ± 0.05	205.8 ± 0.07	427.6 ± 0.15	427.5 ± 0.13
Northing (10^4 m)	60.3 ± 0.08	60.3 ± 0.07	60.0 ± 0.07	60.0 ± 0.06	60.2 ± 0.05	60.3 ± 0.09	65.7 ± 0.19	65.6 ± 0.18
Habitat edge								
Riparian width (m)	287 ± 231	468 ± 235	99 ± 39	107 ± 41	255 ± 193	663 ± 351	No data	No data
Distance to upper edge (m)	209 ± 215	294 ± 217	47 ± 23	65 ± 35	142 ± 148	418 ± 297	No data	No data
Distance to road (m)	52 ± 48	55 ± 50	34 ± 24	28 ± 23	36 ± 28	51 ± 32	9 ± 18	18 ± 24
Distance to river (m)	78 ± 94	174 ± 167	51 ± 36	42 ± 35	112 ± 88	245 ± 162	588 ± 333	624 ± 289
Associated vegetation								
Robinia cover (%)	13 ± 37	3 ± 17	1 ± 8	5 ± 21	15 ± 34	3 ± 17	0 ± 0	0 ± 0
Native perennial (%)	6 ± 19	2 ± 9	3 ± 14	3 ± 13	12 ± 23	5 ± 16	14 ± 15	9 ± 11
n (number of shrubs)	182	1440	93	795	76	798	25	774

Data are means ± 1 SD.

Similarly, the abundance of recent beetle holes was correlated with abundance of old holes ($F_{1,374} = 102$, $R^2 = 0.21$, $p < 0.0001$).

Throughout the study system, beetle holes occurred most frequently (47%) in stems or branches with diameter 2–7 cm or branches and at 0–1 m above ground (79% of occurrences). This result may reflect the size distribution of main stems of shrubs, 60% of which had a basal diameter of 2–7 cm. Holes also were commonly found in stems or branches with diameter 7–12 cm (36% of occurrences) and at heights 1–2 m above the ground (19%). Distribution patterns of holes were similar within each habitat type. Stems and branches >12 cm in diameter hosted proportionally fewer holes. Relatively old, large shrubs (maximum main stem diameter ⩾12 cm), however, were more likely than small shrubs to be occupied and to have multiple holes.

4.   Discussion

A way to improve recovery plans for listed species is to develop definitions of habitat that identify reliable environmental determinants of landscape occupancy and local persistence and abundance. This approach will allow planners to better differentiate high-quality and low-quality habitat for the valley elderberry longhorn beetle, and to assess whether unoccupied sites may be suitable for the beetle. Moreover, this approach should allow conservation planners to prioritize land acquisitions and identify management actions using objective criteria.

We identified several predictors of habitat occupancy by the valley elderberry longhorn beetle in the American River Basin. To some extent these vary among habitat types and, we suspect, as a function of spatial scale (Wu et al., 2000; Talley, 2005; Talley, in press). In general, the most influential predictors are density of elderberry shrubs and shrub size, number of stems, and range of branch sizes. Like Barr (1991) and Collinge et al. (2001), we found that within individual shrubs, smaller stems and branches are more likely to have exit holes than larger stems. This may be due to lower availability of large branches or to the drying and loss of pith, a common phenomenon in older stems (Haack and Slansky, 1987). Contrary to studies revealing that environmental conditions at or near habitat edges may have negative effects on insect occupancy (Collinge and Palmer, 2002), the beetle in our riparian sites was slightly more likely to be present near edges between land cover types. This association may be due in part to increased sunlight, moisture near open water, or nutrients from upland or road runoff (Johnson et al., 1975; Holzapfel and Schmidt, 1990). Access to groundwater and flat topography (slope, aspect) appeared to limit beetle occupancy in our higher elevation habitats.

Based on occupancy rates, the quality of riparian habitat for the valley elderberry longhorn beetle appears to be greater than the quality of non-riparian habitat. Within riparian cover types, habitat quality appeared to be greatest in the upper riparian terrace and, especially, in the lower alluvial plain. Upper riparian or scrub systems might serve as local refugia for the beetle when near-river habitats are disrupted by land use or non-native species. Several species of invasive plants, such as black locust (*Robinia pseudoacacia*), giant reed (*Arundo donax*), and salt cedar (*Tamarix* spp.), have displaced native vegetation along river corridors in California (Bossard et al., 2000). The Argentine ant (*Linepithima humile*) has displaced a number of native riparian invertebrates (Holway, 1998), possibly including the valley elderberry longhorn beetle (Huxel, 2000).

The low shrub occupancy rates, reduced local abundances, and weak associations between environmental variables and beetle presence suggest that shrub occupancy by the beetle may be highly stochastic. Accordingly, the presence of unoccupied elderberry shrubs does not necessarily indicate that a particular cluster of shrubs constitutes poor-quality habitat or is otherwise uninhabitable. Patches of elderberry shrubs that are unoccupied at a given point in time or have low rates of occupancy over time may in fact be important for the long-term local persistence of the beetle (Hanski, 1994). Maintenance of apparently suitable but unoccupied habitat may be especially important in urban areas that are subject to high levels of human land use and associated disturbances, which can combine with natural stochasticity in patch occupancy to increase the frequency of extirpation events.

Against this background it is important that recovery plans and conservation efforts be improved by using scientific information to implement tractable recovery criteria and monitoring plans (Tear et al., 1993, 1995; Schultz and Gerber, 2002). Our work demonstrates that the valley elderberry longhorn beetle has multiple habitat types, that rates of occupancy vary among habitat types, and that measurable environmental variables can help explain those patterns. Turnover in occupancy, and the associated importance of currently unoccupied habitat, means that effective conservation planning for the species must consider not only the current but also the future distribution of the beetle and its habitat (e.g., Fahrig and Paloheimo, 1988; Huxel and Hastings, 1999).

Because the valley elderberry longhorn beetle is extraordinarily cryptic, thus nearly impossible to inventory or census directly in the field, regulatory agencies currently use number of elderberry shrubs as the surrogate measure to assess habitat loss that may accompany development and establish mitigation or compensation for that loss (e.g., USFWS, 1984, 1999). Elderberry shrubs that would be destroyed during land development usually must be translocated to areas slated for conservation, including to previously identified mitigation banks, in which patches of putative habitat are purchased and managed in perpetuity with fees paid by developers (USFWS, 1999). Target recipient sites and mitigation banks, however, to date have not been selected using habitat quality criteria, such as those that have emerged from this study. Despite often dramatic differences between sites in plant densities, age structure, and other fundamental patch characteristics, including occupancy by the beetle (Holyoak et al., submitted for publication), the habitat quality of all patches of shrubs is treated as equal. This may be a primary reason that despite substantial mitigation efforts, the number of beetle populations apparently declined by 4% during the 1990s (Holyoak et al., submitted for publication).

Instead of treating groups of elderberry shrubs as de facto habitat patches, boundaries of habitat patches can be

delineated on the basis of apparently suitable values of environmental attributes such as distance to water and upland edge. Within these patches, mature shrubs in gently sloping areas appear to provide the highest quality habitat in our study system. In such areas, shrub densities, size distributions, and other criteria can facilitate more effective assessment of the potential impacts of take on the beetle and its habitat, identification of alternative actions that might reduce impacts to the species, identification of mitigation and translocation sites that maximize the likelihood of local and regional survival and recovery, and generation of site-specific management actions that increase local rates of occupancy.

A more comprehensive approach to defining habitat coupled with the biological information about the valley elderberry longhorn beetle that has been acquired since its listing can be used to improve its recovery plan, inform future management, and identify those patches of habitat that, if conserved, will contribute to regional persistence of the species (Arnold, 1984; Barr, 1991; Holstein, 1992; Huxel, 2000; Collinge et al., 2001; Talley, 2005). Although adaptive management strategies are often missing from recovery plans (Foin et al., 1998; Crouse et al., 2002), they may be especially valuable in areas like the American River basin where land use requirements are diverse, dynamic, and potentially can be made compatible with conservation goals. Immediate needs to stem and mitigate losses of habitats used by species most at risk need not preclude thoughtful quantification of habitat quality. An ability to describe gradients in habitat quality will enhance our capacity to predict occupancy and dynamics of imperiled species, which in turn facilitates more effective conservation action in multiple-use landscapes.

REFERENCES

Arnold, R., 1984. The Endangered Valley Elderberry Longhorn Beetle in the north Sacramento area. Report to North Sacramento Land Company, 400 Slobe Avenue, Sacramento, CA 95815, 10pp.

Aronson, J., Dhillion, S., Lefloch, E., 1995. On the need to select an ecosystem of reference, however, imperfect – a reply to Pickett and Parker. Restoration Ecology 3, 1–3.

Barr, C.B., 1991. The distribution, habitat and status of the Valley Elderberry Longhorn Beetle, *Desmocerus californicus dimorphus*. U.S. Fish and Wildlife Service, Sacramento, 133.

Bossard, C.C., Randall, J.M., Hoshovsky, M.C., 2000. Invasive Plants of California's Wildlands. University of California Press, Berkeley, CA.

Campbell, S.P., Clark, J.A., Crampton, L.H., Guerry, A.D., Hatch, L.T., Hosseini, P.R., Lawler, J.J., O'Connor, R.J., 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecological Applications 12, 674–681.

CaSIL, 2000. The California Spatial Information Library, State of California, Sacramento, CA. Available from: <http://gis.ca.gov/>.

Chevan, A., Sutherland, M., 1991. Hierarchical partitioning. American Statistician 45, 90–96.

Collinge, S.K., Palmer, T.M., 2002. The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. Landscape Ecology 17, 647–656.

Collinge, S.K., Holyoak, M., Barr, C.B., Marty, J.T., 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. Biological Conservation 100, 103–113.

Crouse, D.T., Mehrhoff, L.A., Parkin, M.J., Elam, D.R., Chen, L.Y., 2002. Endangered species recovery and the SCB study: a US Fish and Wildlife Service perspective. Ecological Applications 12, 719–723.

Darlington, R.B., 1990. Regression and Linear Models. McGraw-Hill, New York.

Fahrig, L., Paloheimo, J., 1988. Effect of spatial arrangement of habitat patches on local population size. Ecology 69, 468–475.

Foin, T.C., Riley, S.P.D., Pawley, A.L., Ayres, D.R., Carlsen, T.M., Hodum, P.J., Switzer, P.V., 1998. Improving recovery planning for threatened and endangered species: comparative analysis of recovery plans can contribute to more effective recovery planning. Bioscience 48, 177–184.

Gerber, L.R., Hatch, L.T., 2002. Are we recovering? An evaluation of recovery criteria under the US Endangered Species Act. Ecological Applications 12, 668–673.

Haack, R.A., Slansky, F., 1987. Nutritional ecology of wood-feeding coleoptera, lepidoptera and hymenoptera. In: Slansky, F., Rodriguez, J.G. (Eds.), Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. Wiley, New York, pp. 449–486 (Chapter 15).

Hanski, I., 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63, 151–162.

Holstein, G., 1992. Ecological factors in valley elderberry beetle habitat creation. A report for Zentner & Zentner Land Planning and Restoration, 95 Linden Street, Suite 6, Oakland, CA 94607. Available from: <www.zentner.com>, Sacramento, CA, 7pp.

Holway, D.A., 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia (Berlin) 116, 252–258.

Holyoak, M., Talley, T.S., Wood, S.E., submitted for publication. How effective are current mitigation practices for imperiled species? A case study of the threatened Valley elderberry longhorn beetle. Biological Conservation.

Holzapfel, C., Schmidt, W., 1990. Roadside vegetation along transects in the Judean desert. Israel Journal of Botany 39, 263–270.

Huxel, G.R., 2000. The effect of the Argentine ant on the threatened valley elderberry longhorn beetle. Biological Invasions 2, 81–85.

Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7, 309–315.

Jenness, J., 2004. Nearest Features, with Distances and Bearings, Jenness Enterprises, Flagstaff, AZ. Available from: <http://jennessent.com/arcview/nearest_features.htm>.

JMP(R), 2005. JMP(R) Statistical Discovery Software, SAS Institute Inc., Cary, NC. Available from: <http://www.jmp.com/>.

Johnson, H.B., Vasek, F.C., Yonkers, T., 1975. Productivity, diversity and stability relationships in Mojave desert roadside vegetation. Bulletin of the Torrey Botanical Club 102, 106–115.

Katibah, E.E., Dummer, K.J., Nedeff, N.E., 1984. Current condition of riparian resources in the Central Valley of California. In: Warner, R.E., Hendrix, K.M. (Eds.), California Riparian Systems: Ecology, Conservation, and Productive Management. University of California Press, Berkeley, CA, pp. 314–321.

Linsley, E.G., Chemsak, J.A., 1972. The Cerambycidae of North America. University of California Press, Berkeley, CA.

Mac Nally, R., 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between and reconciliation of 'predictive' and 'explanatory' models. Biodiversity and Conservation 9, 655–671.

R Development Core Team, 2004. R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org>.

Schultz, C.B., Gerber, L.R., 2002. Are recovery plans improving with practice? Ecological Applications 12, 641–647.

Scott, J.M., Tear, T.H., Mills, L.S., 1995. Socioeconomics and the recovery of endangered species – biological assessment in a political world. Conservation Biology 9, 214–216.

Tabachnik, B.G., Fidell, L.S., 2004. Logistic regression. In: Using Multivariate Statistics, fourth ed. Allyn & Bacon, Portland, OR, pp. 517–581 (Chapter 12).

Talley, T.S., 2005. Spatial ecology and conservation of the Valley elderberry longhorn beetle, Ph.D. Dissertation, University of California, Davis, CA.

Talley, T.S., in press. Which spatial heterogeneity framework? Consequences for conclusions about patchy population structure. Ecology.

Tear, T.H., Scott, J.M., Hayward, P.H., Griffith, B., 1993. Status and prospects for success of the Endangered Species Act – a look at recovery plans. Science 262, 976–977.

Tear, T.H., Scott, J.M., Hayward, P.H., Griffith, B., 1995. Recovery plans and the endangered species act: are criticisms supported by data? Conservation Biology 9, 182–195.

USFWS, 1976. Determination that six species of butterflies are endangered species. Federal Register 41, 22041–22944.

USFWS, 1980a. Listing the Delta green ground beetle as a threatened species with critical habitat. Federal Register 45, 52807–52810.

USFWS, 1980b. Listing the Valley elderberry longhorn beetle as a threatened species with critical habitat. Friday, August 8, 1980. Sacramento, CA. Federal Register 45, 52803–52807.

USFWS, 1984. Recovery Plan for the Valley Elderberry Longhorn Beetle. U.S. Fish and Wildlife Service, Portland, OR.

USFWS, 1997. Determination of endangered status for three plants and threatened status for five plants from vernal pools in the Central Valley of California. Federal Register 62, 14338–14352.

USFWS, 1998. Recovery plan for the Upland Species of the San Joaquin Valley, California. U.S. Fish and Wildlife Service, Portland, OR.

USFWS, 1999. Conservation Guidelines for the Valley Elderberry Longhorn Beetle. U.S. Fish and Wildlife Service, Sacramento, CA.

USFWS, 2000. Final rule to list the riparian brush rabbit and the riparian, or San Joaquin Valley, woodrat as Endangered. Wednesday, February 23, 2000. Sacramento, CA. Federal Register 65 (36), 8881–8890.

USFWS, 2001. 12-Month finding for a petition to list the yellow-billed cuckoo (Coccyzus americanus) in the western continental United States. Federal Register 66, 38611–38626.

USFWS, 2004. Review of species that are candidates or proposed for listing as Endangered or Threatened; annual notice of findings on resubmitted petitions; annual description of progress on listing actions. Tuesday, May 4, 2004. Sacramento, CA. Federal Register 69 (86), 24876–24904.

Walsh, C., Mac Nally, R., 2004. hier.part R package: Hierarchical Partitioning. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available from: <http://www.R-project.org>.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. Bioscience 48, 607–615.

Wu, J., Jelinski, D.E., Luck, M., Tueller, P.T., 2000. Multiscale analysis of landscape heterogeneity: scale variance and pattern metrics. Geographic Information Sciences 6, 6–19.