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CONSERVATION OF THE ENDANGERED OHLONE TIGER BEETLE (*CICINDELA OHLONE*)

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by

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Tara M. Cornelisse

ABSTRACT

The goal of my dissertation was to incorporate habitat quality into metapopulation theory for the conservation of the endangered Ohlone tiger beetle (*Cicindela ohlone*). *Cicindela ohlone* is endemic to the few remaining coastal terrace prairies in Santa Cruz County where it forages and lays eggs in bare ground. The prairies were once dominated by bunch grasses, fire, and large grazers that maintained bare ground but now consist of invasive annual grasses with cattle grazing and recreation creating the little remaining bare ground. My dissertation work approached species conservation from multiple scales and each chapter represents those different approaches: habitat quality of metapopulation patches to predict patch conservation value, habitat restoration and adaptive management, population viability analyses, and investigation on how knowledge affects behavior of recreationists in species habitat and the impact of recreation on beetle behavior.

I, along with my collaborators, found that the majority of the remaining Ohlone tiger beetle populations are sustainable and can persist in Santa Cruz County, but only with habitat management. Specifically, creation of bare ground habitat by scraping the ground free of vegetation augments *C. ohlone* oviposition habitat. Also, requiring cyclists to slow down to speeds of five mph in *C. ohlone* habitat greatly

reduces the negative impact of recreationists on adult behavior. I have shown that these management strategies will increase the growth rates of all *C. ohlone* populations.

Ensuring that the Ohlone tiger beetle will persist will require not only management of occupied habitats, but also unoccupied sites, particularly to maintain metapopulation dynamics and in the face of the unknown effects of global warming. Habitat management that increases bare ground and forb cover and reduces grass cover, such as controlled grazing, vegetation removal, mowing, or burning are the best options for maintaining *C. ohlone* persistence. Finally, education and outreach to hikers and bikers in and around Santa Cruz will result in greater understanding and appreciation for *C. ohlone* conservation and, in turn, result in increased compliance with slowing down in *C. ohlone* habitats. The Ohlone tiger beetle and its unique coastal prairie habitat can persist into the future, but only with our help.

ACKNOWLEDGEMENTS

I would first like to thank my three wonderful committee members, Drs. Deborah Letourneau, Karen Holl, and Tim Duane. As my primary advisor, Deborah improved my work and ecological thinking tremendously. She not only took me through the journey from student to scholar, she also instilled in me the confidence to follow through with and defend my scientific ideas and opinions. While Deborah gave me the confidence to uphold my ideals, Karen gave me the tools and expertise to back them up and state them more effectively. Karen guided me through the ups and downs of the PhD process, always bringing me back to the appropriate path for me, providing me with peace of mind. Both Deborah and Karen endlessly supported me throughout my time at UCSC and have shaped me as the scientist I am today. I feel so lucky that Tim Duane joined the faculty right as I entered the program. Working with Tim was like a breath of fresh air, always uncomplicated, efficient, and enjoyable. Tim really listened and helped me shape a plan of study that was outside of my expertise, while giving me the confidence to own it as it became part of my repertoire. All three are lasting friends and colleagues.

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Introduction

This dissertation was conducted to better understand and conserve the populations and habitats of the endangered Ohlone tiger beetle (*Cicindela ohlone*) in Santa Cruz County. The Ohlone tiger beetle is endemic to Santa Cruz and occurs in only five remnant patches of coastal terrace prairie. Like many tiger beetles, *C. ohlone* require open, bare ground habitat to find mates, prey, and to lay eggs, as larvae also require bare ground for hunting. The main drivers of *C. ohlone* extirpation are habitat destruction and invasive grasses and, in some remaining populations, recreation in the form of hiking and biking. To understand how best to conserve *C. ohlone* and manage its habitat, I sought to determine: effective management techniques that mitigated threats of invasive grasses and recreation, the status of all the populations and how management affected that status, and the future habitat conservation requirements of this unstable metapopulation. The four chapters of my dissertation are the results of those efforts.

Chapter one describes and reports results on the study of *C. ohlone* habitat quality and characteristics that define sites in which *C. ohlone* are currently present, those from which they are extirpated and prairie sites not known to host *C. ohlone*. This chapter will soon be submitted for publication. I found that vegetation, litter and bare ground cover as well as soil compaction clearly defined extirpated from occupied sites and that extirpated sites were not isolated from occupied sites. In this chapter, I argue the importance of managing and conserving extirpated and unoccupied sites for the persistence of species, particularly those in fragmented populations. The management of unoccupied sites for suitable habitat will become more important as fragmentation and global warming continue to displace species around the world.

Chapter two describes and reports the results of our efforts to create *C. ohlone* bare ground habitat by scarping the ground free of vegetation. This work was conducted in collaboration with Mike Vasey, Karen Holl, and Deborah Letourneau and published in the Journal of Insect Conservation (Cornelisse et al. 2013). We found that *Cicindela ohlone* oviposited significantly more in artificial bare ground plots compared to controls both one and two years after the scrapes were created. For *C. ohlone* habitat creation, we recommended creation of scraped plots every two years, particularly in prairie areas not currently used for oviposition, in order to maintain bare ground and to ensure maximum usage by female *C. ohlone* as oviposition sites. The University of California Santa Cruz (UCSC) and the City of Santa Cruz have initiated scraping and trail creation in their respectively managed *C. ohlone* sites.

Chapter three describes and reports the results of interdisciplinary research on the social and ecological relationship between recreation and *C. ohlone* protection. This work was conducted in collaboration with Tim Duane and has been accepted for publication in Conservation Biology. Before this study, it was clear that recreation maintained open trails in *C. ohlone* habitat, benefiting the beetle; however, it was unknown how recreationists perceived *C. ohlone* conservation as well as the impact recreation had on beetle behavior. We found that fast cycling caused the beetles to fly off the trail more often and at further distances, taking them away from their prime habitat and potentially causing them to unnecessarily expend important energy. Upon providing knowledge about the beetle and surveying recreationists, we found that knowledge led to an increase in stated compliance with management strategies, such as slowing down in beetle habitat. Thus, we recommended that recreationists be provided information about the positive impact trail maintenance has on *C. ohlone*, but that negative impacts on the beetle's behavior can be greatly reduced by slowing down to five mph. To disseminate this work, it was covered in a popular article and blog posts that I posted on the Mountain Bikers of Santa Cruz's listserv and Facebook page. Also, signs instructing bikers to slow down have been posted in *C. ohlone* habitat on the UCSC campus.

Chapter four describes and reports the results of a population viability analysis that I conducted on the five *C. ohlone* populations, including analyses of density dependence, effects of management, and the effects of migration between patches on viability. This work was conducted with the help of Deborah Letourneau and Michelle Bennett conducted the study on larval density-dependent survival for her undergraduate thesis. This work is currently under review for publication. We found that four out of the five *C. ohlone* populations had a positive population growth rate (>1.0). The population at Wilder Ranch State Park is declining and the population at

Lower Marshall in upper UCSC campus had a growth rate just slightly over 1.0; together the two have a 50% chance of extinction in the next 10 years. Fortunately, we found that creating bare ground can increase *C. ohlone* growth rate up to 40% and managing cycling up to 25%; however, Wilder Ranch's growth rate remained below 1.0 in all tested scenarios. We recommended that both the prairie in and surrounding Wilder Ranch be managed to enhance *C. ohlone* habitat as well as connectivity to nearby populations.

It is my hope and goal to not only have this research applied for Ohlone tiger beetle protection and recovery, but also to use the ideas and techniques I have learned and developed as a PhD student in my career as a conservation scientist.

Chapter 1

Conserving extirpated sites: using habitat quality to manage unoccupied sites for metapopulation persistence

Introduction

Effective management of fragmented populations entails inclusion of both habitat and metapopulation factors, as they provide different but complementary conservation insights and recommendations (e.g., Soule 1987, Samways 1994, Thomas and Hanski 1997, Tscharntke et al. 2002, Armstrong 2005, New 2007, Holyoak et al. 2010, Vogeli et al. 2010). One of the fundamental predictions of metapopulation theory is that species do not occupy all patches at all times due to stochastic extinction (Hanski 1999). Management of endangered species, however, is often based on incidence data; thus, if a population is extirpated from a former patch, that patch may be excluded from habitat management. Ignoring extirpated patches could be detrimental to species persistence if the species exists as a metapopulation, with recolonization likely to occur. Therefore, maintenance of suitable habitat in extirpated patches is vital for long-term species conservation, especially in the face of increased habitat destruction, global warming, and the hope of future translocation (Griffith et al. 1989, Perez et al. 2012).

Patch occupancy, colonization and extinction of many taxonomic groups are affected by habitat quality (Crone et al. 2001, Pellet et al. 2007, Visconti and Elkin 2009); thus, determining the habitat requirements of threatened species is key to managing for suitable habitat. For rare insects, habitat requirements are often fine-grained such that local scale, within-patch habitat characteristics are central to population persistence (e.g., Thomas et al. 2001, Fleishman et al. 2002, Collinge et al. 2003, Poyry et al. 2009, Beyer and Schultz 2010). Understanding and managing for subtle species habitat requirements can be difficult, but comparing habitat characteristics between occupied and unoccupied patches can elucidate important differences in habitat quality that can be used to focus management efforts in unoccupied sites.

The Ohlone tiger beetle (*Cicindela ohlone* Freitag and Kavanaugh) is an endangered and fragmented species found in only five patches of a once more extensive metapopulation, having been extirpated from at least 5-10 patches since it was discovered 25 years ago (Cooper 2009). *Cicindela ohlone* is endemic to coastal prairies that evolved with disturbances such as grazing by large ungulates and fires that are thought to have promoted and enhanced the beetle's bare-ground habitat (Anderson 2007, Wigand et al. 2007). Human activities have eliminated natural disturbances and spread invasive grasses, which form dense, extensive stands, often replacing native perennial bunch grasses (Hayes and Holl 2003a, D'Antonio et al. 2007). While it is known that *C. ohlone* requires open, bare-ground areas to mate as adults and find prey as both adults and larvae (Pearson and Vogler 2001), it is unclear what specific changes in habitat quality have contributed to *C. ohlone* patch occupancy and extirpation and, in turn, how to manage habitat for *C. ohlone* persistence and recolonization.

The destruction and decline of habitat quality may have compromised *C. ohlone* metapopulation dynamics, causing there to be only five remnant populations (Knisley 2011). However, because there have been two population turnover events in recent years and four out of five *C. ohlone* populations are viable (Cornelisse *et al.* unpublished data), there is reason to believe *C. ohlone* has the capability to recolonize extirpated patches managed to provide suitable habitat. In addition, because *C. ohlone* is a relatively newly discovered species, its past distribution is unknown (Freitag et al. 1993). Thus, patches of coastal prairie that are not known to have been occupied by *C. ohlone* may have been a part its historical range. These patches are important to consider for potential habitat augmentation, assisted migration or translocation for future viability of the species (Hanski and Thomas 1994, Seddon 2010).

I sought to determine the role of habitat characteristics in differentiating habitat quality among sites on which *C. ohlone* are currently found (present), those from which they are extirpated (extirpated), and coastal prairie sites within *C. ohlone*'s habitat range that are thought to have never been occupied (absent). To determine *C. ohlone* habitat requirements and quality differences at a finer scale, I examined the habitat characteristics within present sites that were associated with *C. ohlone* breeding areas. I hypothesized that specific, measureable habitat characteristics, such as percent cover of bare ground or nonnative vegetation, would determine a level of habitat quality such that they successfully differentiated extirpated sites from present and absent sites and larval habitat within present sites. To establish the scale of habitat characteristics needed to specify habitat quality between and within sites, I examined the role and importance of plant species composition in predicting *C. ohlone* occupancy, which I hypothesized would be less important than plant guilds and vegetation cover. Finally, as isolation has been shown to be an important driver of patch extirpation (Hanski 1999, Thomas et al. 2001), I tested the spatial autocorrelation of *C. ohlone* presence and extirpation in patches to determine whether extirpated patches were more isolated than expected by chance.

Methods

Study sites

This study was conducted in 15 coastal terrace prairies in Santa Cruz County, California, USA (36.97°N to 37.07°N and 121.96°W to 122.09°W). Santa Cruz County has a Mediterranean climate that receives an average of 77 (58-120) cm of rain, 95% of which falls from October to April. To determine the local habitat characteristics associated with the incidence of the *C. ohlone*, I compared the five habitat patches on which *C. ohlone* are present (present), five from which *C. ohlone* were extirpated in the recent past (5-10 years) (extirpated), and five in which *C. ohlone* have never been recorded (absent) (Fig. 1.1). The absent sites were coastal terrace prairies chosen based on their presence within the current *C. ohlone* range, having a slope <30% and the same Watsonville-Loam soil family as present and extirpated sites. Grazing management differed among and within site types during the study: no extirpated sites were grazed; two present sites were grazed by cattle, one by horses, and two were not grazed; one absent site was grazed by horses, one by cattle, and three were not grazed.

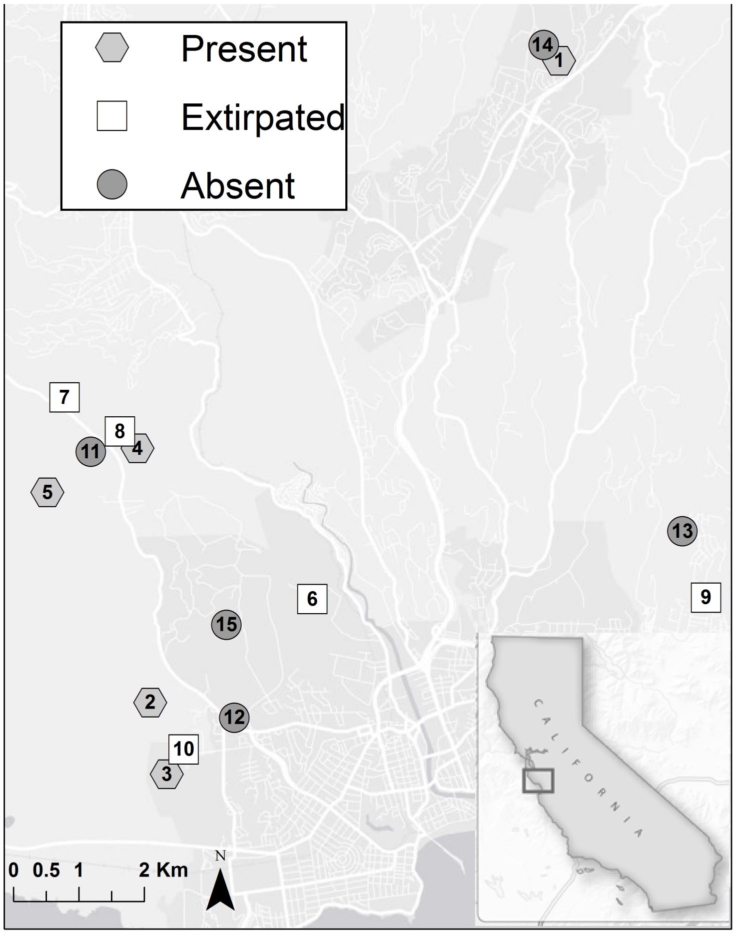

Figure 1.1. Study sites (area): 1. Glenwood (2.9 ha), 2. IAA (7.8 ha), 3. Moore Creek (9.6 ha), 4. Lower Marshall Field (1.5 ha), 5. Wilder Ranch (3.5 ha), 6. Pogonip (7.2 ha), 7. North Marshall Field (2.9 ha), 8. Upper Marshall (6.1 ha), 9. Soquel (1.6 ha), 10. South Meder (2.9 ha), 11. East Wilder Ranch (3.9 ha), 12. IAD (4.5 ha), 13. Santa Cruz Gardens (1.7 ha), 14. Glenwood Out (2.8 ha), 15. Great Meadow (10.4 ha).

To confirm presence or absence of *C. ohlone*, I used a visual index count (Knisley and Schultz 1997) of adults and larvae along transects the width of each patch, two meters apart throughout all patches from January to June in 2011 and 2012. No *C. ohlone* colonized extirpated or absent patches during the study, nor did any present sites become extirpated.

Habitat quality data collection

To test the contribution of habitat factors to *C. ohlone* incidence, I sampled percent bare ground, vegetation, and litter cover as well as vegetation height, litter depth, plant species composition, and soil at all 15 sites in March-May 2011 and 2012. I randomly placed 12 5-m diameter circle plots at each of the 10 extirpated and absent sites. At each present site, I placed 12 5-m diameter circle plots in a stratified random distribution to ensure that half of the plots were located in areas of high *C. ohlone* larval burrow density (>15 burrows/plot) and half were located in paired areas with no larval burrows.

I characterized vegetation and ground cover in four haphazardly placed 0.25-m^2 quadrats in all plots. I measuring vegetation height using the 'direct measurement method' (Stewart et al. 2001) and litter depth to the highest horizontal dead-plant material. I determined vegetation species composition in 5% cover classes, using the mid-point for analysis, and omitting species under 5% cover. I identified vegetation species and determined their source of origin (native vs. nonnative) using the Jepson

Manual (Baldwin et al. 2012) and calculated mean percent cover of nonnative forbs, nonnative grasses, native forbs and native grasses. In 2012, one cylindrical soil core, 5-cm in diameter and 20-cm deep, per plot was analyzed at Brookside Laboratories (New Knoxville, OH, USA) for physical, chemical, and organic matter analysis (Brookside Laboratories Inc. 2013) (Appendix 1).

Data Analysis

To determine habitat and soil factors important in predicting site type (present, extirpated, or absent), I constructed conditional inference trees (Hothorn et al. 2006) with the ctree command in the Party package in R (R Development Core Team 2012). Conditional inference trees utilize an unbiased iterative, binary recursive data-partitioning algorithm that searches for the best predictor variable, splits the dependent variable into distinct groups, and then repeats variable selection until no more significant predictors are found (Hothorn et al. 2006). I used commands table (predict) to determine the number of plots predicted correctly based on the significant variables in the resultant inference trees. I used treeresponse to determine to which site type the incorrectly predicted plots belonged and to which site type they were misclassified; because there were three site types, there was a 33% random chance of correct prediction. I pooled the measurements from the four quadrats by averaging percent cover values so that each circle plot was a replicate and did two analyses with both years combined: one with all predictor variables, including percent cover of all plant species, and one with plant cover grouped by guilds. I also conducted a separate conditional inference tree with just soil factors as predictor variables.

To determine if habitat and soil factors correctly classified larval habitat, I combined data from all present sites and coded plots with burrows (1) and those without burrows (0), and conducted conditional inference trees using ctree. As above, I did two analyses with both years combined: one including percent cover of all plant species and one with plant cover grouped by guilds. For all analyses, I set the minimum criterion of variable inclusion in ctree to p = 0.05 (mincriterion=0.95) and 24 instances (minbucket=24) (Hothorn et al. 2009).

Spatial Autocorrelation

Using ArcGIS, I digitized each site and calculated the area and distance of each site center to all other sites. The small number of site types (five each) precluded any statistical analysis on patch area, but site areas are listed in Fig. 1.1. To determine whether extirpated and present sites were spatially correlated, I used the program joincount.m (Morris and Doak 2002) in Matlab (Student Version 7.12) to estimate the correlation of paired site fates (extirpated=0 or present=1) in different distance categories, using a randomization method to test significance. I used distance classes of 2.5, 5.0, 7.5, 10, and 15 km. The randomization was done by reshuffling, without replacement, the fates of each site (0 or 1) in each distance category to create an expected random distribution of fate pairs (00, 01, or 11) given no spatial association.

The observations that occurred <5% or >95% of the time when compared to the random distribution indicated significant spatial correlations. I did not include the absent sites in this analysis because I chose them based on their proximity to all sites and so their geographic locations were biased.

Results

Predicting site type

Fifty-two plant species with greater than 5% cover were found in all coastal prairies; 44 species in present sites, 42 in extirpated sites, and 46 in absent sites (Appendix 2). Percent cover of plant species correctly classified 61% of present plots and 62% of absent plots, whereas when plants were included as guilds, only 49% of present plots and 48% of absent plots were classified correctly. Classification of extirpated plots was highly successful in both analyses, but more so, 89%, when plants were included as guilds than if species percent covers were included, which correctly classified 80% of extirpated plots. Year and site were not significant factors in any of the analyses, justifying combining the two years and indicating that results were not driven by characteristics of one site.

Present plots were characterized by a high percent cover of bare ground and low litter depth and vegetation cover (Fig. 1.2). Present plots also had a higher percent cover of the nonnative forb *Erodium botrys* and lower cover of the nonnative annual grass *Brachypodium distachyon*, which forms dense stands. Of the 39%

misclassified plots in *C. ohlone* present sites, nearly all were the plots with no larval burrows and 26% were misclassified as belonging to absent sites. Extirpated plots were significantly classified by many factors, including low percent bare ground cover and high vegetation cover and low percent cover of the nonnative forb *E. botrys* (Fig. 1.2). Absent plots were most significantly explained by high percent cover of vegetation and *B. distachyon*, but a few other factors had significant effects (Fig. 1.2).

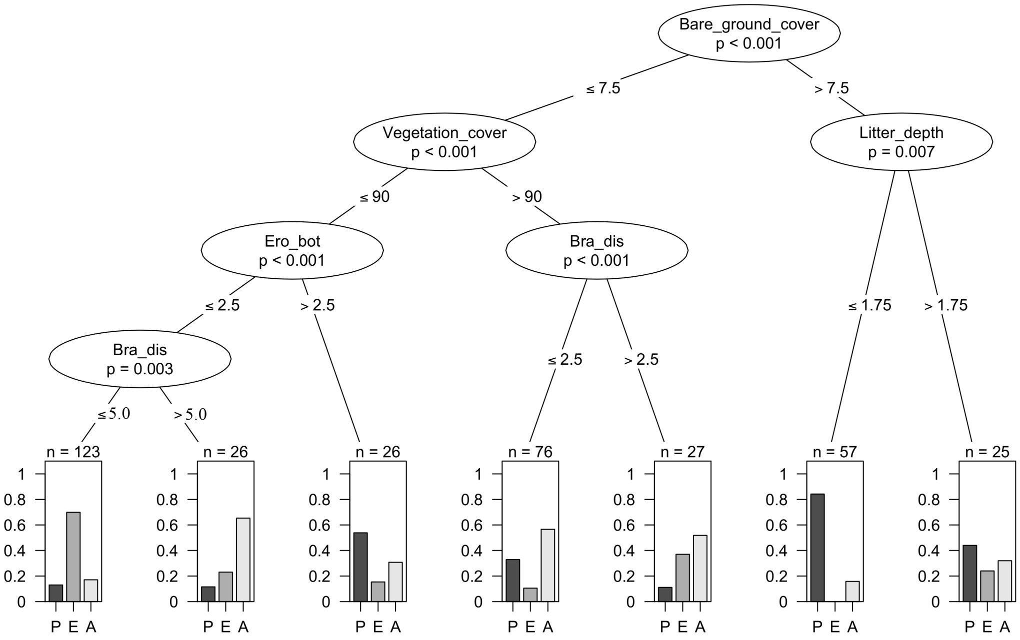

Figure 1.2. Conditional inference trees with percent cover of plant species included showing the habitat factors that significantly classified site types. Significant habitat factors are circled and ranked (top-most variable has highest correlation) with associated p-values and the splitting percent cover or height/depth (in cm) values on the branches. The bar plots show the proportion of total plots classified by predictor variables (indicated by the n-value) from each of the site types; present (P), extirpated (E), and absent (A). Ero_bot= *Erodium botrys* and Bra_dis= *Brachypodium distachyon*.

Including plants as guilds-only did not greatly change the significant predicting factors, as high percent cover of bare ground, low vegetation height, and low percent cover of litter significantly classified plots with beetles present; conversely, extirpated plots were significantly classified by low percent bare cover, high percent cover of litter as well as higher percent cover of native grasses (Fig. 1.3). Low percent cover of bare ground and high vegetation cover significantly predicted the majority of absent plots (Fig. 1.3). In one absent site, Great Meadow (Fig. 1.1, #15), 21 of 24 plots were classified as extirpated.

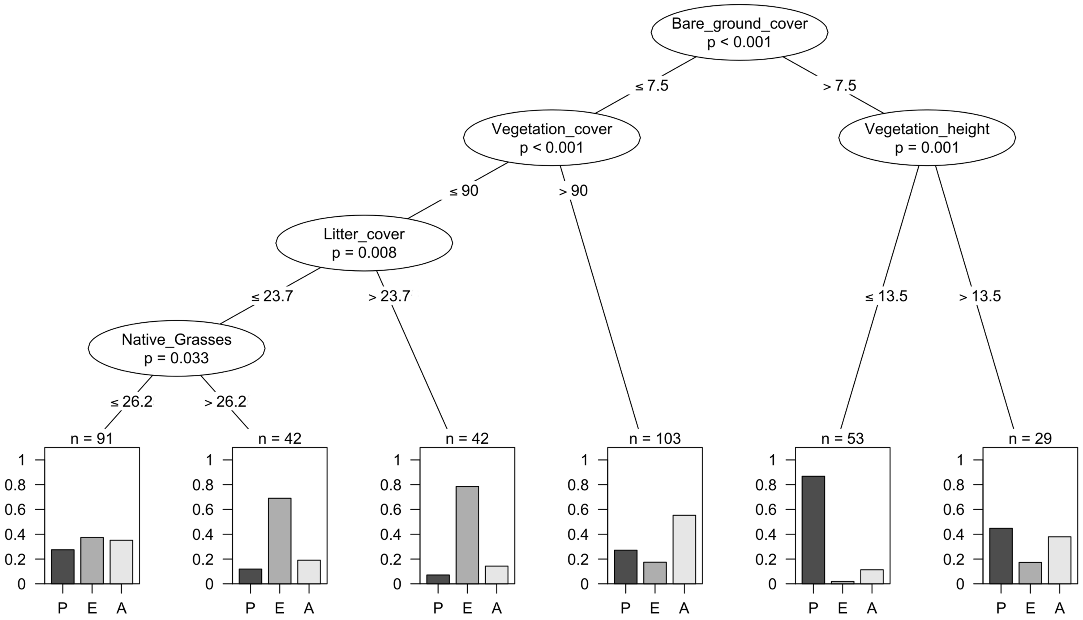

Figure 1.3. Conditional inference trees excluding percent cover of plant species showing habitat variables that significantly classified site type; present (P), extirpated (E), and absent (A).

Soil characteristics did not significantly explain beetle occupancy when combined with vegetation factors. When analyzed separately, however, soil characteristics correctly classified ~65% of plots from all three site types. Bulk density was the most important soil factor differentiating site types, as present plots generally had bulk density >1.01 g/cm^3, extirpated plots ≤1.01 g/cm^3. Plots at Glenwood (Fig. 1.1, #1), a site with beetles, were almost exclusively classified as absent sites based on soil characteristics.

Predicting larval habitat

Plant species composition did not significantly classify presence or absence of larval burrows within occupied sites. Also, whether included or analyzed separately, no soil characteristics were significant in classifying plots with or without burrows. The majority (88%) of plots with burrows were significantly classified by >5% bare ground cover and low vegetation height and litter depth (Fig. 1.4). On the contrary, ≤5% bare ground cover and low percent cover of forbs, native and nonnative, significantly classified 86% of plots without burrows (Fig 1.4).

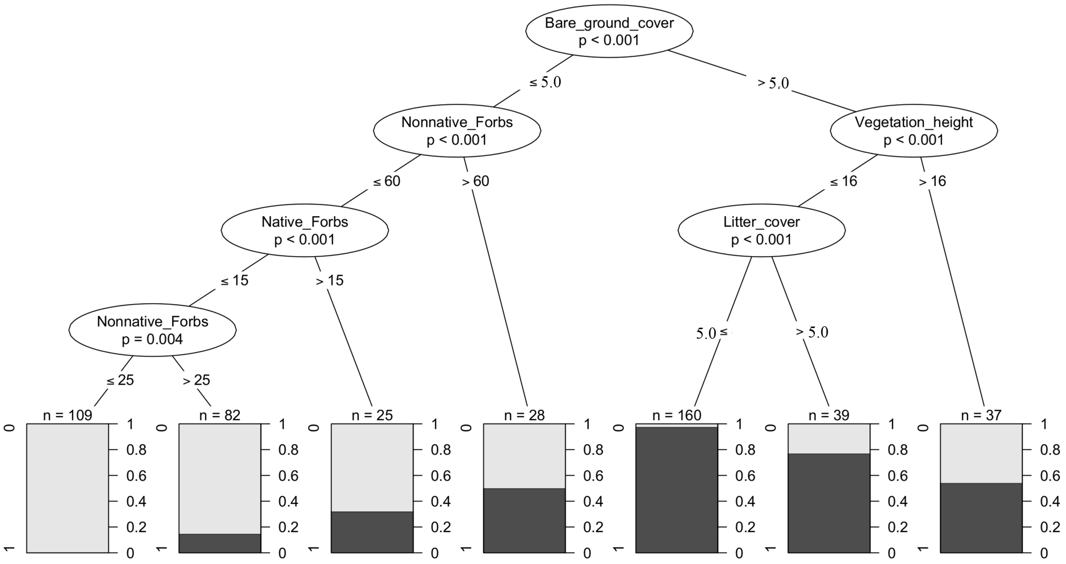

Figure 1.4. Conditional inference trees showing habitat factors that significantly classified larval habitat (1) and non-larval habitat (0).

Spatial autocorrelation of site fates

Occupied sites were not spatially autocorrelated with other occupied sites, as they were not significantly paired at any scale throughout *C. ohlone*'s range (Fig. 1.5). At the smallest scale, 2.5 km, there were significantly *fewer* extirpated-extirpated site pairs observed than expected and significantly *more* present-extirpated site pairs observed than expected (Fig. 1.5). Extirpated sites were, however, correlated at mid-distances, as there were significantly more extirpated-extirpated site pairs than expected at 7.5 km (Fig. 1.5). Thus, extirpation of *C. ohlone* appears to have occurred throughout its range rather than at smaller scales, as extirpated sites are clumped with occupied sites at small distances and regularly occur at mid-distances.

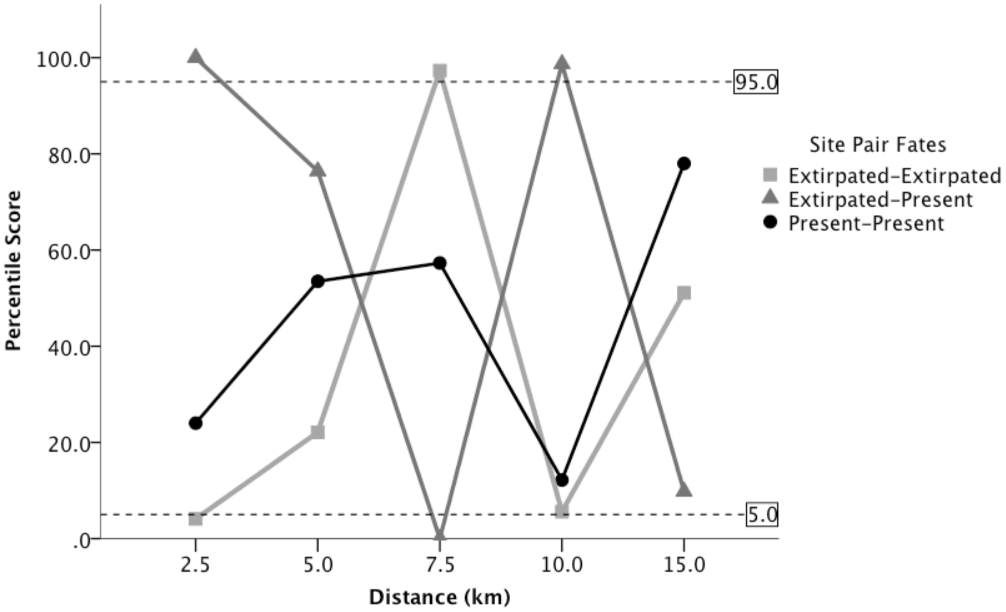

Figure 1.5. Spatial autocorrelation of present (occupied) and extirpated site types; site pairs with percentile scores above 95% are significantly correlated in space, while those with scores below 5% are significantly uncorrelated.

Discussion

The Ohlone tiger beetle has been extirpated from at least ten sites in the last 25 years due to habitat destruction and deterioration assumed to be the result of lack of bare ground habitat, which my results have confirmed. Modeling and comparing habitat features important in classifying current and potential *C. ohlone* habitat in the context of its biology and natural history has revealed how extirpated and absent sites can be managed for conservation. The majority of studies investigating the effects of habitat quality metrics on patch occupancy focus on defining characteristics of occupied sites (e.g., Thomas et al. 2001, Knapp et al. 2003, Heisswolf et al. 2009, Sanford et al. 2011) instead of extirpated sites; yet, ameliorating current threats to *C. ohlone*, and the many species experiencing increased fragmentation and displacement, will require managing extirpated and unoccupied sites for future colonization and translocation (Opdam and Wascher 2004).

Extirpated sites were virtually paired in space with currently occupied sites, suggesting that metapopulation dynamics (i.e. isolation of formerly occupied sites) did not dictate *C. ohlone* population extinctions. The extirpated sites were more likely to be found at intermediate distances from each other, spread throughout the range of *C. ohlone* metapopulation, indicating extinction is caused by local, within-site factors rather than isolation (Morris and Doak 2002). Indeed, extirpated sites were clearly defined by a decreased availability of bare ground and forb cover and an increase in the cover of grasses. The proximity of extirpated sites to currently occupied sites is encouraging for potential recolonization with improvements in habitat quality.

Habitat factors consistently characterized sites from which *C. ohlone* are extirpated as having less than 10% cover of bare ground, higher grass than forb cover, high litter cover and depth, and lower soil bulk density, and occupied sites exhibited these characteristics, indicating that these are important factors for *C. ohlone* survival. Bare ground is essential for both *C. ohlone* adults and larvae because of their visual hunting and mate finding natural history characteristics and creation of bare ground has been shown to augment *C. ohlone* colonization of within patch habitat (Cornelisse et al. 2013). A moderate to high level of soil compaction, a sign of disturbance, has also been shown to indicate high quality larval habitat for some tiger beetle species (Knisley 2011).

For *C. ohlone*, a predator, plant species composition was not important in determining extirpated sites. However, plant guilds were important, as the beetles were not found in areas with high grass cover, including native grasses. Disturbance, such as grazing, mowing or fire, reduces grass and litter cover and reduces competition for space and sunlight resulting in increased forb cover and habitat of lower stature with more bare ground in California coastal prairies (Hayes and Holl 2003b, a, Stahlheber and D'Antonio 2013), features also favorable to the endangered San Francisco Popcorn Flower (*Plagiobothrys diffusus*) and the Scott's Valley spineflower (*Chorizanthe robusta var. hartwegii*) (K. Lyons, personal communication). This suggests that managed disturbance has the potential to create favorable prairie habitat conditions on extirpated sites and is needed for potential *C. ohlone* reintroductions or natural colonizations.

Absent sites were consistently predicted by a high percent cover of vegetation, particularly nonnative grasses; thus, potentially suitable larval habitat could be created in absent sites through creation of bare ground (Cornelisse et al. 2013), conditions for forbs, such as grazing (Hayes and Holl 2003b, Stahlheber and D'Antonio 2013), and control of the invasive grass *Brachypodium distachyon*. Misclassifications and differences between habitat characteristics of present and absent plots can be used to determine the absent sites most appropriate for habitat management and translocation. For example, plots in the absent site Glenwood Out were consistently misclassified as belonging to a present site. Glenwood Out is separated by a marsh from Glenwood, which hosts the *C. ohlone* population with the highest population growth rate (Chapter Four). Thus, because of its present-like habitat quality and proximity to a thriving *C. ohlone* population, Glenwood Out would be an ideal candidate for habitat restoration.

Within-site habitat heterogeneity can also important to consider when managing unoccupied sites, particularly for disturbance dependent species (Platt and Connell 2003) and those dependent on microhabitat features (Kotliar and Wiens 1990). For *C. ohlone*, patches of bare ground and forbs differentiated larval habitat from the grass-covered non-larval habitat in present sites. Insects are particularly sensitive to small-scale, within-patch habitat quality changes because of the distinct habitat requirements and dispersal abilities between the larval and adult stages (Clarke et al. 1997). This has been shown for insects that depend on host plants, such as butterflies (Thomas et al. 2001, Beyer and Schultz 2010) and certain habitat features, such as deadwood for saproxylic beetles (Schroeder et al. 2006). While *C. ohlone* occupy the two largest sites, they only utilize a portion of the prairies for life functions such as mating, hunting, and laying eggs. Thus, site area may be important in that larger coastal prairie sites may have higher habitat heterogeneity (MacArthur and Wilson 1967, Rosenzweig 1995) and be more likely to contain suitable *C. ohlone* habitat.

For metapopulations, unoccupied sites will be increasingly significant in the face of further habitat fragmentation and global warming and an understanding of species' habitat requirements and characteristics is needed to guide protection and restoration of future habitat. While it is important to consider any regional cause of extinction before making conservation management plans, habitat quality ultimately determines whether or not a species goes extinct in a patch (Thomas et al. 2001). I have shown that the measureable characteristics of ground cover, vegetation, and soil defined habitat quality and predicted patches from which *C. ohlone* populations have been extirpated as well as larval habitat within occupied sites. Through managed disturbance that alters these soil and vegetation characteristics, currently unoccupied and extirpated sites can be enhanced for future colonization.

Chapter 2

Artificial bare patches increase habitat for the endangered Ohlone tiger beetle (*Cicindela ohlone*)

Introduction

Habitat loss, including loss of ecosystem processes and natural disturbances, is the primary driver of species extinctions (Laurance 2010). Natural disturbances, such as fire, grazing, and floods, are integral components of some ecosystems and can serve to increase biodiversity and habitat heterogeneity, creating microsite conditions to which certain species are adapted (Sousa 1984, Platt and Connell 2003, Garcia-Gomez et al. 2010, Katayama et al. 2010, Knisley 2011). Thus, often it is not enough to simply protect habitat for species conservation; instead, disturbance-dependent habitats frequently need active management that restores natural processes and disturbances. In cases when restoring natural disturbance regimes is difficult or impossible, the recovery and management of rare species relies on direct anthropogenic habitat alteration or creation to supplement resources, augment populations, and expand ranges (Souter et al. 2004, New 2010, Knisley 2011). Examples of this approach range from removal of encroaching vegetation due to lack of flooding to create gravel bars for Long-billed Plover breeding (Katayama et al. 2010) to construction of artificial burrows, no longer created by burrowing animals, to enhance the population density of the endangered pygmy blue tongue lizard (Souter et al. 2004).

Mimicking natural disturbance and habitat creation has been a central approach for the recovery and conservation of rare ground beetles and tiger beetles (New 2010). Rare beetle species can be sustained by the creation of simple, small-scale habitat features such as hedgerows, beetle banks, and dead wood that provide vital resources in an otherwise unsuitable habitat (MacLeod et al. 2004, Toivanen and Kotiaho 2007, New 2010, Letourneau et al. 2011). These type of anthropogenic analogues of natural habitat have provided the resources needed for 35% of the rare and threatened carabid species in Britain (Eversham et al. 1996). Tiger beetles in particular have benefited from artificial substrates because almost half of tiger beetle species and subspecies in the U.S. are found in human managed or created habitats (Knisley 2011).

Adult tiger beetles are visual predators on small arthropods, and many species require bare ground to both forage and oviposit. Larvae are sit-and-wait predators that generally require bare ground to capture prey from the mouth of their burrows in the soil (Pearson and Vogler 2001). Many tiger beetle species have restricted distributions on substrate surfaces of dynamic, naturally disturbed habitats, such as riparian areas, sand dunes, salt flats, ocean beaches and prairies, which commonly contain areas of bare ground (Pearson and Cassola 1993, Pearson and Vogler 2001, Knisley 2011).

The endangered Ohlone tiger beetle (*Cicindela ohlone* Freitag and Kavanaugh) is endemic to the coastal prairies of Santa Cruz County, California where it is found in five remnant patches. The coastal prairie evolved with disturbances that created conditions for bare ground, such as natural and anthropogenic fire by Native Americans, grazing and soil disturbance by native ungulates and burrowing animals, and periodic drought (Anderson 2007, Wigand et al. 2007). After European settlement, grazing regimes changed, time between fires increased, and annual exotic plants replaced perennial bunch grasses, decreasing the incidence of bare ground (Hayes and Holl 2003a, D'Antonio et al. 2007). Managed disturbance to create bare ground is an important conservation strategy for many threatened and endangered tiger beetles (Knisley 2011). Nevertheless, methods for creating such habitat for conservation have often not been tested experimentally. In this study, we tested whether bare ground plots created by scraping off vegetation would be colonized by *C. ohlone* as oviposition habitat (estimated as first instar larval burrows) compared to otherwise comparable, unscraped control areas. We also examined if *C. ohlone* colonization was influenced by: (1) the distance of scrapes from core habitat and (2) soil compaction.

Currently, recreational trails and/or cattle grazing haphazardly create core, disturbed habitat within each prairie (i.e. around a trail or grazed patch) where *C. ohlone* adults and larvae are primarily found. Prairie radiates out from these core areas for ~100-200 meters before abutting forests, roads, or ravines, depending on the site. We predicted that core habitats represent potential source populations from which individuals could colonize the surrounding prairie if suitable habitat conditions were present (Pulliam 1988, Pulliam and Danielson 1991). To test this, we created scraped, bare ground plots at increasing distances from the core habitat. We expected that *C. ohlone* would colonize bare ground plots close (10 m) to source populations more frequently than more distant scraped plots and unscraped controls (MacArthur and Wilson 1967).

In *C. ohlone* habitat, the conditions of bare ground can vary from a highly compacted bike trail to loose soil excavated during recent gopher activity. Thus, the suitable habitat characteristic of "bare ground" required by all tiger beetles (Pearson and Vogler 2001, Knisley 2011) remains undefined. To qualitatively test the effect of soil decompaction on *C. ohlone* colonization, we mechanically decompacted the soil after scraping. Because *C. ohlone* have been observed to oviposit preferentially in the compacted trails edges (Knisley and Arnold 2004), we expected that *C. ohlone* colonization would be less frequent in the decompacted plots than in plots that have not been decompacted or have been tamped down after decompaction.

Methods and Analyses

Expansion of suitable habitat

This study was conducted in Santa Cruz County, California, USA in three *C. ohlone* habitat patches, all of which are within 12.2 km of each other: Moore Creek Preserve, Wilder Ranch State Park, and Glenwood Reserve. In February 2010 bare ground habitat in treatment plots was created manually by removing vegetation with a McLeod (large rake hoe). At both Wilder Ranch State Park and Glenwood Reserve, four sets and, in Moore Creek Preserve, five sets of 2 × 2 m plots were created by scraping vegetation off the soil surface. Each set included a scraped and adjacent control plot at 10 m, 50 m, and 100 m away from the core *C. ohlone* habitat that radiated out in four or five directions (Fig. 2.1). One of us (TC) surveyed for 1st instar larval burrows in scraped and control plots to check for colonization in May of both 2010 and 2011. In both years, colonization was defined as the presence of a 1st instar larval burrow in a plot. In May 2011, we estimated the percent of bare ground in 5% cover classes, using the mid-point for analysis, in each plot in two randomly placed 0.25-m^2 quadrats.

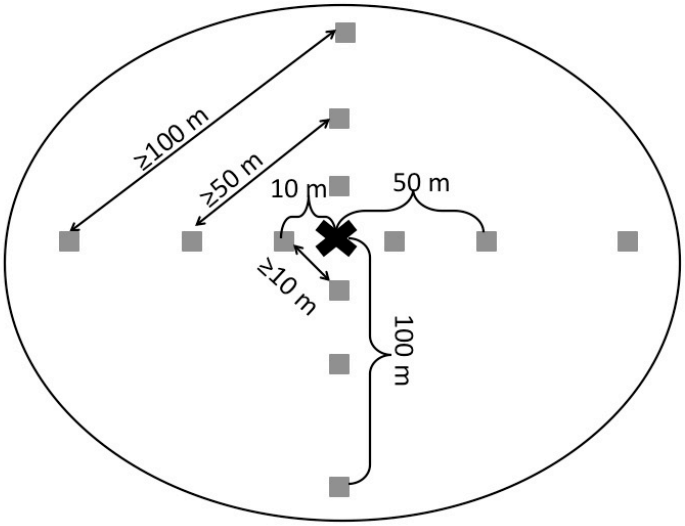

Figure 2.1 Experimental design for expansion of suitable habitat experiment in coastal prairie, with individual plots of artificial bare ground radiating out at 10, 50 and 100 m distances from the core beetle habitat (designated with an X). Gray squares represent 4 m^2 of bare ground plots within the coastal prairie (adjacent controls not shown).

A Chi-square test for independence was used to compare the frequency of colonization in scraped plots versus unscraped control plots and, within scraped plots, the frequency of colonization in plots created 10, 50, and 100 m from the core habitat for each year separately. Colonization in the control plots was too infrequent to test for distance effects, so we only compared distance effects on scraped bare plots. After establishing the assumption of independence of data, paired t-tests were used to compare percent bare ground in scraped versus control plots. The average percent bare ground was estimated from the two quadrats and log transformed to fit assumptions of normality and homogeneity of variances. We used a logistic regression to test the effect of percent bare ground on colonization in a plot.

Soil decompaction

This study was conducted in two different *C. ohlone* habitat patches, Inclusion Area A and Marshall Field on the University of California Santa Cruz campus. In late April 2009, we applied the following treatments within experimental plots: scraped, scraped + ripped, and scraped + ripped + tamped. A front loader was used to rip the top 10-15 cm of soil and to create the different scraping and tamping treatments. The ripping was done to both emulate soil decompaction as done by burrowing animals as well as to test its effect on maintaining bare ground. In addition, tamping of the soil surface was tested because field observations suggest that tiger beetles prefer smooth surfaces for oviposition (T. Cornelisse, personal observation). Three randomized blocks in Inclusion Area A and six blocks in Marshall Field, both with two 2 × 2 meter plots of each treatment type (n=18 for each scraped, scraped + ripped, and scraped + ripped + tamped) were created for a total of n=9 blocks and n=54 plots. The total size for each block was 5 × 8 meters. One of us (TC) checked for colonization by surveying for 1st instar larval burrows in each treatment plot in May of 2010 and 2011(scrapes were created too late in the season for *C. ohlone* oviposition in 2009). Also in May 2010 and 2011, percent bare ground was estimated as in the first experiment. Colonization and percent bare ground were measured in paired control plots in 2011.

A Chi-square test for independence was used to compare the frequency of colonization in scraped plots of any treatment versus unscraped control plots and, within scraped plots, the frequency of colonization in plots scraped, scraped + ripped, and scraped + ripped + tamped, for each year separately. Percent bare ground data were transformed as in the first experiment. The difference in percent bare ground between years 2010 to 2011 in each scraped treatment was analyzed using repeated measures ANOVA. After finding that year was a significant factor, the difference in percent bare ground between the different scraped treatments was analyzed using a separate ANOVA for each year. Percent bare ground in control and treatment plots in 2011 was analyzed using a planned comparison. We used logistic regression to test the effect of percent bare ground on colonization in a scraped plot.

Results

Overall, in both studies, there were 73 colonizations in plots scraped to create bare ground, while unscraped control plots had 9 colonizations over two years. In the study testing the effect of distance on the colonization, scraped plots were colonized significantly more frequently than unscraped control plots in both 2010 (X^2= 8.9, p=0.003, Fig. 2.2) and 2011 (X^2= 6.4, p=0.012, Fig. 2.2) regardless of their placement in the prairie habitat. Similarly, scraped plots of any soil decompaction treatment were colonized significantly more than paired control plots (X^2=24, p<0.0001).

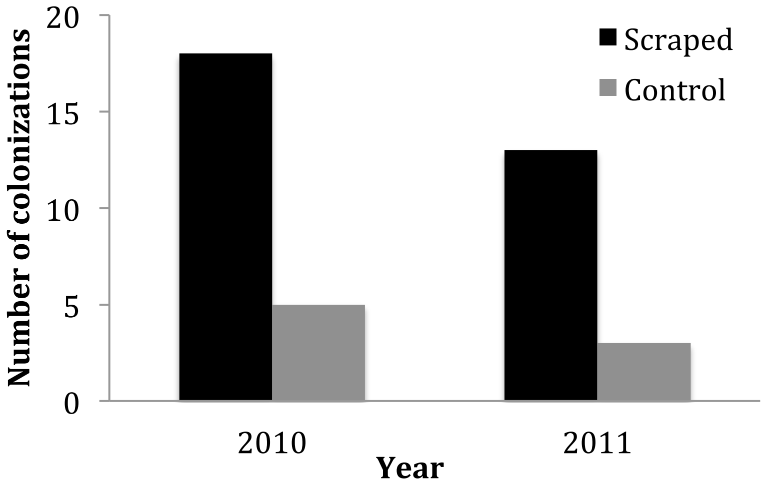

Figure 2.2. Number of colonizations in scraped and control plots at all distances in 2010 (p=0.003) and 2011 (p=0.012).

One year after scraping, in 2011, percent bare ground was significantly higher in experimentally scraped plots at three different distances from the core habitat within a prairie (20 ± 14%) than unscraped control plots [3.7 ± 4.7%, $t_{(38)}$=11, p<0.001]. Scraped plots of all soil decompaction treatments also had significantly more bare ground (18 ± 10%) than control plots [1.9 ± 2.9%, $t_{(95)}=16$, $p<0.0001$] in 2011, two years after scraping.

Expansion of suitable habitat

In 2010, scraped plots 10 m away from the core habitat were colonized significantly more than those 50 and 100 m away from the core habitat ($X^2= 9.9$, $p=0.007$, Fig. 2.3a). In 2011, there was no significant difference in the number of colonizations at different distances away from core habitat ($X^2= 1.6$, $p=0.45$, Fig. 2.3b). Percent bare ground correctly predicted incidence of colonization 80.8% of the time (logistic regression $X^2= 17$, $p<0.0001$).

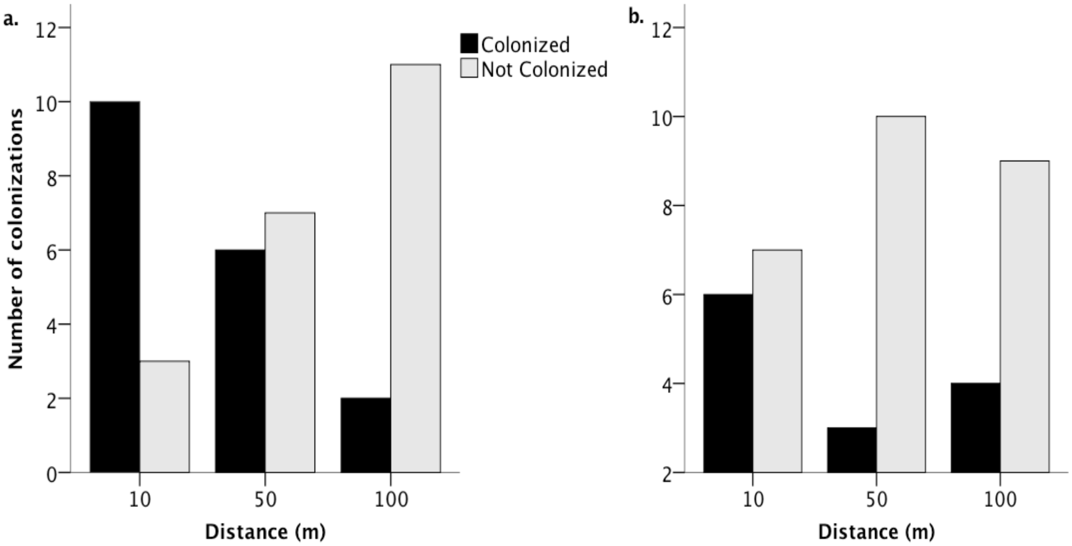

Figure 2.3. Number of colonizations in scraped plots created at 10, 50, and 100 m away from the core habitat in a. 2010, plots at 10 m had significantly more colonizations that plots at 100 m (p=0.007) and b. 2011, no significant difference (p=0.45).

Soil decompaction

Colonization did not differ significantly among scraped, scraped + ripped, and scraped + ripped + tamped treatment plots in either 2010 (X^2= 4.4, p=0.108, Fig. 2.4a) or 2011 (X^2= 2.0, p=0.374, Fig. 2.4b). Percent bare ground significantly decreased between the first and second year after the scrapes were created, from 30% ± 13 in 2010 to 18% ± 10 in 2011 [$F_{(1,51)}$=30, p<0.0001]. Percent bare ground did not differ significantly among the three treatments in either year [2010: $F_{(2,51)}$=3.1, p=0.054, 2011: $F_{(2,51)}$=0.55, p=0.58]. Percent bare ground correctly predicted incidence of colonization 75.9% of the time (X^2= 17, p<0.0001).

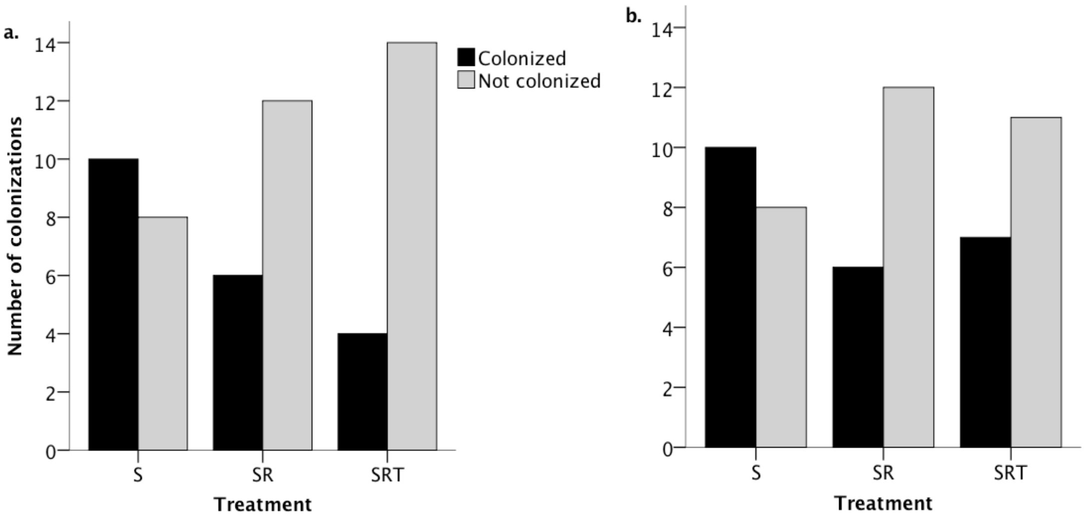

Figure 2.4. Number of colonizations in scraped (S), scraped + ripped (SR), and scraped + ripped + tamped (SRT) plots in a. 2010 (p=0.108) and b. 2011 (p=0.374).

Discussion

The significant number of Ohlone tiger beetle colonizations in cleared soil habitat, an eight-fold rise compared to controls, clearly demonstrates that artificial scrapes in coastal prairie can relieve habitat limitations for colonization by this endangered beetle. *Cicindela ohlone* currently persists in habitat patches that are influenced by local recreation, burns, or grazing practices that maintain patchy, bare-ground refuges. A combination of relatively long-lived (one-two years) larval and pupal stages and the ephemeral nature of the adults are life history characteristics that allow them to persist in such habitats (Platt and Connell 2003). When natural processes that maintain these refuges cannot be restored, artificial disturbances are needed. Practically, we found that a single management event had effects lasting at least two years. The infrequent presence of larval burrows in control habitat sites is most likely a result of the lack of bare ground. This is evidenced by the fact that we found significantly more colonizations in scraped plots than controls, that bare ground was a significant predictor of colonization, and that tiger beetles require bare ground free of dense vegetation and thatch for oviposition (Pearson and Vogler 2001).

Our results suggest that *C. ohlone* are able to use suitable bare ground oviposition sites at least 100 m away from core areas. In much the same way roads, open areas, and forest are dispersal barriers to certain species of Carabidae (New 2010), the tall, thick grasses and thatch may be dispersal barriers to *C. ohlone* within a patch. Yet, the distance of the scraped plots from the core habitat was not a significant factor for *Cicindela ohlone* colonization. Even though we found a significant difference between scrapes created 10 and 100 m from the core habitat in 2010, in 2011 there was no distance effect on colonization. While the results suggest a lack of a source-island effect over the range of distances tested, the increased colonization of 100 m plots in the second year could be a result of the closer plots functioning as stepping stone habitat in the first year (MacArthur and Wilson 1967).

Soil decompaction did not affect *C. ohlone* colonization. A moderate to high level of soil compaction has been shown to indicate high habitat quality for some tiger beetle species (Knisley 2011), yet it is detrimental to others (Cornelisse and Hafernik 2009). *Cicindela ohlone* larval burrows have been found both along compacted trail edges as well as in relatively decompacted feral pig foraging areas (Knisley and Arnold 2004). This pattern further suggests that neither compaction nor decompaction limits *C. ohlone* colonization on bare soils.

Despite the fact that bare ground is important for Ohlone tiger beetle oviposition, percentage bare ground in the plots actually decreased with time and *C. ohlone* significantly colonized artificial bare ground plots both one and two years after they were created. Thus, bare ground *per se* may be only one of several factors associated with the year-old bare ground areas. Microhabitat characteristics are important in tiger beetle oviposition site choice, as females have been shown to choose sites based on shade, soil type, salinity, moisture, and vegetation cover (Shelford 1908, Knisley 1987, Schultz 1989, Hoback et al. 2000, Romey and Knisley

2002, Cornelisse and Hafernik 2009). In addition, some vegetation within bare ground plots can provide both shade and cover from predators (Hoback et al. 2000, Omland 2002, Brust et al. 2006). Shading reduces soil surface temperatures and temperature variability (Cornelisse and Hafernik 2009), and this oviposition preference has been shown to reduce egg and larval heat stress, desiccation, and death in some tiger beetles (Hoback et al. 2000). Future detailed studies will determine factors associated with *C. ohlone* habitat quality.

Based on the results of this study, we recommend continued creation of bare ground plots for the conservation of the endangered Ohlone tiger beetle. Scraped plots do not need to be decompacted and should be created throughout the prairies of currently occupied habitat. Scraped plots should also be created every two years in order to maintain bare ground and to ensure usage by female *C. ohlone* as oviposition sites.

Chapter 3

Managing recreation for endangered species conservation: how knowledge affects recreationists' attitude and stated behaviors and the significance for Ohlone tiger beetle conservation

Introduction

Outdoor recreation has been cited as a leading cause of threatened and endangered species decline on public lands (Losos et al. 1995, Taylor and Knight 2003). Recreational activities can result in direct mortality of plants and wildlife but also cause behavioral and physiological stress that results in reduction of habitat, reproduction rates, and, ultimately, populations (Boyle and Samson 1985, Cole 1993, Cornelisse and Hafernik 2009, Martinez-Abrain et al. 2010, Monz et al. 2010, Martin et al. 2011). However, engagement in recreational activities can enhance one's environmental knowledge and attitudes as well as increase public support for conservation efforts (Peterson et al. 2008, Thapa 2010). Fortunately, science-supported, expert-backed management can often mitigate the negative effect of recreation (Cole 1993, Taylor et al. 2007, Martin et al. 2011) and in certain instances, recreation can be used as a tool for conservation management, particularly in habitats threatened from a lack of natural disturbance (Knisley 2011, Cornelisse et al. 2013). The case of the endangered Ohlone tiger beetle represents an opportunity to investigate the effect of recreation on species behavior as well as the role of recreationists' knowledge and attitudes in conservation management. We demonstrate that recreational activities can be managed in ways that promote endangered species conservation.

The endangered Ohlone tiger beetle (*Cicindela ohlone* Freitag and Kavanaugh) is endemic to the coastal prairies of Santa Cruz County, California where it is found in only five remnant patches. *Cicindela ohlone* requires bare ground habitat (i.e., free of vegetation) to forage, find mates, and oviposit (Knisley and Arnold 2004, Cornelisse et al. 2013). In particular, *C. ohlone* adults are generalist predators that stalk their prey and find mates on large open patches of bare ground whereas the larvae are sit and wait generalist predators that maintain burrows at the site of oviposition, generally in smaller bare ground patches within the prairie vegetation. The coastal prairie evolved with disturbances that created conditions for bare ground, such as fire, grazing and soil disturbance by native ungulates and burrowing animals, and periodic drought (Anderson 2007, Wigand et al. 2007). After European settlement, grazing regimes changed, time between fires increased, and annual exotic plants replaced perennial bunch grasses, decreasing the incidence of bare ground (Hayes and Holl 2003a, D'Antonio et al. 2007). Today, livestock grazing maintains much of the within-prairie larval habitat of *C. ohlone*, whereas adults frequently conduct mating and foraging activities on recreational trails. The *C. ohlone* case is unusual in that recreation can directly disrupt adult foraging and mating, yet, paradoxically, recreation maintains bare ground habitat for these activities.

Recreation has only recently been recognized as a tool to create habitat for this endangered species and, prior to 2005, was considered solely detrimental to *C. ohlone*, as adults were occasionally found crushed on trails (C.B. Knisley, personal communication). From 2001-2005, trails were temporarily closed for *C. ohlone* protection and a widely publicized popular article stated that recreation had an exclusively negative effect on the beetle, going so far as to say that cyclists were the number one cause of its demise (Phelan 2002). However, the effect of recreation on *C. ohlone* has never been systematically evaluated or quantified and it is unknown how the trail closures and popular article influenced recreationists' perceptions toward *C. ohlone* conservation and management. Recreation effects and recreationist perceptions are critically important for the management of the beetle, as four of the five remaining *C. ohlone* habitat patches are currently open to recreation. Here, we tested both the effect of different types of recreation on adult *C. ohlone* behavior as well as how both prior and new knowledge about *C. ohlone* affected recreationists' attitude toward the beetle and stated willingness to comply with management strategies.

Recreationists' knowledge of their effects on species may influence both their perceptions of management and attitude toward the species and, in turn, their behavior in protected habitat (Kaiser and Fuhrer 2003, Taylor and Knight 2003, Frick et al. 2004). Knowledge of ecological issues affects behavior in a significant, yet indirect way; specifically, knowledge provides the basis through which mediators, such as attitudes, values, incentives, and social consequences change behavior (Kaiser and Fuhrer 2003, Frick et al. 2004, Farrior 2005, Randler et al. 2007). We hypothesized that prior knowledge of *C. ohlone* would affect recreationists' attitude and stated behaviors in a negative way; specifically, we predicted that recreationists with prior knowledge would rate the conservation of *C. ohlone* as less important, the effect of recreation on the beetle as negative and be less likely to state compliance with management actions in *C. ohlone* habitat. We based this hypothesis on the assumption that most of recreationists' prior knowledge of *C. ohlone* was a result of the popular article and trail closures. Alternatively, we predicted that recreationists with no prior knowledge would rate the conservation of *C. ohlone* as more important and be more likely to state compliance with *C. ohlone* management if provided with new knowledge.

To complement our study of recreationists' stated compliance with management strategies, we tested the effect of different recreation types and management on beetle behavior. Our goal was to determine if adult *C. ohlone* management should include requiring cyclists to dismount their bikes (equivalent to hiking) or if simply requiring cyclists to slow down in beetle habitat would minimize the negative disturbance of beetle behavior. We hypothesized that the recreational types would differ in the magnitude in which they disrupt *C. ohlone* behavior; specifically, based on observations, we predicted that cyclists riding at fast speeds would cause adult *C. ohlone* to cease their behaviors and fly off the trails more often and at further distances than would cyclists at riding at slow speeds and hikers, assuming the later two represent less disruptive recreational activities. The goal of our study was to identify the most effective recreation management approaches and to increase awareness of and compliance with *C. ohlone* conservation strategies.

Methods

Effect of recreation on beetle behavior

Site description

We conducted this study in Santa Cruz County, California, USA in the *C. ohlone* habitat known as Inclusion Area A (IAA) on the University of California Santa Cruz campus (36°N 122°W). Inclusion Area A contains an 850-meter fire road open to recreation, including cycling, on which *C. ohlone* adults are often found foraging and mating. The trials were conducted on eight days between 24 February and 10 March, the peak of *C. ohlone* adult activity in 2012, during which time around 350 *C. ohlone* adults were surveyed in IAA (Chapter Four).

Data collection

We conducted 30 trials each of hiking, slow cycling, fast cycling, and control treatments (120 total trials) during which we observed the affect of the recreation activity on *C. ohlone* behavior. For all trials T. Cornelisse observed the beetles while a research assistant hiked or cycled as the “recreationist”. Slow cycling was defined as 8-12 kph (5-7 mph) and fast cycling as 30-35 kph (18-22 mph). We measured bicycle speed using a Schwinn 20-Function Bike Computer (Schwinn, Chicago, IL) attached to the bicycle that was monitored by the "recreationist" during each trial.

To conduct the trails, we walked along the road until an individual *C. ohlone* adult was sighted. Once sighted, the "recreationist" backed up at least 30 m away from the beetle and T. Cornelisse walked into the grassland, perpendicular to the trail, until three to five meters away from the beetle. We then observed the beetle for two minutes with no recreation and recorded behavior and distance moved, if any. The "recreationist" was then signaled verbally to begin hiking or cycling and told where on the trail to aim to avoid direct impact with the beetle (i.e., off to either side if the beetle was in the center of the trail). In all cases the "recreationist" was at least 0.25-0.50 m away from the beetle. The "recreationist" continued the activity another 10 m down the trail before stopping. We recorded whether the beetle remained stationary, flew off the trail, walked off the trail, or walked along the trail, as well as the distance moved by the beetle during each of these behaviors. We observed the beetle for an additional two minutes after the recreational activity and recorded the beetle's behavior and distance moved. For control trials we observed a beetle for four minutes with no recreation. We used a Bosch GLR225 Laser Distance Measurer (Bosch, Farmington Hills, MI) to measure the distance moved by the beetle. Once we reached the end of the fire road, trials were stopped for the day to avoid testing individual beetles more than once on a trial day.

Data analysis

We used a Chi-square test for independence to determine if the frequency of flight off the trail differed among the recreation treatments. We used a z-test of column proportions for pairwise comparisons between recreation treatments, with Bonferroni adjustments indicating significant differences at the 0.05 level. We determined if distances flown by beetles off of the trail depended on recreation treatments using One-way analysis of variance (ANOVA) with Post Hoc Tukey Honestly Significant Difference test (HSD) for pairwise comparisons. We did not include controls in this analysis because the beetles never flew off the trail during the control trials, resulting in all zeroes and thus a non-normal distribution without homogeneity of variances. This is justified because we are not looking to exclude recreation as a management strategy. We determined if total distance moved along the trail depended on recreation treatment using One-way ANOVA with Tukey HSD test for pairwise comparisons. All statistical analyses were done using SPSS v. 19.0.0 (SPSS, Inc., IBM).

Effect of recreationist knowledge on attitude and stated behaviors

Site description

We conducted this study on the University of California, Santa Cruz north campus (37°N, 122°W) at a trailhead leading into both campus natural lands and Wilder Ranch State Park, with connections to all active *C. ohlone* habitats open to recreation. Over the course of one year (2011: 8 July, 14 July, 21 August, 5

September, 16 October; 2012: 4 January, 7 April, 28 April), we conducted 302 in person surveys at the trailhead. We set up a table with copies of the survey, a lock-box, informational signs about the areas populated by *C. ohlone*, and refreshments. We asked every recreationist (cyclists, runners, and hikers) that passed by if they would be willing to take a survey in regards to the Ohlone tiger beetle and the management of the area.

Data collection

On each survey date, we gave information about the Ohlone tiger beetle to half of the participants prior to providing them with the survey. In particular, we provided three types of knowledge that have been recognized as important precursors to changing attitudes: systems knowledge, the understanding of ecosystem properties in which a behavior is conducted; effectiveness knowledge, the understanding of how actions affect the environment; and action-related knowledge, the understanding of what can be done about a problem (Frick et al. 2004). We told half of participants that "the Ohlone tiger beetle finds food and mates on bare ground, including trails" (systems knowledge), "while recreation can harm and directly kill beetles, it also creates essential bare-ground habitat for the population as a whole" (effectiveness knowledge), and "complying with management and posted signs can reduce the negative affect of recreation on the Ohlone tiger beetle" (action-related knowledge). The other half of participants on that date received no information prior to the survey. We coded the surveys with a small "1" for new knowledge and "0" for no new knowledge at the top of the paper, which were hidden under the clipboard when handed to participants. On the survey, we asked participants if they had heard of the Ohlone tiger beetle and we interpreted an affirmative response as prior knowledge of the beetle. Thus, we had four experimental groups: recreationists with neither prior nor new knowledge, recreationists with prior knowledge but no new knowledge, recreationists with new knowledge but no prior knowledge, and recreationists with both prior and new knowledge.

To determine participants' attitude toward *C. ohlone* conservation and their perception of the effect of recreation, we asked participants to rank the importance of Ohlone tiger beetle conservation and how they felt recreation affected the beetle, respectively. We also asked participants whether they "do", "would", or "would not" comply with five different management strategies including, stay off closed trails, dismount and walk bike, and slow down in *C. ohlone* habitat. Finally, we asked participants to answer demographic questions on place of residence, sex, age, income, and education. The complete survey is included in Appendix 3.

Data analysis

We coded survey responses for statistical analyses by assigning each response a number and combined "would comply" and "do comply" responses to the management strategy questions as one number. To determine how participant responses to the question "How do you feel recreation affects the Ohlone tiger beetle?" depended on experimental group, we compared the frequency of responses among groups using a Chi-square test for independence. We also used a Chi-square test for independence to determine how the frequency of participant compliance to management strategies depended on experimental group. To determine how participant responses to the question “How important is conservation of the Ohlone tiger beetle to you?” depended on experimental group, we used a non-parametric Mann-Whitney *U* test to compare ranked responses among experimental groups. We used Chi-square tests for independence to compare the frequency of responses to the questions on both the importance of *C. ohlone* conservation and how recreation affects the beetle between participants that stated compliance or noncompliance to management strategies. Pairwise comparisons of responses were done using a built-in z-test with Bonferroni adjustments.

We used summary statistics to describe participant demographics. We compared participant ages among survey dates and among experimental groups using One-way ANOVA with Tukey HSD for both tests. We compared participant income and education among survey dates using Kruskal Wallis Sum of Ranks and among experimental groups using Mann Whitney *U* tests. We compared participant sex among survey dates and among experiment groups using a Chi-square test for independence. We compared place of residence between participants with prior knowledge and those without prior knowledge of *C. ohlone* with a Chi-square test for independence. To determine if stated compliance with the various management strategies depended on participant demographics, we used a Chi-square test for independence to compare frequency of responses (would/do comply vs. would not comply) between participants residing in Santa Cruz County zip codes and those residing outside of the County and among education levels, income levels, and between sexes; we used logistic regression to compare compliance responses among participant ages. All analyses were done in SPSS v. 19.0.0 (SPSS, Inc., IBM).

Results

Effect of recreation on beetle behavior

All recreation treatments (hiking, slow cycling, and fast cycling) caused the beetles to fly off the trail significantly more than no recreation wherein the beetles never flew off the trail during the 30 trials ($\chi^2=43.125$, df=3, $p<0.0001$). Among the recreation treatments, fast cycling caused the beetles to fly off the trails 25 times, which was significantly more ($p=0.014$) than slow cycling (15 times) and hiking (14 times), which were not significantly different. Similarly, the beetles flew significantly further off the trail when approached by fast cycling than hiking or slow cycling ($F=6.433$, df=2, $p=0.002$, Fig. 3.1). Thus, the distance of beetle displacement caused by fast bikes was significantly greater than that of both slow bikes and hiking, which were not significantly different from each other. There was no difference in the total distance moved along the trail among the three recreation types and control treatment ($F=0.822$, df=3, $p=0.484$, Fig. 3.1). Therefore, if the beetle stayed on the trail during a recreation event, it did not move along the trail any more than if there was no recreation.

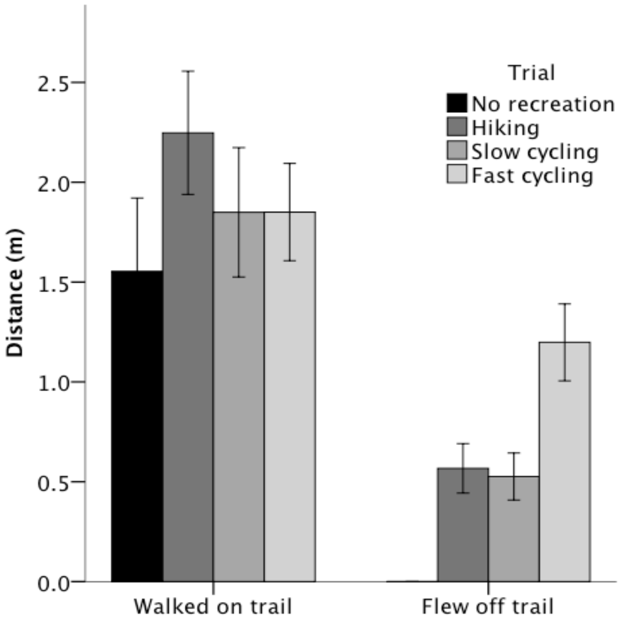

Figure 3.1. Mean distance walked by an individual beetle when it remained on the trail during each recreation trial type (p=0.484) and mean distance flown by an individual beetle when it left the trail during each recreation trial type (p = 0.002, no recreation had a mean of zero and was not included in the analysis). Error bars show SE.

Effect of recreationist knowledge on attitude and stated behaviors

Ninety-five percent of passing recreationists agreed to take the survey. On average, survey participants were 40 (SD 13) years old (18 to 70 years), held bachelor's degrees, earned $50,000/year, and had recreated in the area for 11 (SD 10.2) years (from first time to 40 years). Seventy-seven percent of the participants were from Santa Cruz County and another 16% from the surrounding Bay Area/Monterey counties. Only 1% of participants were from outside of the Bay

Area/Monterey counties in California, while 3% lived outside of California and 3% did not provide their zip code.

Participant demographics were generally not clustered on a survey date; yet, participants on survey date five (16 October 2011) were significantly older (51 SD 9.7 years old) than participants on survey dates two (14 July 2011, 39 SD 13 years old, p=0.022), seven (7 April 2012, 37 SD 13 years old, p=0.001), and eight (28 April 2012, 38 SD 14 years old, p=0.004). There were no demographic differences (age, sex, income, and education level) among experimental groups. Sex was the only demographic factor that significantly affected stated compliance with management strategies, as females were significantly more likely to state that they would slow down (χ^2=5.065, df=1, p=0.023) and dismount their bike (χ^2=9.445, df=1, p=0.003) than males. We also found no difference in stated compliance between participants from Santa Cruz County and those from surrounding counties (all above p=0.270).

Participants who had heard of the Ohlone tiger beetle prior to taking the survey were significantly older (43 SD 13 years, F=16.534, df=1, p<0.0001) and had a higher education level (Bachelor's degree, *U*=7825.5, p=0.039) than those who had not heard of the beetle, who were younger (36 SD 13 years) and had a lower education level (between some college and a Bachelor's degree). Participants living in Santa Cruz County had heard of the Ohlone tiger beetle significantly more than those who lived in surrounding counties (χ^2=26.356, df=1, p<0.0001).

There was no difference in the number of participants who had previously heard of the Ohlone tiger beetle between those who were given new knowledge and those who were not (χ^2=0.642, df=1, p=0.423). Participants given new knowledge did not rank the importance of Ohlone tiger beetle conservation higher than those who were not given new knowledge (U=10263, p=0.297). However, participants who had heard of the Ohlone tiger beetle prior to the survey ranked its conservation as "very important" significantly more than those who had not heard of the beetle before the survey (U=8318, p=0.005, Fig. 3.2). Participants who had both heard of the Ohlone tiger beetle prior to the survey *and* were given new knowledge at the time of the survey rated the effect of recreation as positive significantly more, and negative significantly less, than those with prior knowledge but no new knowledge of the beetle (χ^2=14.804, df=3, p=0.002, Fig. 3.3).

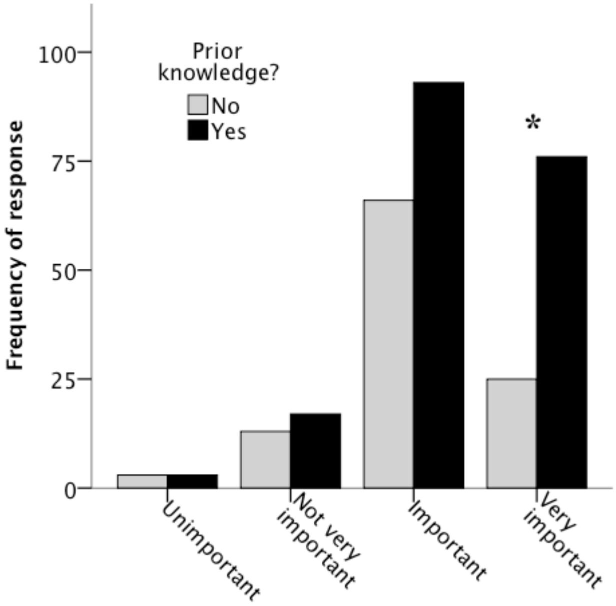

Figure 3.2. Frequency of responses to the survey question, "How important is conservation of the Ohlone tiger beetle to you?" between participants with prior knowledge of the beetle and those with no prior knowledge (*p=0.005).

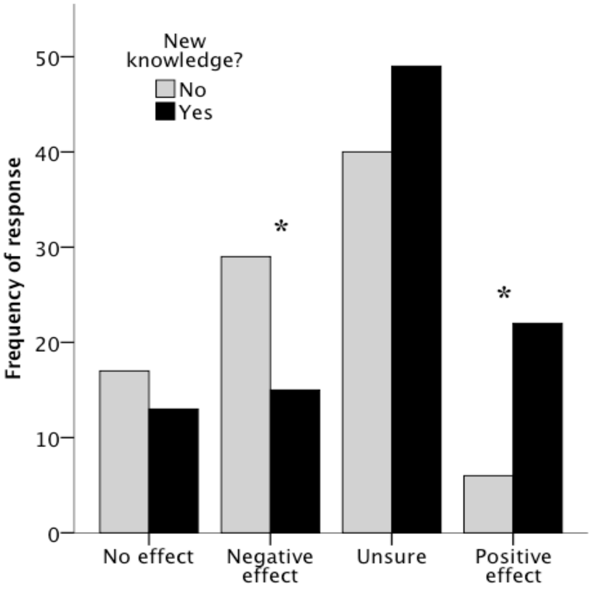

Figure 3.3. Frequency of responses to the survey question "How do you feel recreation affects the Ohlone tiger beetle?" from participants with prior knowledge of the beetle that either received new knowledge of the beetle or received no new knowledge (*p=0.002).

Stated compliance was high for all management strategies: 90% for slow down in beetle habitat, 90% for stay off closed trails, 95% for use alternative trails, 89% for create new trails, and 62% for dismount bike; neither prior knowledge, new knowledge, nor their interaction significantly affected stated compliance. Stated compliance was, however, affected by participant's ranking of Ohlone tiger beetle conservation importance and rating of recreation's effect on the beetle. In particular, participants who marked Ohlone tiger beetle conservation as "very important" were more likely to state that they would (or do) slow down in beetle habitat (χ^2=24.671, df=3, $p<0.0001$, Fig. 3.4a) and more likely to state that they would dismount their bike in beetle habitat (χ^2=16.380, df=3, p=0.001, Fig. 3.4b). If participants who received no new knowledge thought that recreation had no effect on the Ohlone tiger beetle, then they were more likely to state that they would not slow down in beetle habitat (χ^2=10.347, df=3, p=0.016).

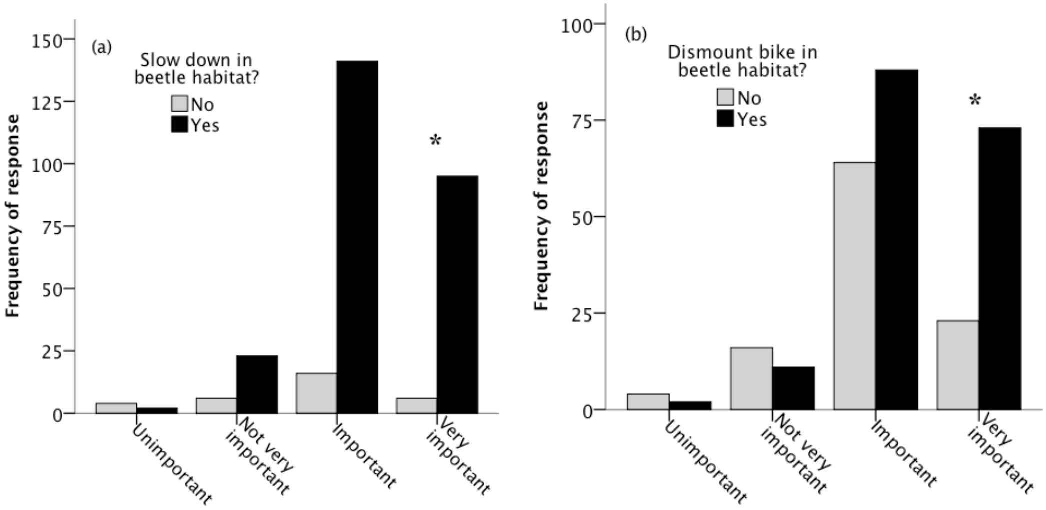

Figure 3.4a. Frequency of participant stated compliance (“Yes”) and stated noncompliance (“No”) with a. slowing down in beetle habitat (*p<0.0001) and **b.** dismounting their bike in beetle habitat (*p=0.001) as it depended on participants’ responses to the question, “How important is conservation of the Ohlone tiger beetle to you?”.

Discussion

In line with the knowledge, attitude, behavior literature, we found a direct link between recreationists’ knowledge and their attitudes towards *C. ohlone* conservation as well as their rating of the recreation’s effect on *C. ohlone* (Kaiser and Fuhrer 2003, Frick et al. 2004, Farrior 2005, Randler et al. 2007). Recreationists were more likely to rate Ohlone tiger beetle conservation as very important if they had heard of the beetle *prior* to taking the survey. This finding was contrary to our hypothesis and may be a result of the 10 years that have passed since the publicized conflict, as time can significantly reduce perceived conflict (Watson et al. 1997). In addition, recreationists negatively affected by the conflict may have been displaced from the area due to the trail closures and management in *C. ohlone* habitat (Schneider and Hammitt 1995, Vorkinn 1998). Alternatively, since prior knowledge of *C. ohlone* was associated with older and more educated participants, this finding may be a result of greater awareness and experience, which results in reduced conflict perception (Cessford 2003) and increased support for conservation efforts (Peterson et al. 2008, Thapa 2010). In line with our hypothesis, however, gaining *new* and *different* types of knowledge on top of prior awareness proved to be a significant indicator of the correct and more positive understanding of recreation's effect on *C. ohlone*; indicating that building on prior knowledge was central to impart the correct understanding of environmental interactions (Kaiser and Fuhrer 2003, Frick et al. 2004).

It was through recreationists' attitudes and perceptions that knowledge positively affected stated behavior in our study. Of the five management strategies we suggested on our survey, only "slow down in beetle habitat" had a positive association with both recreationists' importance rank of *C. ohlone* conservation and perception of recreation's effect on the beetle. If knowledge does affect attitude and understanding, as our results indicate, then education could lead to increased compliance with signs explaining the positive effect of slowing down on *C. ohlone* and rules to slow down in beetle habitat. While we only investigated stated behaviors, theory and empirical research show that stated behavioral intentions account for a large portion of variance in actual behavior (Ajzen 1991, Hughes et al. 2009), particularly if the behavioral intention is made while conducting the activity of interest (Lehman and Geller 2004), such as learning of and committing to slowing down while on the trail, as in our study. Based on our results of the effects of recreation on beetle behavior, detailed below, we now know that this behavior change is likely to have positive outcomes on *C. ohlone* adult survival and conservation.

Despite the limitations of the scope of the behavioral trials, we found that the effect of cycling on adult *C. ohlone* behavior could be reduced by 50% if cyclists slow down to speeds of 8-12 kph (5-7 mph) in beetle habitat. Beetles tended to stay on or near the trail more often when cyclers go slowly through their habitat, allowing the beetles to remain closer to their area of activity (i.e. the trail). Tiger beetles are highly active insects that expend upwards of 56% of their energy maintaining an internal body temperature just below their lethal limit (Pearson and Lederhouse 1987). The relatively constant thermal energy tiger beetles receive in open, bare habitats allows them to maintain an optimal foraging temperature (Schultz 1998) as well as visually locate and capture prey (Layne et al. 2006). When *C. ohlone* flies off the trail away from a disturbance (i.e. recreationist), it flies into the surrounding tall, dense grassland, causing the beetle to leave a microenvironment of high thermal quality to one of low thermal quality (Schultz 1998) as well as to expend energy escaping the disturbance. This behavioral response also takes the beetle away from its optimal foraging location, the trail, and reduced prey capture has been shown to significantly decrease the number of eggs produced by female tiger beetles (Pearson and Knisley 1985). While this study is limited in space and time due to the endangered and ephemeral nature of *C. ohlone,* it is the only empirically based depiction of the effect of recreation on adult *C. ohlone* behavior. No recreation would be least disturbing to *C. ohlone* behavior, but it would be detrimental to the overall population, as lack of recreation would be followed by loss of critical bare ground habitat. Thus, requiring cyclists to slow down in beetle habitat is likely to reduce the negative effect of recreation on adult *C. ohlone* and we now know that providing knowledge will enhance compliance with this management strategy.

Outreach campaigns should therefore be geared towards educating recreationists with little or no knowledge of *C. ohlone*; thus, the factors associated with that demographic are important to consider when planning management foci. Our results show that older and/or more educated participants were more likely to have heard of the Ohlone tiger beetle prior to the survey. This indicates that educational outreach should be geared toward younger, less educated recreationists, such as local schools and youth mountain bike clubs. In addition, since recreationists from Santa Cruz County are more likely to have heard of the Ohlone tiger beetle, the educational campaign should also extend to surrounding counties. Of course, it is important to educate the entire public, because not all veteran recreationists will have heard of the beetle. In addition, because both larval and adult stages of the Ohlone tiger beetle are dependent on bare ground, the recreation community can be directly involved in habitat creation, such as by creation of new and more beetle-friendly trails for adults or removal of within-prairie grasses to create bare patches for larval habitat (Cornelisse et al. 2013).

Our study investigates both the ecological effects and the social considerations of managed recreation in a conservation area with the unique attribute of using human disturbance to create habitat for an endangered species. Reconciling and balancing species habitat requirements with human activity is an essential component of species conservation in the Anthropocene (Kareiva et al. 2007, New 2007, Caro et al. 2012, Ramalho and Hobbs 2012). By incorporating communities directly affected by conservation actions into the management or science of species conservation, we can begin to enhance environmental literacy and support for biodiversity conservation (Bickford et al. 2012) as well as achieve more effective conservation outcomes.

Chapter 4

The implications of habitat management on the population viability of the endangered Ohlone tiger beetle (*Cicindela ohlone*) metapopulation

Introduction

Although the ultimate causes of species endangerment are most commonly habitat loss and invasive species introductions (Sodhi and Ehrlich 2010), proximate causes are reduced viability of small populations via genetic degeneration and demographic and environmental stochasticity (Lawton 1994, Simberloff 1994, Brook et al. 2008). Thus, while habitat protection is vital to species conservation, management is often needed to ensure viability of populations within protected habitat and across landscapes (Rodrigues et al. 2004, Fuller et al. 2010, Bonnot et al. 2011, Laurance et al. 2012). It is particularly important to understand the effect of management actions on tangible population viability goals of endangered species to ensure efficient and effective use of resources to prevent species extinctions (Morris and Doak 2002, Brook et al. 2008, Traill et al. 2010).

Despite their significance in ecosystem functions, insects are frequently overlooked in conservation actions and endangered insect recovery plans often lack quantitative population goals to ensure long-term viability (Losey and Vaughan 2006, Cardoso et al. 2011). More than 20 species of tiger beetles (Coleoptera: Cicindelinae) have been listed as threatened, endangered, or extinct and many more as federal species of concern (Knisley 2011). Pearson et al. (2006) estimate that at least 33

(15%) of the 223 named species and subspecies of tiger beetles in the US and Canada may be declining at a rate that justifies their listing as threatened or endangered. Tiger beetles are associated with distinct disturbance-dependent bare-ground habitats needed to forage, find mates, and oviposit; thus, while they are sensitive to habitat degradation, they are increasingly dependent on anthropogenic disturbance (Pearson and Vogler 2001, Knisley 2011).

The endangered Ohlone tiger beetle metapopulation (*Cicindela ohlone* Freitag and Kavanaugh) is endemic to the coastal prairies of Santa Cruz County, California. The remaining *C. ohlone* populations are present in habitat patches of a once more extensive metapopulation that consisted of 10-15 patches in the last 25 years (Cooper 2009). Adult *C. ohlone* are generalist predators that stalk and chase down prey in open areas using visual cues and larvae are sit-and-wait predators that construct a cylindrical burrow flush with the soil surface from which they lunge to capture passing arthropods; thus, both require bare ground for capturing prey (Pearson and Vogler 2001). The coastal prairie habitat evolved with disturbances such as large ungulate grazing and fires that created conditions for the beetle’s bare-ground habitat (Anderson 2007, Wigand et al. 2007); however, human activities have eliminated natural disturbances and spread invasive grasses, which form dense, extensive stands, reducing the incidence of bare ground (Hayes and Holl 2003a, D'Antonio et al. 2007).

Management of livestock grazing, recreation and artificial habitat creation currently maintains bare-ground in the remaining *C. ohlone* habitat patches. Creation of bare-ground plots by scraping the ground surface free of vegetation successfully augments egg-laying habitat for *C. ohlone* (Cornelisse et al. 2013). However, tiger beetle larval habitat augmentation within areas already limited by quality habitat could create a potential for negative density-dependence, with increased larval density leading to increased competition and reduce larval survivorship (Takeuchi and Hori 2007). Recreational (i.e. hiking and cycling) trails also create bare ground, but high-speed cycling can disrupt the mating and foraging behaviors of *C. ohlone* adults (Chapter Three). Thus, while systematic management of bare ground creation and recreation maintains *C. ohlone* habitat, it is unknown how these actions affect *C. ohlone* population viability.

The metapopulation dynamics of *C. ohlone* may be compromised because of habitat destruction and decline of habitat quality resulting in a few remnant populations; but because there have been two population turnover events in recent years, we have reason to believe *C. ohlone* has the capability of recolonization provided suitable habitat is available and managed in extirpated patches. However, recolonization of extirpated patches depends on asynchrony of *C. ohlone* population dynamics and their ability to migrate between populations (Hanski 1999), both of which are unknown.

We use population viability analysis (PVA) to model the effects of conservation management and metapopulation dynamics on *C. ohlone* viability. We hypothesized that artificial bare ground creation and managed recreation would augment the population growth rate of all *C. ohlone* populations when accounting for density-dependent effects, which we hypothesized would be a significant factor in determining larval survival. We also hypothesized that *C. ohlone* vital rate dynamics would be asynchronous among populations and that any migration would reduce *C. ohlone* extinction risk. To test our hypotheses, we used PVA to model the growth rates of all *C. ohlone* populations and associated vital rate sensitivities as well as to determine how each rate was affected by management strategies and metapopulation dynamics in order to plan for the recovery of this endangered species.

Methods

Study sites

We conducted this study from January 2010 to August 2012 within the five remaining populations of *C. ohlone*, located in different coastal terrace prairie sites within a 24 km^2 area in Santa Cruz County, California: Lower Marshall (LM, 1.5 ha, 37.02°N 122.07°W) and Wilder Ranch (WR, 3.5 ha, 37.01°N 122.09°W), 1.3 km apart in the center of the range; Moore Creek (MC, 9.6 ha, 36.97°N 122.07°W) and University of California Campus (UC, 7.8 ha 36.98°N 122.07°W), 0.75 km apart in the south of the range; and Glenwood (GW, 2.9 ha, 37.07°N 121.99°W), 10 km north of the other sites. This work was completed under USFWS permit #TE-39184A-0.

Adult *C. ohlone* emerge from oviposition burrows, oviposit, and are active from late January to May. From February through early April, females deposit eggs singularly in the soil and the larvae develop at the site of oviposition. The first instars hatch in April through May, remaining in the first instar stage for four to six weeks (Pearson and Vogler 2001, Knisley and Arnold 2004), then progress to the second instar in May through June. Development to the third instar almost always occurs during the same summer, in July, after which the third instar plugs its burrow and pupates in late September through January, completing a one-year cycle. In addition, a few individuals have been observed to delay pupation until the following spring when the third instars unplug their burrows after winter inactivity (Knisley and Arnold 2004).

Data collection

We surveyed adults once or twice per week late January to early June 2010 to 2012. We did not include UC in 2010 because it was thought to be an extirpated site at that time. We estimated the number of *C. ohlone* adults and surveyed for larval burrows using a visual index count (Knisley and Schultz 1997). First instar larval burrows were surveyed in March to late April 2010 to 2012, identified by burrow diameter (Fig. 4.1) and assumed to be active if it was clearly delineated with a clean entrance, a sign of recent larval activity (Pearson and Vogler 2001). We overlaid the burrow(s) with a 0.25 m^2 gridded quadrat, marked the corners with a 3-cm wide metal washer and 5-cm long nail and the locations with a GPS to avoid disturbing larvae. We mapped all burrows in the quadrat on a gridded datasheet resembling the quadrat. In 2012, we identified and marked oviposition burrows in early March in the same manner as first instars. In 2010 and 2011 we marked 20 quadrats at each site and in 2012 we marked nine quadrats of oviposition burrows and 18 quadrats of first instar burrows, for a total of 27 quadrats at each site, which was dictated by the number of burrows found during surveys.

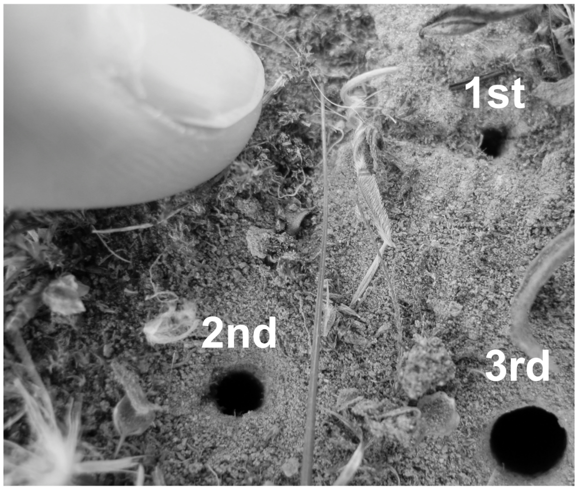

Figure 4.1. *C. ohlone* larval burrows, the three instars shown with index finger for scale.

To determine if eggs survived to first instar, first to second, and second to third, or remained in the same stage, we revisited each site in late April and May, June, and July, respectively, sufficient time for all stage transitions to occur (Pearson and Vogler 2001). Quadrat markers were located via GPS and then either visually or using a metal detector. We lined up the gridded quadrat to the metal markers and considered the transitions to have occurred based on the increase in burrow entrance diameter (Fig. 4.1). The following year, we revisited the locations of the previous year's third instar burrow once per week from late January though mid-March to check marked burrows for third instar larva survival and transition to adults by the presence of an irregular exit hole ≥ 6 mm.

Parameter estimates

We counted the total number of adults surveyed as females in the projection matrix model because visual index counts underestimate tiger beetle adults by ~50% (Knisley and Schultz 1997) and sex ratios are not significantly different from 1:1 (Shivashankar and Pearson 1994, Knisley and Schultz 1997, Tigreros and Kattan 2008, Cooper 2009). We assigned fertility rate (Sf4) as 40 because it is the best estimate of eggs a female *C. ohlone* oviposits in her lifetime (Knisley and Arnold 2004). We calculated larval growth rate within a stage (Sg*i* , *i* = instar stage 1, 2, or 3) as the proportion of individuals in the same stage at the next census. Transition rates (Ss*i* , *i* = the stage that transitioned to instar stage 1, 2, 3, or adult) were calculated as the proportion of individuals that transitioned from one stage to the subsequent stage in the next census (Morris and Doak 2002). Adult survival rates were included as zero because all adults senesce during the activity year. To estimate fecundity (F), we averaged three different estimates: (1) assuming a breeding pulse and mid-breeding census of eggs by multiplying the fertility rate by the square root of egg survivorship (Ss0); (2) assuming a constant breeding flow and mid-breeding census by multiplying the fertility rate by both the square root of (Ss0) and the square root of an estimate of adult survivorship; and (3) assuming a post-breeding census by multiplying the fertility rate by Ss0 (See Morris and Doak 2002, Ch. 6 for explanation of assumptions). We constructed a stage-class population model for *C. ohlone* (Fig. 4.2) and used the model parameters to construct a stage-class matrix model:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & Sf4*Ss0 \\ Ss0 & Sg1 & 0 & 0 & 0 \\ 0 & Ss1 & Sg2 & 0 & 0 \\ 0 & 0 & Ss2 & Sg3 & 0 \\ 0 & 0 & 0 & Ss3 & 0 \end{bmatrix}$$

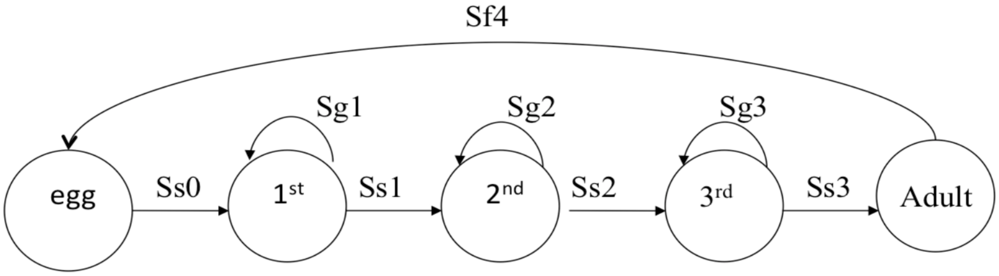

Figure 4.2. Stage class population model for *C. ohlone*; The parameters presented are those we measured: survival of egg to 1st instar (Ss0), growth of 1st instar (Sg1), survival of 1st to 2nd instar (Ss1), growth of 2nd instar (Sg2), survival of 2nd to 3rd instar (Ss2), growth of 3rd instar (Sg3), survival of 3rd instar to adult (Ss3), and fertility of adults (Sf4).

Density Dependence

To test for density dependent effects on larval survival, we used a random number generator to select an individual in each of the marked quadrats. We recorded survivorship from first to second and from second to third instar as survived (1) or dead (0) for each selected individual as well as the number of larval burrows in each quadrat surrounding the selected individual. Individuals still in the second instar stage during the last field visit were marked as survived (1). We tested the effect of larval density on the survival of selected individuals among sites using logistic regressions. Larval density was log-transformed to fulfill assumptions of normality. Logistic regressions were carried out using SPSS v. 19.0.0 (SPSS, Inc., IBM).

Matrix Modeling

All matrix analyses were done using Matlab Student Version 7.12 and methods described in Morris and Doak (2002). To account for demographic and environmental stochasticity, we constructed one matrix per study year and conducted the multiple matrices approach to estimate population growth rate (Morris et al. 1999). Stochastic log growth rate, log λ_s, was determined both via simulation using the program stoc_log_lam and using Tuljapurkar's approximation (τ^2), which accounts for the covariance and variability of matrix elements among years. (Tuljapurkar 1982, Morris and Doak 2002). We assumed all matrices had equal probability of occurring and simulated 50,000 iterations. We used simext.m (Morris and Doak 2002, Box 7.5), to evaluate the fraction of simulated populations that reach the quasi-extinction threshold after a designated time t_{max} set to 25 and 50 years and the quasi-extinction threshold to 25, 10, and 1 individual(s) and weighted all matrices equally.

Sensitivity Analysis

We conducted a stochastic sensitivity and elasticity analysis for each population by simulating multiple matrices using low, average, and high estimates of each vital rate using limitsens.m (Morris and Doak 2002, Box 9.2). Maximum likelihood estimates of Ss1, Ss2, and Ss3 were calculated using Kendall.m (Kendall 1998, Morris and Doak 2002, Box 8.2) and we used the resulting confidence interval values as our high and low estimates of the survivorship vital rates in limitsens.m. Vital rates associated with the three measures of fecundity were used for fertility estimates; 40 for average, 60 for the high (highest estimated by Knisley and Arnold 2004), and lowest fecundity value for the low estimate.

Sensitivity to management effects

To test the effect of creation of bare-ground and mandated slower cycling in *C. ohlone* habitats on population growth rates, we explicitly included a management scalar, *h*, in a deterministic matrix model using the program vitalsens.m (Morris and Doak 2002, Box 9.1). We averaged vital rates for all years and used 40 for the fertility value in the matrix.

Creating bare ground in *C. ohlone* habitat will likely increase the number of eggs laid by females, as up to eight times more larval burrows were found in scraped ground compared with vegetation-covered controls (Cornelisse et al. 2013). Females will also obtain more food with more bare ground (e.g. hunting ground), increasing their fecundity and egg survivorship (Pearson and Knisley 1985, Pearson and Vogler

2001). Furthermore, larvae that develop in bare ground experience increased prey availability and, in turn, reduced development time from 160 to 110 days, a 30% reduction (Pearson and Knisley 1985, Pearson and Vogler 2001, Knisley and Arnold 2004, Takeuchi and Hori 2007, Knisley 2011). Since female *C. ohlone* will lay up to 60 eggs in captivity (Knisley and Arnold 2004), we assumed females would lay 60 eggs with increased bare ground. We included bare ground creation as a management strategy that increases the survivorship and growth of eggs, 1st, 2nd, and 3rd instar by 30%, *h*=1.3, and the number of eggs by 1.5 times (1.15**h*). The resulting matrix is:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & (\mathrm{Sf4}*1.15\mathrm{h})*\mathrm{Ss0}*h \\ \mathrm{Ss0}*h & 0 & 0 & 0 & 0 \\ 0 & \mathrm{Ss1}*h & \mathrm{Sg2}*h & 0 & 0 \\ 0 & 0 & \mathrm{Ss2}*h & \mathrm{Sg3}*h & 0 \\ 0 & 0 & 0 & \mathrm{Ss3}*h & 0 \end{bmatrix}$$

We also modeled a hypothetical strategy that required all cyclists to slow down to speeds of 8-12 kph in *C. ohlone* habitats that allow bicycles: UC, LM, and WR. Reducing bicycle speed to 8-12 kph has the potential to reduce recreational disruptions to adult mating and foraging behavior, increasing adult survivorship and the number of eggs laid because of both increased fertility and increased reproductive period (Cornelisse and Duane in press, Pearson and Knisley 1985, Pearson and Vogler 2001). We incorporated the management strategy of reducing the bicycle speed allowed in *C. ohlone* habitat by adding a scalar, *h*, to the matrix vital rates that increased the number of eggs laid to 80. This is justified in that tiger beetles are able to lay up to 200 eggs per female lifetime if a female lives for 30 days, an estimate for the average life span for adult tiger beetles (Pearson and Vogler 2001). We also increased the fecundity, or survivorship of eggs, by 30%, as justified above. The resulting matrix is:

$$\begin{bmatrix} 0 & 0 & 0 & 0 & (\mathrm{Sf4} * 1.5h) * \mathrm{Ss0} * h \\ \mathrm{Ss0} * h & 0 & 0 & 0 & 0 \\ 0 & \mathrm{Ss1} & \mathrm{Sg2} & 0 & 0 \\ 0 & 0 & \mathrm{Ss2} & \mathrm{Sg3} & 0 \\ 0 & 0 & 0 & \mathrm{Ss3} & 0 \end{bmatrix}$$

Metapopulation Dynamics

We calculated vital rate correlation coefficients among sites from 2010-2012 using Pearson’s correlation to check for asynchrony. To determine the overall metapopulation growth rate as well as the quasi-extinction risk, we created a metapopulation matrix composed of the individual population vital rates and used DemoMetaSim.m (Morris and Doak 2002, Box 11.5). We capped the egg and larval stages at 100 individuals and adults at 300, high estimates of observed numbers, and the quasi-extinction thresholds to five, 10, and 20 individuals in each stage, and maximum time to 100 years for 500 runs. We ran the program first assuming no migration and including all sites and then by excluding sites one by one to test the extirpation or complete isolation of each site.

We also simulated quasi-extinction probability for LM and WR alone, as they are clumped in space. We simulated population growth and quasi-extinction risk for WR and LM assuming no migration, assuming one out of 50 adult females migrate between the two sites, or m=1/50=0.02; one out of 25, or m=1/25=1.04; and one out of 10, or 10% m=1.10; thus, each adult vital rate (Sf4) was multiplied by 1.02, 1.04, and 1.10, respectively.

Results

The number of adults, marked burrows, and vital rates varied between sites and years (Table 4.1). First instars never remained in the 1st instar stage between two successive censuses, thus we did not include a measure of Sg1 in the models. Egg survivorship estimates were similar between all populations except WR where we found the lowest estimate (Table 4.1), resulting in lower fecundity estimates. By averaging the three fecundity measurements described in the methods, we obtained the following fecundity (F) estimates for each population: GW 22.9; LM 14.8; WR 6.49; MC 19.7; UC 26.3.

Table 4.1. Number of adult *C. ohlone* counted using the visual index method and number of eggs and first instars marked (all quadrats combined); growth and survival parameters for each stage (see text for parameter explanation and calculation method); na indicates not marked that year.

	Glenwood (GW)			Lower Marshall (LM)			Wilder Ranch (WR)			Moore Creek (MC)			Campus (UC)	
Year	‘10	‘11	‘12	‘10	‘11	’12	‘10	‘11	‘12	‘10	‘11	‘12	‘11	‘12
Eggs	na	na	58	na	na	31	na	na	36	na	na	27	na	28
1stinstar	69	99	159	48	117	67	110	66	59	125	79	72	80	88
Adults	41	39	226	59	51	68	124	25	86	100	64	428	67	166
Ss0	na	na	0.59	na	na	0.32	na	na	0.06	na	na	0.41	na	0.54
Ss1	0.45	0.69	0.94	0.79	0.51	0.67	0.29	0.38	0.71	0.22	0.54	0.60	0.51	0.74
Sg2	0	0	0	0.05	0.03	0.27	0.03	0	0.05	0	0	0.02	0	0.2
Ss2	0.74	0.85	0.80	0.42	0.53	0.51	0.31	0.52	0.57	0.54	0.77	0.70	0.68	0.45
Sg3	0.74	0.21	0.20	0.75	0.69	0.69	0.3	0	0	0	0	0	0.14	0.14
Ss3	0.26	0.64	0.75	0.13	0.25	0.25	0.7	0.85	0.85	1.0	0.88	0.88	0.82	0.82

Density Dependence

The number of larvae in a quadrat ranged from 1-13, with an average of 3.3 (± 2.4). There was no effect of larval density (number of larval burrows in a quadrat), site, or site × larval density interactions on survivorship of first instars to second (R^2= 0.029, p=0.469), nor second instars to third (R^2= 0.015, p=0.692). Thus, we found no evidence of density-dependent larval survival.

Matrix Modeling

The simulated growth rates (λ_s) with 95% confidence intervals were: GW 1.41(1.405-1.415); LM 1.03 (1.028-1.032); WR 0.598 (0.596-0.601); MC 1.164

(1.153-1.174); and UC 1.163 (1.153-1.174). The growth rates calculated by Tuljapurkar's approximation were within the 95% confidence intervals of λ_s. For every population except WR, the stochastic quasi-extinction rate was zero in all time frames modeled. In all time frames and quasi-extinction thresholds, the extinction probability of the population at WR was 1.00, or definite extinction, by 21 years. The quasi-extinction probability or reaching 25 and 10 individuals was 1.00 by eight and 14 years, respectively.

Sensitivity Analysis

The elasticities of Ss1, Ss2, Ss3, and Sf4 were equal with relatively small confidence intervals, whereas Sg2 elasticities were very small with narrow confidence intervals (Fig. 4.3a). Egg survivorship (Ss0) and 3rd instar growth (Sg3) elasticities varied greatly among populations and uncertainties of those parameters were high in both LM and WR, as indicated by the wide confidence intervals (Fig. 4.3a).

For UC, MC, and WR, maximizing the survivorship of eggs has the greatest potential to maximize population growth rate (Fig. 4.3b) with corresponding r^2 values (a measure of influence on the population growth, λ) of: 0.4437, 0.3941, and 0.4503, respectively. The population growth rate of WR remains below λ=1 despite maximizing egg survivorship (Fig. 4.3b). For GW and LM, maximizing both egg survivorship (r^2 = 0.5917 and 0.6941) and survival of 3rd instars (r^2 = 0.0224 and 0.0918) maximized population growth rate (Fig. 4.3b).

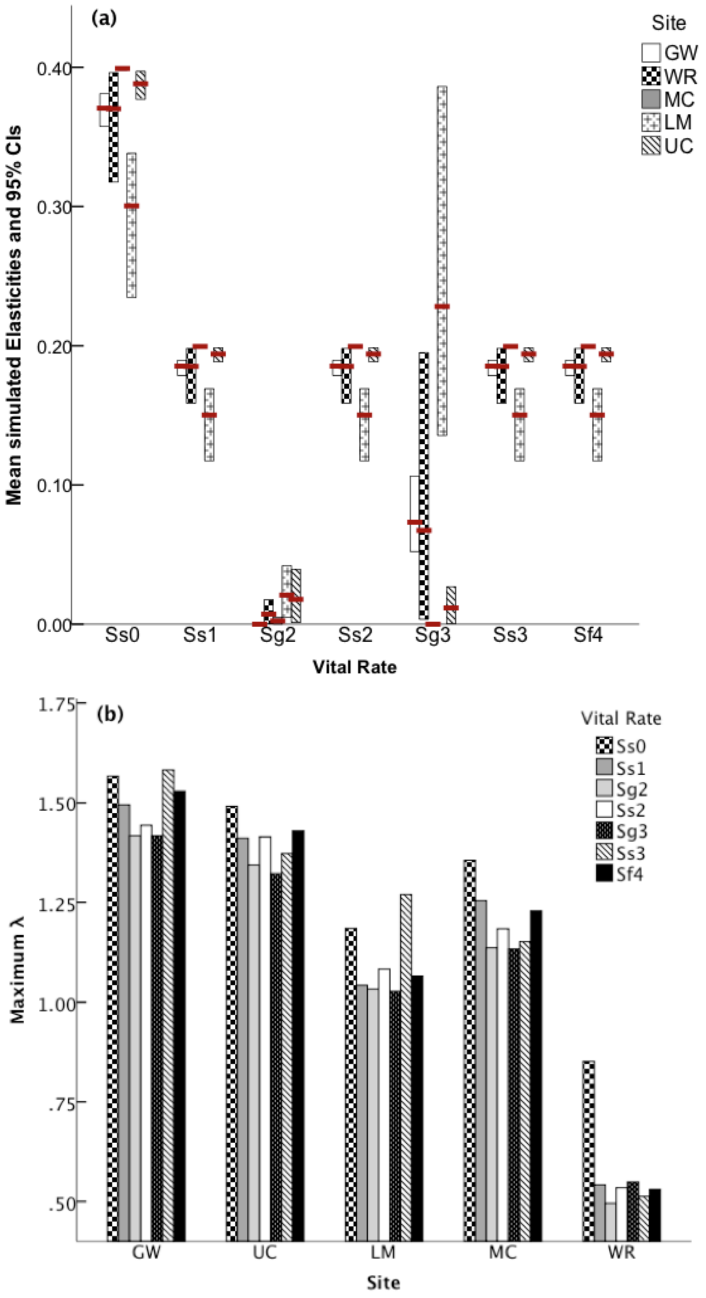

Figure 4.3a. Elasticities of each vital rate as they relate to population growth rates (λ) for each population. Black dashes represent mean elasticities and bars represent the 95% confidence intervals. **b.** The maximum possible population growth rate (λ) obtained when maximizing each vital rate, for each site. See text for vital rate meanings.

Sensitivity to management effects

The simulated management strategies had positive effects on the growth rates of all populations, indicated by the large, positive sensitivity and elasticity values of *h*, the management scalar (Fig. 4.4). Increasing the amount of bare ground resulted in larger population growth rates for all populations compared to the status quo (Fig. 4.4). Proposed slowing of bicycle speed also resulted in increased growth rate of all applicable populations, albeit by a smaller magnitude than increasing bare ground, and only slightly for WR (Fig. 4.4).

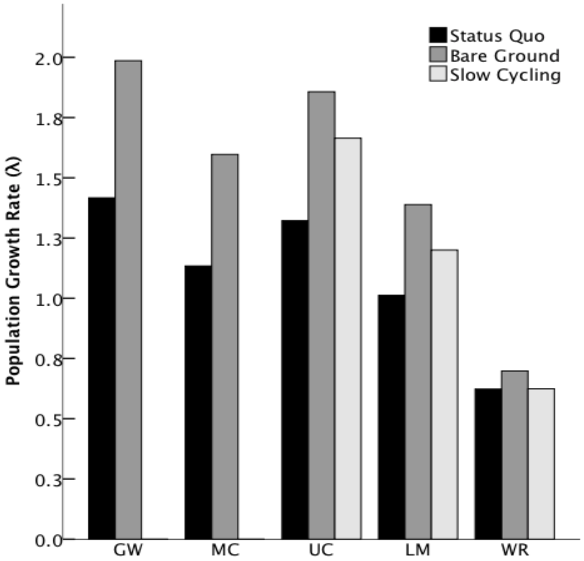

Figure 4.4. Population growth rates for all populations with current management (Status Quo (λ_1)), with increased bare ground, and with slower cycling where recreation is permitted. Sensitivities (and elasticities) for bare ground *h* are: GW 1.81 (1.19); MC 1.47 (1.20); UC 1.70 (1.19); LM 1.22 (1.14); WR 0.639 (1.19). Sensitivities (and elasticities) for slow cycling *h* are: LM 0.423 (0.458); WR 0.275 (0.572); UC 0.745 (0.582).

Metapopulation Dynamics

The Pearson correlation analysis revealed that while vital rates were largely correlated among sites, Ss1, Ss2, and Ss3 were asynchronous between LM and all other sites, WR and UC, MC and GW, and MC and LM, respectively.

The simulated metapopulation growth rate ranged from 1.2935 to 1.6282 and the quasi-extinction probability was zero for all simulations containing the GW, MC, and UC populations. Since all combinations of sites that included GW, UC, and MC had a positive population growth rate and a zero chance of quasi-extinction at any threshold with no migration we did not simulate migration including these sites because migration only acts to decrease the risk of extinction, with our assumption of no negative density dependence.

The maximum population growth rate and probability of quasi-extinction for WR and LM in 100 years, assuming 10 individuals in each stage and no migration, was 0.9396 and 0.5160, respectively (Fig. 4.5). Assuming 2% migration, or one per 50 adult females migrate between the two sites, population growth was 1.0131 with quasi-extinction probability reduced to 0.4880 in 100 years; for 4% migration, the growth rate was 1.0115 and quasi-extinction probability 0.4640 in 100 years; for 10% migration, the growth rate was 1.0133 and quasi-extinction probability 0.4320 in 100 years (Fig. 4.5). Thus, migration increased the population growth rate for WR and LM to $\lambda>1$and reduced the quasi-extinction probability by 5-10%.

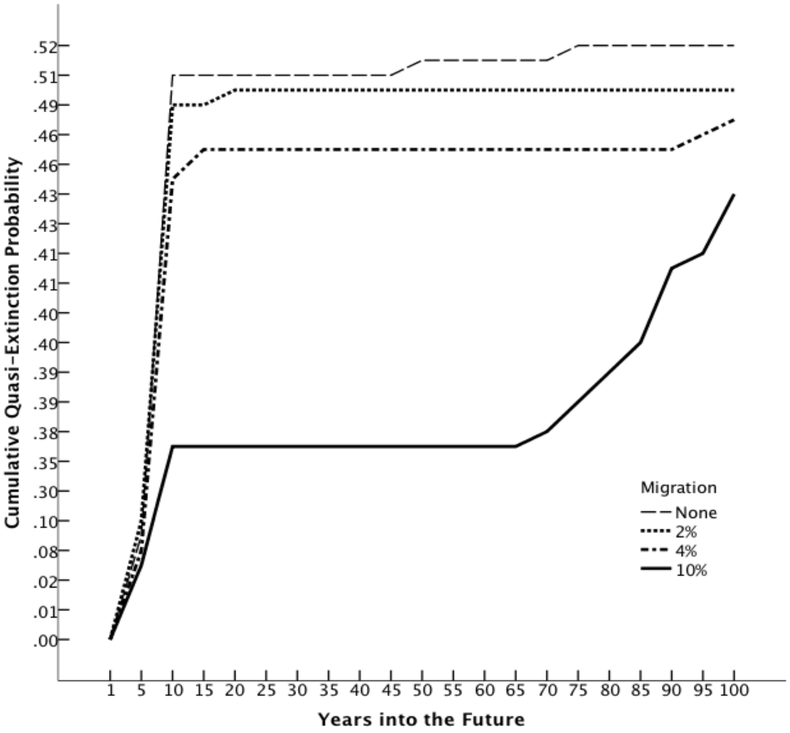

Figure 4.5. Cumulative quasi-extinction probability (set at ten individuals per stage class) for WR and LM populations combined with different migration scenarios.

Discussion

The endangered Ohlone tiger beetle represents the fragmented status of many threatened species for which coordinated, scientifically based and data driven management is desperately needed. By understanding population growth between and among populations as well as the effect of management strategies, we were able to evaluate the consequences of conservation actions on the recovery of *C. ohlone*.

Environmental and demographic stochasticity did not appear to be important factors of *C. ohlone* population growth, as matrix elements were not highly variable among years, Tuljakurpur's approximation fell within the narrow confidence intervals of the stochastic population growth, and we found no evidence of a density-dependent effect on larval survival. Despite these findings, environmental stochasticity should not be ignored as we only have three years of data, which is perhaps not enough to predict insect population fluctuations (Schultz and Hammond 2003). In addition, the impact of environmental stochasticity on variable population growth will increase as global warming continues to alter climate patterns around the world (Brook et al. 2008).

The stochastic projection matrices revealed some large differences in growth rates among *C. ohlone* populations. GW had the highest growth rate, yet since it is the most physically isolated site, metapopulation theory would predict it to be at high risk of extirpation (Hanski 1999). While several studies show that metapopulation theory is useful in explaining some patterns of extinction, many show that local scale, within patch, habitat characteristics are important for the conservation of insect species (Thomas et al. 2001, Fleishman et al. 2002, Collinge et al. 2003, Heisswolf et al. 2009, Hodgson et al. 2009, Poyry et al. 2009, Beyer and Schultz 2010). GW is grazed by horses year round and has a high percentage of bare ground and low standing vegetation. GW is also managed by the Land Trust of Santa Cruz County, which employs biological consultants to improve the land specifically for *C. ohlone* viability. Thus, GW is an example of how extinction risk of isolated patches can be reduced with increased habitat quality and management.

WR was the only population that had a negative population growth and high extinction risk across all projected models. While it seems that the reason for this was the low egg survivorship, all WR vital rates were generally lower than for other populations. Indeed, if we substitute the egg survivorship and mean fecundity values from LM (which is mostly likely a high estimate for true WR values) into the WR population projection matrix, the growth rate remains below 1.0 at 0.97. In contrast to GW, WR represented how a more connected habitat patch can become non-viable as habitat quality declines, suggesting that increased habitat management in WR could increase *C. ohlone* viability.

The sensitivity analyses revealed that, for all populations, the population growth rate was most sensitive to egg survivorship. The wide confidence intervals around the egg survivorship estimates for LM and WR indicated a greater uncertainty in those values and while we recognize the limited predictive power of a single estimate of egg survivorship, our estimates fall well within those published for tiger beetles (Hoback et al. 2000). The LM population growth rate was also highly sensitive to the growth of third instar larvae. This is important for viability in that larvae will prolong their pupation without sufficient food, increasing their risk of mortality (Knisley and Schultz 1997, Pearson and Vogler 2001). As the LM population growth rate was near 1.0, management that augments food availability, such as increased bare ground, may become important for population viability.

Increasing bare ground and requiring cyclists to slow down in *C. ohlone* habitat created large, positive changes in all populations. We based our assumed increase of 1.5 times the number of eggs laid on our previous study (Cornelisse et al. 2013), which follows that as little as 9-m^2 of bare ground per site would be beneficial. Similarly but less so, management that requires a reduction in bicycle speed increased population growth rates in the three sites that allow bicycle recreation. We assumed that this management action only affected fecundity because recreation mainly affects the mobile adult stage. Our elasticity results showed that reducing bicycle speed to 8-12 kph increased population growth by 42-58%.

We found that any amount of migration between *all* sites ensured that the *C. ohlone* metapopulation would not go extinct within the next 100 years, assuming current management remains in effect. Despite the fact that vital rates were generally asynchronous among sites regardless of the distance separating them, *C. ohlone* dispersal dynamics are unknown and because remaining patches are fragmented, we are unsure if *C. ohlone* retains colonization ability. When we removed the populations with high growth rates, GW, UC, and MC, equivalent to no migration between these populations and the other two, WR and LM had a 35% probability of quasi-extinction in the next 10 years, even with a high degree of migration. WR and LM are in a habitat cluster that has lost two populations in recent years (Knisley and Arnold 2004, Cooper 2009); this increased isolation could be contributing to the non-viable status of WR and low growth rate in LM via inbreeding depression. Fortunately, the coastal prairie habitat between these two sites is protected but management efforts focused on augmenting habitat quality in extirpated patches would be a necessary first step in promoting recolonization and maintaining *C. ohlone* viability in this area.

Cicindela ohlone declined across the landscape due to habitat destruction prior to its listing as an endangered species; however, as is the case with many threatened species, protection of occupied habitat alone is not enough to prevent its extinction (Fuller et al. 2010, Laurance et al. 2012). At the site level, management actions that maintain bare ground and reduce incidental mortality of *C. ohlone* must be in place to maintain stable populations (Knisley 2011, Cornelisse et al. 2013), whereas at a landscape level both recently extirpated sites and potential coast prairie habitat should be managed to maintain suitable *C. ohlone* habitat for future colonizations. We are currently analyzing the potential for unoccupied sites to contribute to *C. ohlone* habitat and range expansion and the results of this population viability analysis clearly illustrate that *C. ohlone* has four viable populations that, with habitat management, could recolonize extirpated sites and avoid species extinction.

Appendices

Appendix 1. Soils Factors

pH
Total Exchange Capacity (meq/100 g)
Bulk Density
Organic Matter (%)
Estimated Nitrogen Release (#'s N/acre)
S (ppm)
P (mg/kg)
Bray II P (mg/kg)
Ca (mg/kg)
Mg (mg/kg)
K (mg/kg)
Na (mg/kg)
Ca (%)
Mg (%)
K (%)
Na (%)
Other Bases (%)
H (%)
B (mg/kg)
Fe (mg/kg)
Mn (mg/kg)
Cu (mg/kg)
Zn (mg/kg)
Al (mg/kg)

Appendix 2. Vegetation species found in the Coastal Terrace Prairies, their source of origin, and incidence in sites in which *Cicindela ohlone* is present (P), extirpated (E), and not historically known, or absent (A).

Species	Origin	Guild	Life History	P	E	A
Anagallis arvensis	Nonnative	Forb	Annual	X	X	X
Aphanes occidentalis	Native	Forb	Perennial	X		X
Aira caryophyllea	Nonnative	Graminoid	Annual	X		X
Avena barbata	Nonnative	Graminoid	Annual	X	X	X
Brachypodium distachyon	Nonnative	Graminoid	Annual	X	X	X
Briza maxima	Nonnative	Graminoid	Annual	X	X	X
Briza minor	Nonnative	Graminoid	Annual	X	X	X
Bromus diandrus	Nonnative	Graminoid	Annual	X	X	X
Bromus hordeaceus	Nonnative	Graminoid	Annual	X	X	X
Carex densa	Native	Graminoid	Perennial	X	X	X
Carduus pycnocephalus	Nonnative	Forb	Annual	X	X	X
Chlorogalum pomeridianum	Native	Forb	Perennial	X	X	X
Convolvulus arvensis	Nonnative	Forb	Annual		X	X
Danthonia californica	Native	Graminoid	Perennial	X	X	X
Deschampsia cespitosa	Native	Graminoid	Perennial	X	X	
Dodecatheon clevelandii	Native	Forb	Perennial	X		
Erodium botrys	Nonnative	Forb	Annual	X	X	X
Eryngium armatum	Native	Forb	Annual	X	X	X
Eschscholzia californica	Native	Forb	Annual	X		X
Festuca myuros	Nonnative	Graminoid	Annual	X	X	X
Festuca perennis	Nonnative	Graminoid	Annual	X	X	X
Gastridium phleoides	Nonnative	Graminoid	Annual			X
Geranium dissectum	Nonnative	Forb	Annual	X	X	X
Holcus lanatus	Nonnative	Graminoid	Perennial	X	X	X
Hypochaeris glabra	Nonnative	Forb	Annual			X
Hypochaeris radicata	Nonnative	Forb	Perennial	X	X	X
Juncus bufonius	Native	Graminoid	Annual	X	X	X
Juncus occidentalis	Native	Graminoid	Perennial	X	X	X
Juncus phaeocephalus	Native	Graminoid	Perennial	X	X	X
Lasthenia californica	Native	Forb	Annual	X		
Leontodon saxatilis	Nonnative	Forb	Perennial		X	X
Linum bienne	Nonnative	Forb	Annual	X	X	X
Logfia gallica	Nonnative	Forb	Annual	X		X
Lupinus nanus	Native	Forb	Annual	X	X	X
Medicago polymorpha	Nonnative	Forb	Annual	X	X	X

Plantago lanceolata	Nonnative	Forb	Annual	X	X	X
Plantago maritima	Native	Forb	Perennial	X		
Poa annua	Nonnative	Graminoid	Annual	X	X	X
Prunella vulgaris	Nonnative	Forb	Perennial	X	X	X
Ranunculus californicus	Native	Forb	Perennial	X	X	X
Raphanus sativus	Nonnative	Forb	Annual			X
Rumex acetosella	Nonnative	Forb	Annual	X	X	X
Sherardia arvensis	Nonnative	Forb	Annual	X	X	X
Silybum marianum	Nonnative	Forb	Perennial		X	
Sisyrinchium idahoense	Native	Graminoid	Perennial		X	
Sisyrinchium bellum	Native	Graminoid	Perennial	X	X	X
Stipa pulchra	Native	Graminoid	Perennial	X	X	X
Trifolium dubium	Nonnative	Forb	Annual	X	X	X
Triteleia hyacinthine	Native	Graminoid	Perennial		X	X
Trifolium macraei	Native	Forb	Annual	X	X	X
Trifolium subterraneum	Nonnative	Forb	Annual	X	X	X
Vicia villosa	Nonnative	Forb	Annual	X	X	X

Appendix 3. Recreation Survey

Please complete this survey to aid in our understanding of recreation needs for Ohlone tiger beetle conservation

1. Purpose of your trip (hiking, biking, etc.): ________________

2. How long have you been recreating in this area? _______________

3. How often do you come to this site? (circle one)

Daily 2-3 times/week Weekly Monthly Few times/year Yearly

4. Have you heard of the Ohlone tiger beetle? Y / N If so, when did you first hear?
____

5. How important is conservation of the Ohlone tiger beetle to you? (circle one)

Unimportant Not very important important Very Important

6. How do you feel recreation affects the Ohlone tiger beetle? (circle one)

Negative effect No effect Positive effect Unsure

7. The following management strategies have been employed or proposed to protect the endangered Ohlone Tiger beetle in its breeding habitat from January through May. Please indicate by checking whether you currently do comply, would comply, or would not comply with the following strategies in beetle habitat:

	Do comply	**Would Comply**	**Would Not Comply**
1. Slow down in beetle habitat	☐	☐	☐
2. Dismount and walk your bike	☐	☐	☐
3. Stay off closed trails and areas	☐	☐	☐
4. Use alternative trails	☐	☐	☐
5. Create/use new trails in grassland	☐	☐	☐

8. Are there other management strategies you can suggest or would support?

____

____

____

9. Other comments/concerns about the Ohlone tiger beetle or recreation in the area?

____

____

____

10. Resident Zip Code: ______________

Please write or circle a response to the following questions for demographic information:

1. Sex: F / M
2. In what year were you born: __________

3. Income: 0-30,00030,000-50,000 50,000-70,000 70,000-100,000 100,000+

4. Highest level of education completed:____________________

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