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Biology and Conservation of *Cicindela ohlone* Freitag and Kavanaugh (Coleoptera: Carabidae: Cicindelinae), the Endangered Ohlone Tiger Beetle. II. Population Ecology of Adults and Larvae and Recommended Monitoring Methods

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Abstract

Population ecological and monitoring results are presented for the endangered Ohlone tiger beetle, *Cicindela ohlone* Freitag and Kavanaugh, at six study sites near Santa Cruz, CA, covering the years 2000 through 2017. Mapping of larval burrows and nearest neighbor analysis found a highly clumped distribution pattern. The numbers of both larvae and adults exhibited substantial year-to-year fluctuations. The range of adult seasonal activity varied over the years, with extreme dates from 13 January to 21 May. Daily, study period, and generation population sizes of adults were estimated using three absolute population estimation methods: capture-recapture; frequency of capture; and repeated counts along fixed belt transect routes throughout the entire adult activity period. In a 12-day capture-recapture study, daily population estimates using four different models ranged from 35 to 146 adults, with estimated average life spans of 3.0–7.2 days. Estimated adult generation sizes using belt transect counts over the 18 years ranged from 136 to 1,025 at Glenwood, 139 to 1,000 at Marshall Field, 284 to 944 at Grey Whale, and 504 to 1,808 at Moore Creek. Temporal trends in generation sizes at these four sites were associated with land use and habitat management activities, including grazing, controlled burns, and trail use by hikers and bikers, plus annual and seasonal precipitation amounts. Results of these studies suggest that both larvae and adults should be monitored as part of adaptive management programs specifically designed for this endangered beetle.

Key Words: insect conservation, population monitoring, capture-recapture, transect counts, spatial distribution

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Population size estimates from different generations over time are frequently used to measure the success of adaptive management efforts to conserve and recover endangered insects (Samways 1994; New 1997; Samways *et al.* 2010). In addition, basic data on a population's demographics, such as sex ratio, survivorship, dispersal, and spatial distribution of life stages within the preferred habitat, provide insights on an insect's habitat requirements and utilization, as well as factors that regulate its population numbers (New 2010; Cornelisse *et al.* 2013a; Henderson and Southwood 2016). The information derived from population monitoring may also provide early warning signs of population declines or extirpation.

Long-term population monitoring should be based on standardized census methods that are easy to execute and require minimal time and expense to complete (New 1998, 2009). Monitoring should be repeated at regular intervals and with appropriate sampling effort to accurately estimate population numbers for detecting short-term changes and long-term trends in the population (Thompson *et al.* 1998; Conrad *et al.* 2007; Samways *et al.* 2010). However, many current conservation management and recovery programs for endangered insects do not adequately census populations in a manner that accurately monitors their status and detects long-term trends to properly guide adaptive management efforts.

In less than a decade after the Ohlone tiger beetle, *Cicindela ohlone* Freitag and Kavanaugh, was described (Freitag *et al.* 1993), it was recognized as an endangered species by the US Fish and Wildlife Service (2001). Since that time, there have been several studies to better understand the ecology of this species and inform management for its conservation. In Part 1 of this series, we (Knisley and

Arnold 2013) documented the Ohlone tiger beetle's historical geographic range and its extirpation at several sites, reported results of field and laboratory studies on survivorship, identified existing threats, and suggested management strategies to improve habitat quality to benefit the beetle. Other important studies included an examination of the habitat characteristics of occupied and extirpated sites (Arnold *et al.* 2012a, b; Cornelisse 2013) and how creation of artificial bare patches can be a useful management strategy by providing new habitat (Cornelisse *et al.* 2013b). Cornelisse *et al.* (2013a) identified factors affecting the survival and viability of existing populations by using simulation models based on short-term population data sets.

In this paper, we present the results of long-term population studies conducted on adult and larval life stages over an 18-year period from 2000 to 2017 at six study sites in Santa Cruz County, CA. Although several remaining occupied sites have been protected from development, they require continued management to maintain suitable habitat conditions favorable to support the Ohlone tiger beetle. It is also essential to identify the most appropriate methods for population monitoring of the beetle at these sites. For these reasons, we evaluated a variety of ecological census techniques to assist resource managers in deciding which method(s) best satisfy their particular Ohlone tiger beetle population monitoring needs and to measure the success of the adaptive management activities at remaining sites under their care. Daily, study period, and generation population sizes of adult beetles were estimated, as well as their survival rates, sex ratios, and dispersal parameters. Larval burrows were inventoried and mapped at selected study sites to determine their spatial distribution patterns.

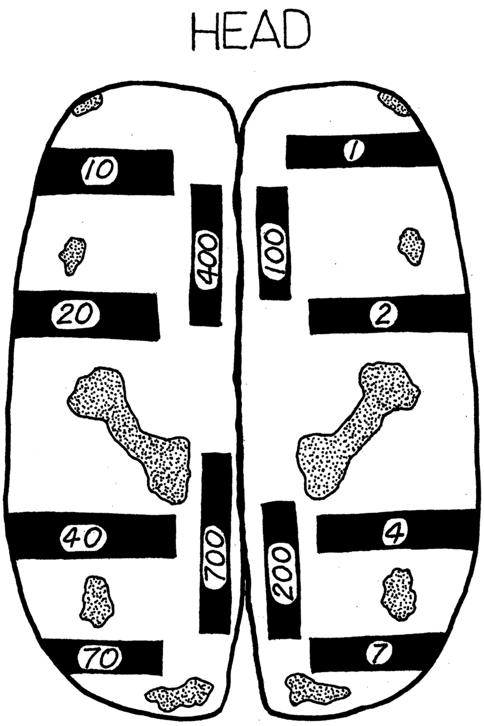

Fig. 1. Marking scheme for individual identification of Ohlone tiger beetle adults used during the capture-recapture and frequency of capture studies. Some variation in the maculations exists. Numbers on the elytra represent the positions for marking each beetle with a unique identification number. Marks applied to single or multiple locations uniquely identify each marked beetle. For example, beetle #1 would have a mark at the #1 position, beetle #12 would have marks at the #2 and #10 locations, and beetle #147 would have marks at the #7, #40, and #100 locations.

Material and Methods

Census estimates of adult population numbers were obtained using three absolute population estimation techniques: capture-recapture; frequency of capture; and repeated counts along belt transect routes throughout the entire adult season. Nearest neighbor statistics were used to determine the spatial distribution pattern of active larval burrows.

Capture-Recapture Studies. During 2002, the first author conducted capture-recapture (also commonly referred to as "mark-recapture" or "mark-release-recapture") studies between 21 February and 4 March at two Ohlone tiger beetle sites that no longer support the species, Santa Cruz Gardens (site #1 in fig. 1 of Knisley and Arnold 2013) and Poliski-Gross (site #13). The Ohlone tiger beetle was studied at Santa Cruz Gardens because it supported an isolated population and at Poliski-Gross because it is close to other occupied Ohlone tiger beetle sites and probably functions as a deme or local population of a larger meta-population of the beetle.

Individual adult beetles were uniquely marked upon their initial capture on the dorsal portion of the elytra with acrylic paint pens (Sharpie, formerly Sanford, Downers Grove, IL) according to the numerical marking code (Fig. 1) of Watt *et al.* (1977). Pen tips were modified from blunt to pointed to minimize the amount of paint applied, which enabled the application of small marks on the elytra and expedited their drying time. All captured beetles at a particular study site were marked with the same paint color, but different paint colors were used for different study sites to readily detect dispersing adults. Manly's (1971) test was used to determine whether capturing and marking adversely affected survival of the marked beetles. This test was applied to beetles initially captured and marked during the first eight days of the capture-recapture study. If the chances of dying are increased by the acts of capture and marking, then the marked individuals will be under-represented in subsequent samples. The CAPTABLE program (Gullette and Arnold 2009) performed the calculations for Manly's test.

Beetles were netted, marked, and released immediately at the point of capture or recapture on eight of the 12 days. Inclement weather prevented sampling on the other four days at both sites. A mapping-grade Trimble GPS unit (Trimble, Inc., Sunnyvale, CA) was used to obtain UTM coordinates for all capture and recapture events. In a few instances, marks of re-sighted individuals could be accurately read without re-netting the beetles, which minimized subsequent handling. The assigned identification number, date, sex, behavior, time, physical condition, and UTM coordinates were recorded in the data dictionary of the GPS unit for the initial capture and all recapture or re-sighting events for every individual. All positional coordinates were differentially corrected.

Every capture-recapture model has inherent assumptions, all of which may not be satisfied during a particular census study, thus it is beneficial to analyze data sets with more than one model to compare estimated population parameters and determine which models provide the most similar estimates. For this reason, daily population sizes were estimated using the Bailey's Triple Catch (1951), Fisher-Ford (1947), Jolly-Seber (Jolly 1965; Seber 1965), and Manly-Parr (1968) statistical models that have frequently been used to analyze populations of other insects (Henderson and Southwood 2016). Both the Bailey's and Fisher-Ford methods are deterministic methods, meaning that they assume a constant survival rate, which may be observed in short-lived insects or during short sampling periods. Also, Bailey's method requires only three sampling occasions to estimate several population parameters, while Fisher-Ford is a robust method for small samples. The Jolly-Seber and Manly-Parr methods are stochastic, meaning that survival rate is treated as probabilistic over time, but these methods require more data and sampling occasions, plus their estimated parameters are more reliable when recapture rates exceed 25%. Manly-Parr is preferable when age-dependent mortality may occur.

Average daily vagility statistics (Scott 1975) were calculated for recaptured individuals. Using the positional coordinates for each capture and recapture event, minimum straight-line movements (d_i) in meters and time (t_i) in days between captures i and ($i + 1$) were determined. The CAPTABLE program (Gullette and Arnold 2009) was used to estimate population parameters and for calculation of the vagility statistics.

Frequency of Capture Methods. Craig's (1953) and Eberhardt's (1969) frequency of capture methods were used to estimate population numbers for the same 12-day study period as used for the capture-recapture studies. Both methods utilize data on the capture history of each marked individual to estimate the frequencies of capture for individuals in the population and to estimate its population size for the entire 12-day study period. Craig's method assumes that the capture frequencies follow a Poisson distribution, while Eberhardt's method utilizes a geometric distribution. Both methods assume that the population is closed (*i.e.*, no births, deaths, immigration, or emigration during the study period) and that each individual has a constant probability of capture. These analyses were performed by the CAPTABLE program (Gullette and Arnold 2009).

Belt Transect Counts and Adult Generation Size Estimates. Repeated counts of adult Ohlone tiger beetles observed along fixed belt transect routes were conducted throughout the entire adult season at four study sites as illustrated in fig. 1 of Knisley and Arnold (2013):

a) from 2000 to 2017 at Glenwood Open Space Preserve (site #2);
b) from 2000 to 2017 at Marshall Field (sites #6 and #16);
c) from 2001 to 2017 at Moore Creek Open Space (site #3); and
d) from 2002 to 2017 at Grey Whale portion of Wilder Ranch State Park (site #14).

Existing dirt trails at each study site were used as fixed routes for the belt transects. We walked slowly along the trails to observe and tally the numbers of adult Ohlone tiger beetles within an approximately 5 m wide area on either side of the center line of a transect, for a total observation zone of about 10 m for each belt transect. This observation zone included the dirt trail, its sparsely vegetated shoulders, and more densely vegetated grassland beyond the trail shoulders. Individual trail widths varied from year to year along the transect route at a particular site as vegetation colonized the trail or more bare ground was created by trail use. Weather permitting, counts were performed at approximately weekly intervals throughout the Ohlone tiger beetle's entire adult season at all study sites. Counts were performed at different times of day at each site, but only when temperatures were warm enough for adult activity ($\geq$16° C).

Since the Ohlone tiger beetle is univoltine, annual adult population numbers or generation size were estimated during each year and at each study site using the methodology of Holmes and Arnold (2015). This method combines the frequencies of observed life spans (*i.e.*, days in residence) of marked individuals during a single capture-recapture study with the weekly transect counts to estimate the population size and its standard error for an entire adult generation.

Population Trends. Although there are numerous statistical methods for determining trends in time-series data such as Ohlone tiger beetle adult generation size estimates, most of these require substantially more years of data ($n \geq 30$) than are currently available from any particular Ohlone tiger beetle site. For short-term data sets, simple linear regression has been demonstrated as a powerful technique to detect trends (Hatfield *et al.* 1996; Thompson *et al.* 1998) when compared to other parametric and non-parametric statistical methods for analysis of time series. Thus, generation estimates were log transformed and simple linear regression analyses were performed to determine temporal trends across monitoring years for each site. Use of log transformed data instead of the raw estimates reduced the size of the variance and tended to equalize variances among the generation sizes (Elzinga *et al.* 2001). The slope of the linear regression equation provided an estimate of a population's trend over time. A slope <0 indicates a population decline over the entire period of study, and a slope >0 indicates a population increase, whereas a slope that is not statistically different from 0 indicates that the population has been stable. The null hypothesis is that there is no trend.

Spatial Distribution of Larvae. From 2003 to 2017, larval burrows were mapped annually during June or July at the Glenwood and Marshall Field study sites. The on-trail areas used for the adult sampling and off-trail areas were surveyed. Although our surveys may not have detected all burrows present, our methodology and areas searched were the same in all years, so comparison of annual results should be valid. In addition, the diameter of each burrow and whether it was active, abandoned, or plugged was recorded. At that time of the year, the majority of larvae are third instars. Positional coordinates for each larval burrow were obtained using the aforementioned Trimble GPS unit. Coordinates were differentially corrected to improve their positional accuracy and then transferred to a geographic information system, ArcGIS version 10.5 (ESRI, Redlands, CA), to calculate the nearest neighbor statistics and determine the spatial dispersion pattern of larval burrows for each year at both study sites.

Results and Discussion

Capture-Recapture. At Santa Cruz Gardens, 168 adults (103 males and 65 females, sex ratio = 1.58:1.00) were marked during the 12-day study period. Seventy-four of these individuals were recaptured at least once (44.0% recapture rate), with a mean of 1.77 recaptures throughout the study. Daily population estimates generated by the stochastic Manly-Parr and Jolly-Seber models ranged from 56 to 113 adults, while estimates from the deterministic Fisher-Ford and Bailey's Triple Catch models ranged from 35 to 120 and from 56 to 146 adults, respectively (Table 1). Manly's test determined that capturing and marking had no adverse effect on survival of the adult beetles ($\chi^2 = 12.81$, df = 7, $P \approx 0.15$).

A total of 165 adults (97 males and 68 females, sex ratio = 1.43:1.00) were marked at Poliski-Gross. Only two were recaptured or re-sighted, both at the neighboring Moore Creek site (#3 in fig. 1 in Knisley and Arnold 2013), which suggests that this site is actually part of a larger Ohlone tiger

Table 1. Estimated daily Ohlone tiger beetle population numbers and standard errors for the study period of 21 February through 4 March 2002 at the Santa Cruz Gardens study site.

	Daily population estimates and standard errors (** = unavailable)			
Sampling Date	**Bailey's Triple Catch**	**Fisher-Ford**	**Manly-Parr**	**Jolly-Seber**
21 February	56.1 ± 28.8	**	**	**
22 February	**	**	**	**
23 February	98.4 ± 33.6	34.7	57.5 ± 30.1	67.1 ± 33.7
24 February	145.6 ± 42.0	98.3	55.7 ± 10.5	60.1 ± 13.2
25 February	**	**	**	**
26 February	144.0 ± 37.9	98.8	89.3 ± 17.2	93.0 ± 17.5
27 February	**	**	**	**
28 February	134.8 ± 31.9	119.7	106.4 ± 21.2	112.5 ± 21.7
1 March	**	**	**	**
2 March	118.4 ± 27.4	93.2	87.8 ± 11.4	92.9 ± 12.9
3 March	**	120.3	82.0 ± 15.9	83.0 ± 15.2
4 March	**	104.4	**	**

beetle population than was sampled during our capture-recapture study. Because the recapture rate was so small, no population parameters could be accurately estimated.

Hori (1982) found that the adult sex ratio for *Cicindela chinensis japonica* Thunberg was closer to 1:1, different than what we observed for the Ohlone tiger beetle. His capture-recapture studies were conducted throughout the full adult activity period. In contrast, our capture-recapture studies of the Ohlone tiger beetle only included the first two weeks of its adult activity period, which is generally about 90 days in duration. Like many insects, the observed protandry of male Ohlone tiger beetles during the early portion of the adult activity period insures that they are plentiful before most females emerge. Consequently, the sex ratio of the Ohlone tiger beetle is probably closer to 1:1 throughout its entire adult generation.

Estimated daily survival rates (φ_i) using the different estimation techniques and capture-recapture models were similar, ranging from 0.717, which is the slope of the fitted regression line for the recapture decay plot in Fig. 2, to 0.868 using the Fisher-Ford model, which assumes a constant daily survival rate. Estimated φ_i generated from stochastic capture-recapture models of Manly-Parr and Jolly-Seber ranged from 0.769 to 0.870. These daily survival rates indicate that the average adult lifespan ranged from 3.0 to 7.2 days. However, the maximum observed lifespan based on the capture-histories for all marked individuals was 12 days (n = 2), and the average time between handling events was 6.1 days. Since this study was conducted at the beginning of the Ohlone tiger beetle's adult season, when nightly and daily temperatures are lower than later in the beetle's adult season, estimated lifespans for the early portion of the adult season may be lower than during the warmer mid-season and late-season portions of the adult activity period. Hori (1982) conducted capture-recapture studies of *C. chinensis japonica* for seven years and estimated survival rates between 0.56 and 0.81, which are comparable to our Ohlone tiger beetle estimates.

At Santa Cruz Gardens, 39 males and 35 females were recaptured at least once, all at this study site, which is approximately 8.5 km from the nearest occupied Ohlone tiger beetle location. Distances moved between consecutive capture and recapture events (d_i of Scott 1975) ranged 9–180 m for males over spans of 1–12 days, while distances for females ranged 8–148 m over spans of 1–6 days (Fig. 3). About 92% of all movements for either sex between consecutive handling events were 100 m or less. The cumulative distances (D_i of Scott 1975) moved throughout all capture and recapture events by individual adult beetles ranged from 299 m for males (1–12 days) to 316 m for females (1–8 days).

In contrast, the only two recaptured adults at Poliski-Gross dispersed to neighboring Moore Creek, 402 m and 485 m from where they were initially captured. Knisley and Hill (unpublished data, cited in Knisley and Schultz 1997) observed individuals of *Habroscelimorpha dorsalis dorsalis* Say that moved distances upwards of 25 km, but studies with *Cicindela albissima* Rumpp found most adults moved only several hundred meters (Knisley and Hill 2001). We have also observed Ohlone tiger beetle adults quickly colonize disturbed patches of soil created by rooting behavior of feral pigs, ground squirrels, and anthropogenic

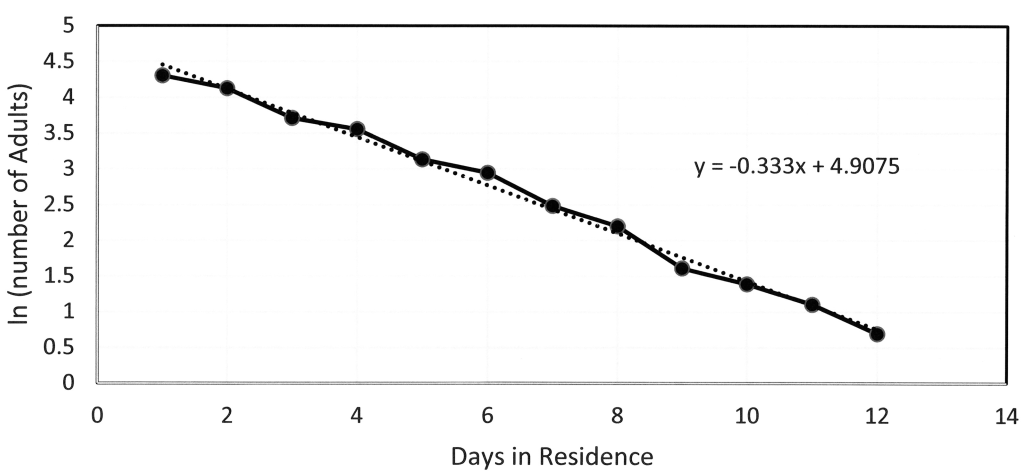

Fig. 2. Recapture decay plot of observed Ohlone tiger beetle adult lifespans (*i.e.*, residence) and fitted trend line (dotted line).

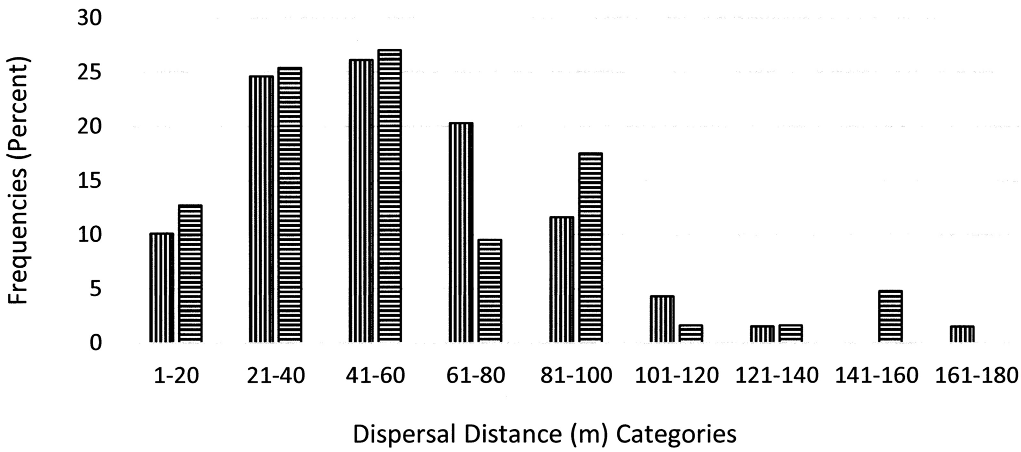

Fig. 3. Frequency of observed dispersal distances (m) by Ohlone tiger beetle males (bars with vertical lines) and females (bars with horizontal lines).

activities that are separated by several hundred meters from the nearest occupied beetle habitat. Other studies found adults also moved to and oviposited in manually created bare patches in dense vegetation up to 100 m from adult concentrations (Knisley and Arnold 2004; Cornelisse *et al.* 2013b). It is likely that Ohlone tiger beetle adults probably possess the ability to disperse even farther distances than were detected during our capture-recapture studies.

Frequency of Capture. The estimated population size at Santa Cruz Gardens during the 12-day study period was 209 using Craig's method and 385 using the Eberhardt method. However, the frequency of capture population size estimates may not be reliable since emergence (births) and deaths of adult beetles occurred during the study period, which violated the assumption of a closed population. Capture-recapture methods assume that emergences and deaths occur, but to properly compare the population sizes estimated by frequency of capture to those estimated by the capture-recapture methods, the daily capture-recapture size estimates must be converted to population size estimates for the entire 12-day study period. This calculation was performed by CAPTABLE using the sums of the daily capture-recapture population estimates multiplied by the average daily survival rate as determined by each of the statistical models. Estimated population sizes for this 12-day period ranged from a low of 372 using the Manly-Parr model to a high of 581 using Fisher-Ford, while estimates were 442 using Jolly-Seber and 500 using Bailey's Triple Catch.

Belt Transect Counts and Adult Generation Size Estimates. A total of 69 annual data sets, which included 26,352 adult observations for the four Ohlone tiger beetle monitoring sites, were analyzed. Using the Holmes and Arnold (2015) method, a curve was fitted to the weekly transect counts for an entire adult generation at a particular study site. In many years, the Ohlone tiger beetle's population curve resembles a triangle (Fig. 4a) with a single peak in numbers, as was the case at Glenwood in 2016. However, seasonal weather conditions or other factors may cause more than one peak in adult numbers to occur, as seen in 2017 for the Glenwood population (Fig. 4b).

Adults normally become active during the first warm spell of the winter rainy season. Observed starting dates for initial adult activity ranged from 13 January to 1 March, while ending dates ranged from 5 April to 21 May 21. In some years, an early- or late-emerging adult was observed several days before or after this seasonal range. Duration of the adult activity period ranged from 59 to 112 days ($\bar{x}$ = 90) but varied considerably among sites and years. For example, Ohlone tiger beetle populations at sites closer to the ocean frequently remained active 7–14 days longer than populations at inland or higher elevation locations. The observed peak in population numbers ranged from 12 to 53 days ($\bar{x}$ = 32) after the start of the adult activity period.

Estimated adult generation sizes ranged 136–1,025 ($\bar{x}$ = 392) at Glenwood, 139–1,000 ($\bar{x}$ = 387) at Marshall Field, 284–944 ($\bar{x}$ = 660) at Grey Whale, and 504–1,808 ($\bar{x}$ = 985) at Moore Creek (Fig. 5). Substantial fluctuations in generation sizes occurred at all four sites. The multi-year average for each study site is illustrated as a dashed horizontal line (Fig. 5). Only 39% of the 69 estimated generation sizes exceeded the multi-year average at these sites. Long-term trends in the time series of log-transformed generation sizes indicated a substantial

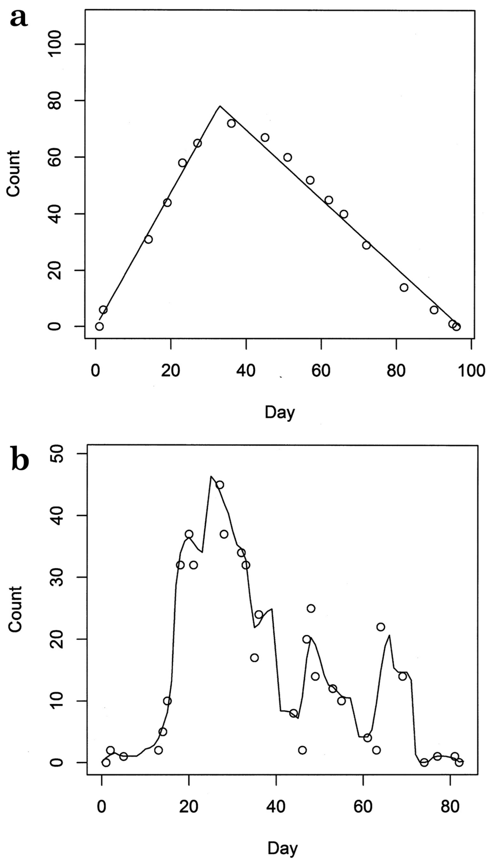

Fig. 4. Population curves for adult Ohlone tiger beetle generations at Glenwood, Santa Cruz Co., CA. a) Triangular model in 2016, b) Multi-peak model in 2017.

decline at Marshall Field (r^2 = 0.80), while modest increases occurred at Glenwood (r^2 = 0.37), Grey Whale (r^2 = 0.38), and Moore Creek (r^2 = 0.62).

Population Trends. Our observations of these temporal trends in generation sizes suggest they are associated with land use and habitat management activities, plus annual and seasonal precipitation amounts. During the early years of our population monitoring, we infrequently encountered users on the Chinquapin Trail, which traverses the Grey Whale Ohlone tiger beetle site, and they were primarily hikers and equestrians. However, trail usage noticeably increased in subsequent years, especially by mountain bikers and joggers, along with students and staff commuting on their bicycles to the nearby Santa Cruz campus of the University of California. This increased usage likely impacted Ohlone tiger beetle life stages on this dirt trail. We observed crushed Ohlone tiger beetle adults, eggs (whose locations were previously identified), and first instars. While Cornelisse and Duane (2013) noted that recreational trail use disrupted Ohlone tiger beetle adult foraging and mating behaviors, we also observed disruption of thermoregulation and oviposition. Beginning in 2003, one of two parallel legs of this trail at Grey Whale was closed in alternate years to reduce these impacts. This management practice enabled Ohlone tiger beetle generation sizes to increase in most subsequent years compared to their estimated numbers during early years of our monitoring (Fig. 5).

In contrast, Ohlone tiger beetle generation sizes were higher during the first five years of our monitoring at Marshall Field (Fig. 5), when local fire agencies used it as a training site for wildland fire-fighting. Controlled burns occurred in most of those years, resulting in less woody vegetation colonizing the coastal prairie, minimal accumulated thatch, and increased bare or sparsely vegetated ground along the dirt trails and in widely scattered patches throughout the coastal prairie. This combination of factors maintained favorable habitat that supported high beetle numbers. Unfortunately, the local fire agencies subsequently discontinued the wildland fire-fighting training events, further reducing the amount of off-trail bare or sparsely-vegetated ground in the prairie, conditions that are unfavorable to the Ohlone tiger beetle.

During this same period, increased trail usage at Marshall Field led to covering of selected primary trails with gravel to make them "all-weather", which reduced available bare ground in on-trail areas that had previously been occupied by the Ohlone tiger beetle. Observed impacts to Ohlone tiger beetle life stages led to closures of secondary trails during the winter and early spring. The control of feral pigs, whose rooting behavior created patches of bare ground, further reduced off-trail areas that could be occupied by the Ohlone tiger beetle. Beetles ceased to be observed at two nearby Ohlone tiger beetle demes (#4 and #15, fig. 1 of Knisley and Arnold 2013), which increased the inter-deme distances for dispersing adults. Thus, this combination of factors is likely responsible for the substantial decline in generation sizes observed from 2004 to 2006. In the absence of other habitat management, these secondary trails were reopened to bikers and other trail users to control the colonizing vegetation, and Ohlone tiger beetle generation numbers increased slightly from 2007 to 2012. Observations of crushed Ohlone tiger beetle adults ranged from 0.2% of the estimated generation size in 2003 to 4.4% in 2013, thus this mortality factor along with the reduced numbers of larvae and area occupied by larval burrows (see next section) may have contributed to the observed decline from 2013 to 2017.

During this same 18-year period, Ohlone tiger beetle numbers at Glenwood (Fig. 5) generally

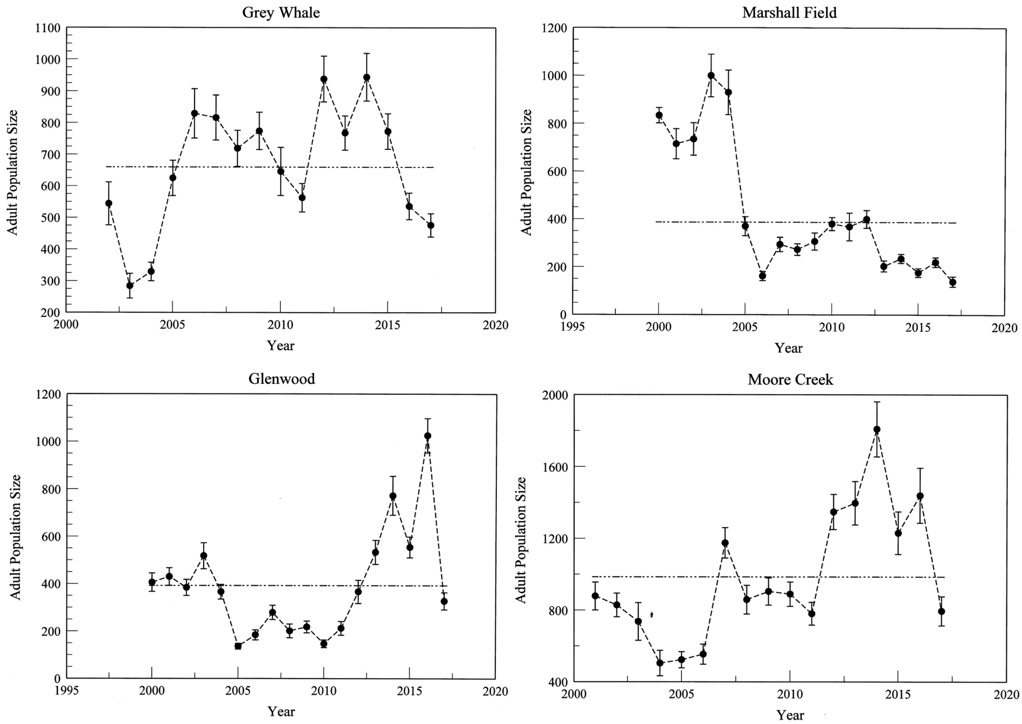

Fig. 5. Annual Ohlone tiger beetle adult generation population estimates from 2000 through 2017 at four study sites near Santa Cruz, CA. Horizontal line represents the average generation size of all annual estimates for each site.

increased as habitat management activities were implemented to benefit the beetle. Public access has been prohibited to-date, but the site is expected to be opened to some recreational activities in the near future. From 2000 to 2012, a small herd of horses grazed the habitat and reduced vegetation, but it was replaced by cows in 2013 because the horse grazing did not maintain adequate bare ground for the Ohlone tiger beetle. Even during the drought years of 2011 through 2016, Ohlone tiger beetle numbers increased as more bare ground was created by the cow grazing. In addition, some brush patches were manually thinned or removed and selected noxious weeds were controlled. Bare ground along a trail used by the Ohlone tiger beetle has been routinely maintained both by grazing and, as necessary, by manual vegetation removal. The steep decline observed in 2017 was probably due to the very high precipitation that occurred then.

Moore Creek Open Space, a public park since 1998, is the largest Ohlone tiger beetle site, and neighboring properties have historically also supported demes of the beetle. The lack of parking and prohibition of bicycles and dogs has limited its use to primarily hikers, joggers, and equestrians. The same program of extensive cattle grazing was in effect at this site throughout our entire period of study. Scraping along one of the trails occupied by the Ohlone tiger beetle happened in 2015. Thus, unlike the other three Ohlone tiger beetle study sites, the land management activity at this site was fairly consistent throughout the multiple years of our monitoring. Ohlone tiger beetle generation sizes (Fig. 5) were less than the multi-year average in 10 of our first 11 monitoring years; however, Ohlone tiger beetle generation sizes were well above the multi-year average during the drought years of 2011–2016. As is discussed later, the 2017 Ohlone tiger beetle generation size declined substantially, probably due to the exceptionally wet 2016–2017 rainfall period.

Annual and seasonal precipitation totals may have both positive and negative effects on Ohlone tiger beetle populations and at least partially explain some of the observed fluctuations in their numbers and trends over time. For example, oviposition activity is noticeably greater immediately after a rain event, perhaps because the soil is easier to manipulate when burying an egg. Although the coastal prairie was historically characterized primarily by native perennial grasses and forbs, numerous invasive annual grasses and herbs have colonized the prairie remnants occupied by the Ohlone tiger beetle (Ford and Hayes 2007). From

2000 to 2017, average annual rainfall (measured between 1 July and 30 June) was about 17.7 cm (Bergholz 2018). During dry years, less herbaceous plant growth results in more sparsely vegetated to bare ground areas that can be occupied by the Ohlone tiger beetle, whereas in wetter years the increased vegetation growth, especially of annuals that colonize former areas of bare ground, reduce the amount of suitable habitat for the beetle. Higher soil moisture during wet years may also result in higher mortality of immature stages living in their earthen burrows due to an increased incidence of pathogens and even drowning during extended seasonal rainy periods. We have also noticed that hooves of grazing animals as well as various foot or bike traffic can dislodge eggs and first instars from their burrows, especially when the soil is moist after a ground-soaking rain. Although the trampling of vegetation by grazing animals and humans to maintain bare or sparsely vegetated soil is detrimental to the beetle, it is probably more beneficial to the Ohlone tiger beetle at sites that lack other habitat management activities.

Results of linear regression analyses indicate that Ohlone tiger beetle generation numbers at all four sites were inversely correlated (*i.e.*, negative slopes) with annual rainfall totals. The degree of correlation, r^2, ranged from only 0.02 at Marshall Field, where the population declined dramatically during our monitoring, to 0.27 at Moore Creek, where the population increased. Distinguishing the effect of rainfall on Ohlone tiger beetle generation size is likely confounded by the varying degree of anthropogenic impacts and variation in land management practices that occurred at the Marshall Field, Glenwood, and Grey Whale study sites during our monitoring years. As noted earlier, land management activities at Moore Creek were more consistent throughout our entire monitoring period, and the inverse correlation between generation size and annual rainfall is more apparent (Fig. 6). We did not assess biotic factors, particularly natural enemies and food availability, which may be related to or independent of rainfall and have important impacts on tiger beetle populations (Knisley 1987; Knisley and Juliano 1988; Pearson and Vogler 2001).

During the course of our field study, we observed several adult behaviors. Because adults of the Ohlone tiger beetle emerge during the late winter and early spring when ambient air temperatures can be cool, much of their time is spent basking to remain active. We found about 61% of all observations were of basking adults. Other behaviors included mating (30%), foraging (5%), ovipositing (3%), and running (1%). We observed adults feeding on ants, flies, earthworms, bumble bees, spiders, caterpillars, and sow bugs.

Spatial Distribution of Larvae. Annual numbers of larval burrows ranged from 167 to 1,229 at Glenwood (Table 2) and 30 to 336 at Marshall Field (Table 3). During most years, larval burrow numbers at Glenwood were similar to or exceeded the estimated adult numbers. At Marshall Field, however, the numbers of larval burrows were lower than the estimated adult population sizes during all years. A possible explanation may be that the Glenwood population is quite isolated from other nearest Ohlone tiger beetle populations, and immigration is unlikely. In contrast, the Marshall Field population is close to other Ohlone tiger beetle sites that may function as a metapopulation with routine interdeme

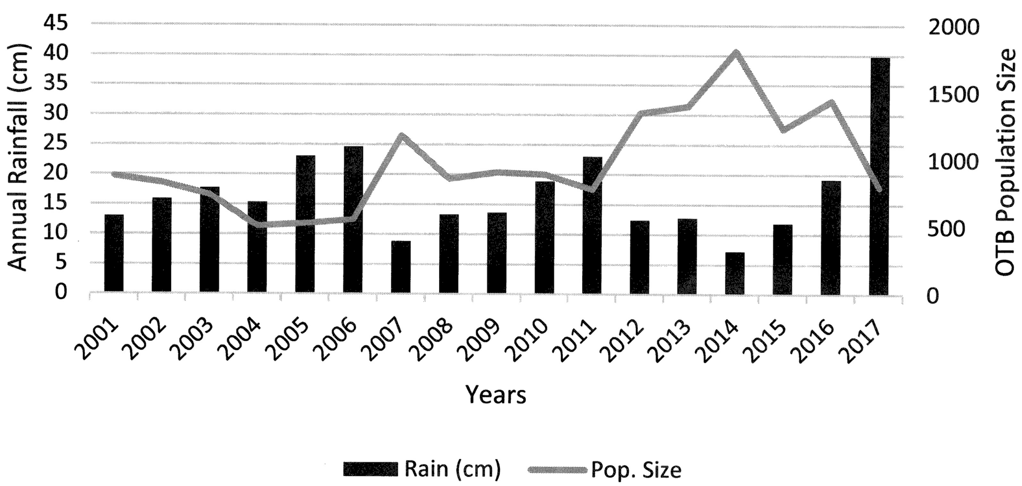

Fig. 6. Inverse correlation between annual (July 1 – June 30) rainfall amounts (cm) and estimated Ohlone tiger beetle (OTB) adult generation population sizes for Moore Creek, Santa Cruz Co., CA.

Table 2. Annual nearest neighbor spatial statistics for active Ohlone tiger beetle larval burrows at the Glenwood study site. Note: p-values for all years are <0.0001.

Year	Number of burrows	Occupied area (m^2)	Nearest neighbor ratio	*z*-score
2003	546	832	0.1715	-37.0350
2004	364	478	0.1289	-31.7958
2005	167	288	0.1570	-20.8405
2006	271	485	0.1731	-26.0416
2007	303	397	0.1524	-28.2241
2008	583	809	0.2132	-36.3452
2009	470	874	0.2406	-31.4970
2010	411	591	0.2549	-28.8988
2011	428	677	0.2429	-29.9652
2012	1,229	1,369	0.3516	-43.4843
2013	507	630	0.2765	-31.1654
2014	946	1,011	0.3264	-39.6355
2015	584	1,414	0.4863	-23.7490
2016	599	773	0.2686	-34.2446
2017	175	457	0.4231	-14.6003

dispersal by adults. Thus, its adult population likely consists of both resident beetles and those that immigrate from nearby Ohlone tiger beetle sites.

As noted by Knisley and Arnold (2013), the Ohlone tiger beetle is associated with mima mound topography on soils known as Watsonville loam (Bowman and Estrada 1980). However, at each Ohlone tiger beetle site in our study, larval burrows were usually patchily distributed and restricted to only small portions of these soils. All of the nearest neighbor ratios (Tables 2 and 3) computed by the nearest neighbor analyses were less than 1.0, which indicates that the spatial distribution of the burrows exhibited highly clustered or aggregated patterns rather than random or uniformly dispersed patterns at both sites for all years (negative z-scores, $p < 0.0001$ in Tables 2 and 3).

The portion of the Glenwood site underlaid with Watsonville loam was too small to be mapped by Bowman and Estrada (1980), but it became apparent after the Ohlone tiger beetle was discovered there (Knisley and Arnold 2013). The presence of a small inclusion of Watsonville loam within the mapped Bonny Doon loam was subsequently confirmed by field and laboratory tests. However, the larval burrows have been restricted to less than 15% (Table 2) of this inclusion's area.

The entire Marshall Field site is Watsonville loam, but the occurrence of soggy soils, shading by the surrounding wooded areas, and limited bare to sparsely vegetated ground restricts where the Ohlone tiger beetle larval burrows can occur. Since the cessation of wildland fire-fighting training, the primary management tool has been recreational

Table 3. Annual nearest neighbor spatial statistics for active Ohlone tiger beetle larval burrows at the Marshall Field study site. Note: p-values for all years are <0.0001.

Year	Number of burrows	Occupied area (m^2)	Nearest neighbor ratio	*z*-score
2003	211	1,195	0.0700	-25.8430
2004	336	1,217	0.0832	-32.1510
2005	134	983	0.0960	-20.0189
2006	72	285	0.0988	-14.6290
2007	74	212	0.0667	-15.3591
2008	65	127	0.0727	-14.3029
2009	54	90	0.0976	-12.6866
2010	71	111	0.0727	-14.9477
2011	70	88	0.0755	-14.7982
2012	68	135	0.0467	-15.0390
2013	62	130	0.1471	-12.8485
2014	55	109	0.1912	-12.3640
2015	41	97	0.2437	-11.6271
2016	45	86	0.3386	-11.0395
2017	30	71	0.4715	-9.8639

activities along the primary and secondary trails to maintain bare ground. During our 15-year study at this site, the area occupied by larval burrows declined dramatically from 1,217 m^2 to 71 m^2 (Table 3).

Recommended Monitoring Methods. Assessing changes in populations of endangered insect species is key to understanding their temporal dynamics, determining if observed generation fluctuations are within a normal range of variation, evaluating the effectiveness of adaptive habitat management actions intended to benefit the population, and documenting compliance with regulatory requirements. However, accurate estimates of population sizes for endangered insects can be challenging to obtain because the insects are often difficult to capture or observe, individuals may be harmed during the census process, or the associated costs of making absolute counts or censuses are usually greater than available funding. Appropriate census methods frequently need to be determined by pilot studies to verify that the estimates of population sizes and other vital parameters are sufficiently accurate to detect changes that occur between generations and population trends over time, while being accomplished at a reasonable cost and expenditure of time.

Population monitoring of rare tiger beetles has often relied on visual index counts, along a fixed route of habitat, often one count per year, not because they are more accurate but primarily because of funding limits. This is especially true for species with multiple populations like *H. dorsalis dorsalis* (Knisley *et al.* 2016), *Ellipsoptera puritana* (G. H. Horn) in Maryland (Knisley 2017), *Cicindelidia floridana* (Cartwright) (Knisley and Brzoska 2018), *Ellipsoptera nevadica lincolniana* (Casey) (S. Spomer, personal communication), and *Cicindelidia highlandensis* (Choate) (Knisley and Hill 2013). A limitation of this relative census method is that it typically underestimates the population by 2–3X (Knisley 2009, Knisley *et al.* 2016). A recent study with *C. albissima* found a removal method was the most accurate method for determining population size in this sand dune species, while the mark-recapture method overestimated its population size (Gowan and Knisley 2014).

The three population estimation methods used to monitor the Ohlone tiger beetle are considered absolute techniques (Henderson and Southwood 2016), and each method is suitable for monitoring the beetle under different situations. The choice of method depends upon the goals of population monitoring and how the results will be used to guide habitat management. Capture-recapture methods estimate a daily population size, frequency of capture methods provide a population size estimate for the duration of the period sampled, and the repeated belt transect counts estimate the number of adults in a single generation. In contrast, the aforementioned visual index counts, popularized by Pollard and Yates (1993) and by the United Kingdom's Butterfly Monitoring Scheme (www.ukbms.org), are considered a relative population census estimation technique (Henderson and Southwood 2016) because only the raw counts or averages are reported and based upon the assumption that these values are closely correlated with the actual population size, even though the precise relationship between the counts and the actual population is rarely quantified.

Our study indicates that larval burrows are generally restricted to smaller portions of occupied sites where microhabitat conditions are presumably best for larval development. Because the larval burrows occur in highly aggregated clusters and may be restricted to very small portions of occupied sites and habitat conditions can deteriorate rapidly, annual monitoring and mapping is needed to confirm that appropriate management activities are being used.

Because both adult and larval stages are essential to understanding population trends and implementing management strategies, we recommend that future population monitoring include both life stages. Resource managers should continue the use of belt transects for future adult monitoring, since this method is easier to implement and provides a population size estimate for an entire adult generation, which facilitates comparison of monitoring results from different years. Capture-recapture and frequency of capture methods may be appropriate in some situations, but both methods require personnel skilled in the capture, handling, and marking of adult beetles. Weather permitting, they require daily sampling for a short-lived beetle such as the Ohlone tiger beetle. Recapture rates should exceed 25% to obtain accurate estimates of population parameters for each day (capture-recapture) or study period (frequency of capture). During our 18-year monitoring period, the timing and duration of annual adult activity periods varied substantially for the same site between years. Thus, results of capture-recapture and frequency of capture monitoring from different years may not be directly comparable unless sampling is performed during the same portion(s) of each respective adult generation. Due to their short adult lifespans, beetles active at any particular time within their activity period represent only a portion of the total adult generation. Because activity and detectability of adult beetles may be reduced by weather conditions, only a portion of the adult generation is represented in a sampling period. The belt transect counts we used eliminate these complications because the entire adult season was monitored. Thus, the estimated population size was for an entire adult generation rather than from a shorter portion the full adult activity period.

Remarkably, despite its low generation sizes, the Ohlone tiger beetle continues to persist at degraded remnants of coastal prairie habitat, including the small and isolated Glenwood site as well as the larger, meta-population(s) west of Santa Cruz. The latter consists of a complex of breeding sites or demes that are likely interconnected to varying degrees by dispersing adults and were considered four populations by Cornelisse *et al.* (2013a). As we document here, generation numbers fluctuate annually in response to environmental stochasticity and ever-changing habitat conditions at these remaining locations. It is apparent that the long-term survival of the Ohlone tiger beetle depends on improving habitat quality at formerly occupied sites and establishing demes at historic sites by translocation of beetles from existing sites or from captively-bred livestock. The results of our long-term population monitoring, in conjunction with those of earlier studies, should enable resource managers to implement adaptive management programs that include effective monitoring of Ohlone tiger beetle populations.

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