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Source: The Coleopterists Bulletin, 67(4):569-580. 2013.
Published By: The Coleopterists Society
DOI: http://dx.doi.org/10.1649/0010-065X-67.4.569
URL: http://www.bioone.org/doi/full/10.1649/0010-065X-67.4.569

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Biology and Conservation of *Cicindela ohlone* Freitag and Kavanaugh, the Endangered Ohlone Tiger Beetle (Coleoptera: Carabidae: Cicindelinae). I. Distribution and Natural History

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Abstract

The objective of this study was to determine the current distribution and natural history of *Cicindela ohlone* Freitag and Kavanaugh, the endangered Ohlone tiger beetle, and to provide information essential for its conservation and recovery. Laboratory and field studies were conducted on the beetle's life cycle, seasonality, developmental times of immature stages, fecundity, and survivorship. The species is restricted to Watsonville loam soil in coastal terrace grassland in Santa Cruz County, California but was found at only 17 of over 200 sites of this habitat type surveyed. Most sites were unsuitable because they lacked bare ground surface needed by adults and larvae. During the course of our studies between 1996 and 2012, *C. ohlone* disappeared from eight of these sites as a result of land use changes that destroyed the habitat totally or altered it by eliminating sufficient bare soil due to increased vegetation. Laboratory studies yielded a mean high of 42 eggs per female over a 4-week period. Larvae reared at *ad libitum* feeding levels developed from first instar through third instar in 109 days compared to 144 days for larvae fed at lower levels. Field studies indicated a 12% survival rate for first instars after one year; 7% emerged as adults and 4% continued development into the second year. This species' unusual winter pattern of adult activity from late January into April coincides with the area's rainy season. Adult activity was limited to days with air temperatures above 16°C. Most of the bare or sparsely vegetated area occupied by *C. ohlone* adults and larvae is maintained by animal or human disturbances, including those by gophers, ground squirrels, feral pigs, cattle, horses, mountain bikers, and pedestrian foot traffic. Our studies suggest that this insect is seriously threatened by increased vegetation growth at most sites and is now more endangered than when we began our studies. New and expanded habitat management strategies must be quickly implemented at all sites to improve habitat conditions and increase recruitment.

Key Words: insect conservation, ecology, development, life cycle, invasive vegetation

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Tiger beetles have become an important focus group in insect conservation, specifically as indicator organisms for assessing species diversity (Pearson and Cassola 1992), as well as habitat degradation and loss (Nagano 1982; Knisley and Hill 1992; Arndt *et al.* 2005). In the USA, four tiger beetle taxa are currently recognized by the U.S. Fish & Wildlife Service as endangered or threatened and two others are candidates for listing pursuant to provisions of the Endangered Species Act of 1973. Pearson *et al.* (2006) noted that at least 33 (15%) of the named tiger beetle taxa in the USA and Canada warranted consideration as threatened or endangered species.

The Ohlone tiger beetle (OTB), *Cicindela ohlone* Freitag and Kavanaugh, was first collected in 1987 at a remnant patch of coastal terrace grassland near Santa Cruz (Santa Cruz County), CA, and subsequently described by Freitag *et al.* (1993). It is distinguished from its closest relatives in the *C. purpurea* species-group by several morphological characters, its separate geographic range, and a different seasonality. Despite the considerable interest and collection of tiger beetles throughout the USA and in California, this insect was apparently overlooked because of its localized range, atypical seasonality, and habitat specificity. *Cicindela ohlone* is considered to be restricted to coastal prairie habitat (Ford and Hayes 2007) on marine terraces characterized by mima mound topography. Freitag *et al.* (1993) noted that California oatgrass (*Danthonia californica* Bol.) and purple needlegrass (*Nassella pulchra* (A. S. Hitch.) Barkworth (both Poaceae) are two native grasses known to occur at all sites. More recently, this coastal terrace prairie community has been called the *Danthonia californica*-herbaceous alliance (Sawyer *et al.* 2009) when this grass is dominant or co-dominant with various native perennial grasses or forbs. Freitag *et al.* (1993) suggested that *C. ohlone* is likely rare because most of the coastal grassland has already been lost to development and agriculture. Because of these factors and apparent threats to its survival, it was listed as endangered in 2001 (U.S. Fish & Wildlife Service 2001; Cornelisse *et al.* 2013).

Between 1996 and 2012, we conducted field and laboratory investigations on *C. ohlone* to determine its geographic distribution and abundance, habitat characteristics, life history, and threats to its survival. These data are important for the implementation of effective habitat management actions and eventual recovery of this declining species.

Material and Methods

Habitat and Distribution. Many species of tiger beetles occur in open habitats such as grasslands, beaches, salt flats, and riverbanks with specific edaphic conditions. To find as many extant populations of the OTB, we surveyed all coastal terrace grasslands throughout Santa Cruz County with a soil series that was characteristic of the known locations for this species. During 2002, we were assisted by agronomists from the Natural Resources Conservation Services (NRCS) of the U.S. Department of Agriculture, who conducted field and lab investigations, including excavation of soil pits at selected OTB sites to obtain data needed to identify the soil series where there were questions about the identity of soils used by the beetle.

Initially, a location was identified using a geographic information system (GIS) and soils information as mapped by Bowman and Estrada (1980). Aerial photographs then were examined to determine the vegetation types and current land uses to narrow down the suitable OTB habitat to be surveyed. Between 1996 and 2009, RAA visited 212 potential locations to examine habitat conditions and to survey for the beetle. Presence-absence data were collected for OTB adults and larvae for multiple years. At sites supporting the OTB, we determined adult and larval population trends over several years, and we will present those findings in a future paper.

Life Cycle and Seasonality. To measure fecundity and adult life span, as well as developmental times of the instars, we conducted laboratory rearing studies using methods previously described for other tiger beetles (Pearson and Knisley 1985; Knisley and Schultz 1997). Due to the rarity of *C. ohlone*, we used small numbers of adults (10 females, 3 males) that were field-collected on three dates in March 2001. Females were confined alone or with a male in small plastic terraria (24 cm long × 12 cm wide × 15 cm high) with a 10-cm layer of sandy-clay soil and covered by a screen top. Water was added on alternate days to maintain soil moisture that varied from well-saturated to surface-dry. Food was provided *ad libidum* by placing 10–15 *Tribolium* (mixed adults and larvae) into the chambers each day. Terraria were kept in a controlled temperature chamber at 25–27°C and 14L:10D photoperiod for the duration of the studies. To determine fecundity over the life span of adults, they were transferred to new terraria every seven days. Watering of these terraria was continued after adults were removed and checked daily for the presence of first instars. When it was estimated that all of the larvae in a terrarium had hatched (within 15 days after adults were removed), we emptied the soil from the terrarium into an enamel pan and examined the soil for the presence of eggs and first instars. These were counted and the larvae transferred to individual 2 cm diameter × 20 cm long acrylic tubes filled with soil that was saturated with water and stopped at one end with a foam plug (Knisley and Schultz 1997). The larvae were placed on top of the damp soil into which they rapidly dug burrows. The tubes were subsequently watered from the top at weekly intervals.

To assess the effects of food level on rate of larval development and to test possible variations in feeding level that larvae may experience in the field, we provided larvae with one of two food levels. The first instars in the low-food group were provided with one small (0.2 cm) *Tribolium* larva every two-three days; second instars were fed one medium (0.3 cm) *Tribolium* larva at the same interval; and third instars were fed one large (>0.4 cm) *Tribolium* larva at the same interval. Larvae in the high-food group were given one of the same-sized *Tribolium* per day. From daily checks of each larval rearing tube, we determined for each instar the number of days from the beginning of a stadium to the time the larva plugged its burrow prior to molting and the length of time before re-opening its burrow and emerging as the next stadium.

To measure larval development and survival rates in the field, we chose a single site (#13 in Fig. 1) where we marked 180 oviposition burrows with numbered aluminum tags when they first appeared during a two-week period in March 2002. We monitored them for larval activity one or two times per week through June and subsequently one or two times per month until the following spring

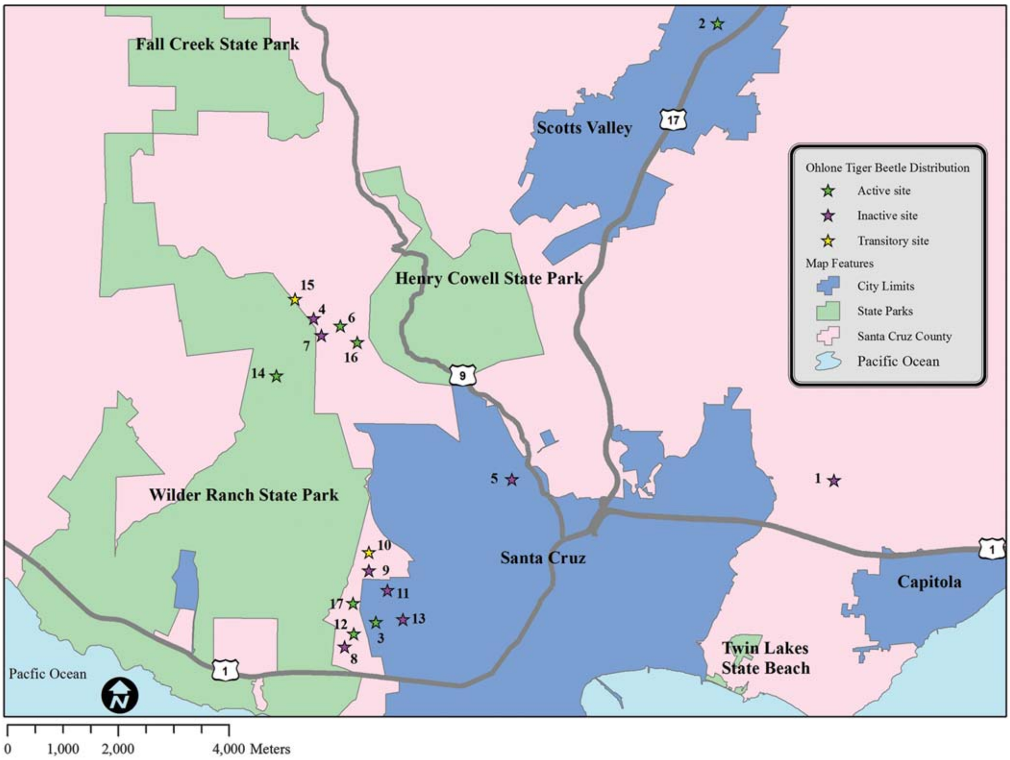

Fig. 1. Map of Santa Cruz County, California showing all known sites for *Cicindela ohlone*.

to determine seasonality, survival, developmental stage, and adult emergence time.

Results

Habitat and Distribution. As of 1994, the OTB was known from sites #1, #2, #3, #4, #5, #6, #7, #11, and #15 (sites are referred to by numerical identifiers in Fig. 1 and Table 1 because illegal collecting is a potential threat to OTB populations, according to the U.S. Fish & Wildlife Service (2001)). By 2012, we had increased the number of known sites with the OTB present to 17 (Fig 1, Table 2). Soil maps (Bowman and Estrada 1980) indicated that Watsonville loam was the soil series at most of these sites. Although a few OTB sites were mapped as Bonny Doon or Pinto loams, field and laboratory investigations by NRCS agronomists subsequently confirmed that the beetle-occupied portions of these sites were actually inclusions (*i.e.*, areas too small to map at the county mapping level) of Watsonville loams within the larger mapped soil types. Thus our efforts to determine the OTB's geographic distribution focused on identifying locations characterized by coastal prairie habitat underlain by Watsonville loam soils.

Overall, 436 locations in Santa Cruz County were mapped as Watsonville loam soil series (Fig. 2), with most of these on old marine terraces, primarily in coastal portions of the county and collectively had an area of 6,392 ha (Table 2). The Watsonville loam soil series includes five soil types, as described in Table 2. Based on this soil and habitat information, we found the OTB at nine additional sites (Fig. 1). Since the time of its discovery in 1987, OTB has been observed on Watsonville loams, totaling only 646 ha, or 10.1% of the entire geographic extent of this soil series in Santa Cruz County.

Prior to its discovery, the OTB may have occurred in a greater portion of Santa Cruz County characterized by Watsonville loams. Our GIS analyses and ground surveys (summarized in Table 2) indicate that a total of 5,467 ha (85.5%) of mapped Watsonville loam soils presently are not suitable for the beetle due to past or current land uses such as agriculture (especially crops), development, and mining. Also, some areas of Watsonville loam are characterized by vegetation types, such as forest or

Table 1. Estimated areas of historically and recently occupied grassland and trail habitats at sites inhabited by *Cicindela ohlone*.

		Habitat area (ha)			Trail length (m)				
OTB site identifier (Fig. 2)	Elevation (m)	Total coastal prairie	Historically occupied	Recently occupied	Total trail length	Historically occupied	Recently occupied	Peak adult OTB numbers	Last year adults observed
1	93	2.26	0.54	-	367	191	-	75	2008
2	230	2.80	0.79	0.51	423	300	254	75	2012
3	128	33.49	8.49	3.29	2,422	1,203	997	108	2012
4	347	1.28	0.38	-	195	97	-	7	2004
5	108	28.77	2.80	-	1,107	1,107	-	3	2004
6	323	6.51	1.94	0.07	1,397	1,101	216	78	2012
7	322	7.57	0.52	-	1,053	250	-	8	1999
8	79	10.32	0.19	-	980	292	-	7	2002
9	122	14.00	9.06	-	1,279	679	-	66	1999
10	134	33.03	8.22	0.24	2,450	1,521	246	14	2012
11	122	3.96	0.22	-	482	300	-	11	2000
12	91	12.30	0.12	0.12	568	568	-	18	2009*
13	67	9.71	2.38		617	358	-	55	2004
14	317	3.58	0.50	0.40	583	459	160	122	2012
15	329	3.65	2.28	0.01	675	386	50	16	2012
16	317	1.88	0.84	0.43	335	269	34	53	2012
17	92	26.29	2.86	1.81	1,792	1,088	379	32	2009*
		201.40	**42.13**	**6.88**	**16,725**	**10,169**	**2,336**		

* No surveys after 2009 because landowner denied access.

coastal scrub, that are not known to support the OTB. Many of the grasslands underlaid by Watsonville loams have been converted to predominately annual grasses and forbs, exhibit accumulated thatch, or have been degraded by the intrusion of forest and coastal scrub. Outside of the historical locations of the beetle, only 279 ha (4.4%) of grasslands represent potential, but unoccupied, habitat for the beetle based on surveys conducted between 1996 and 2012 by RAA. The primary missing parameter at these locations is sufficient patches of bare ground. Additional locations with inclusions of Watsonville loams may exist within other previously noted soil series, but were not included in this analysis.

Soil maps for the three counties that surround Santa Cruz County were also examined as part of our GIS analysis. Watsonville loams were not identified from either Santa Clara or Monterey Counties, but in San Mateo County they occur in 230 polygons that collectively encompass approximately 2,068 ha (Lindsey 1969). Grassland habitat on these sites makes up approximately 818 ha, but our GIS analysis suggests that only 454 ha represent potential habitat for the beetle. RAA has surveyed roughly 30% of this area to-date without finding any new locations for the endangered beetle.

Life Cycle and Seasonality. First-instar burrows measured in the field had a mean diameter of 1.7 mm (range of 1.5–2.2 mm) and mean depth of 4.6 cm. Second-instar burrows had a mean diameter of 2.9 mm (range of 2.4–3.2 mm) and depth of 5.9 cm, whereas third-instar burrows had a mean diameter of 4.6 mm (range of 3.7–5.2 mm) and depth of 8.2 cm.

Although the small sample sizes in our laboratory studies did not allow for statistical analysis of most of our results, we were able to obtain useful information on these life history parameters. Fecundities were highly variable among the females with a range of 2–62 eggs per female over the four-week period that some of the females survived. The three females (kept without males) collected on 7 March produced a mean of 3 eggs per female over a three-week period, while the four females (without males) collected on 12 March produced a total of 127 eggs and a mean of 42 eggs per female (Table 3). In this group, some eggs were produced in each of the four weekly periods, but most were laid in weeks two and three. The four females collected on 20 March and kept with males produced a total of 51 eggs (one female produced no eggs) in three weeks and an overall mean total of 13 eggs per female. This level of fecundity is comparable to that reported for several other tiger beetles studied in the laboratory. Shelford (1908) found a range of 10–50 eggs for several Illinois species, while Gwiazdowski *et al.* (2011) found no more than 26 per female. Brust *et al.* (2012) found a lifetime range of 30–60 eggs for *Cicindela sexguttata* F. and

Table 2. Estimated number of hectares of habitat types associated with Watsonville loam soils in Santa Cruz County, California.

		Watsonville loam soil type					
Current habitat types	Habitat for *Cicindela ohlone*	0–2% slopes	2–15% slopes	Thick surface, 0–2% slopes	Thick surface, 2–15% slopes	Thick surface, 15–30% slopes	Totals
Agriculture	No	87	1,134	295	424	6	1,946
	Potential	0	0	0	0	0	0
	Yes	0	0	0	0	5	11
Agriculture Total		**87**	**1,134**	**295**	**424**	**11**	**1,951**
Developed or Mined	No	218	1,200	790	637	57	2,902
	Potential	0	0	0	0	0	0
	Yes	0	0	0	0	0	0
Developed or Mined Total		**218**	**1,200**	**790**	**637**	**57**	**2,902**
Developed and Grassland	No	0	0	0	0	0	0
	Potential	0	69	0	0	0	69
	Yes	0	5	0	28	0	33
Developed and Grassland Total		**0**	**74**	**0**	**28**	**0**	**102**
Grassland and Agriculture	No	0	0	0	0	0	0
	Potential	0	0	0	17	0	17
	Yes	0	0	0	0	0	0
Grassland and Agriculture Total		**0**	**0**	**0**	**17**	**0**	**17**
Grassland-Annual	No	0	160	0	180	0	340
	Potential	0	0	0	0	0	0
	Yes	0	2	0	0	0	2
Grassland-Annual Total		**0**	**162**	**0**	**180**	**0**	**342**
Grassland-mixed Perennial and Annual	No	0	11	0	32	0	43
	Potential	0	44	0	56	17	117
	Yes	0	35	6	112	0	153
Grassland-mixed Perennial and Annual Total		**0**	**90**	**6**	**200**	**17**	**313**
Grassland and Scrub	No	0	6	0	0	0	6
	Potential	0	5	21	0	0	26
	Yes	0	0	0	0	0	0
Grassland and Scrub Total		**0**	**11**	**21**	**0**	**0**	**32**
Grassland and Forest	No	0	9	0	5	0	14
	Potential	0	0	0	15	0	15
	Yes	0	453	0	0	0	453
Grassland and Forest Total		**0**	**462**	**0**	**20**	**0**	**482**
Forest, Scrub, and Grassland	No	0	0	0	0	15	15
	Potential	0	0	3	0	32	35
	Yes	0	0	0	0	0	0
Forest, Scrub, and Grassland Total		**0**	**0**	**3**	**0**	**47**	**50**
Scrub and/or Forest	No	0	128	0	53	20	201
	Potential	0	0	0	0	0	0
	Yes	0	0	0	0	0	0
Scrub and/or Forest Total		**0**	**128**	**0**	**53**	**20**	**201**
All Habitat Types	No	305	2,648	1,085	1,331	98	5,467
	Potential	0	118	24	88	49	279
	Yes	0	495	6	140	5	646
Grand Totals		**305**	**3,261**	**1,115**	**1,559**	**152**	**6,392**

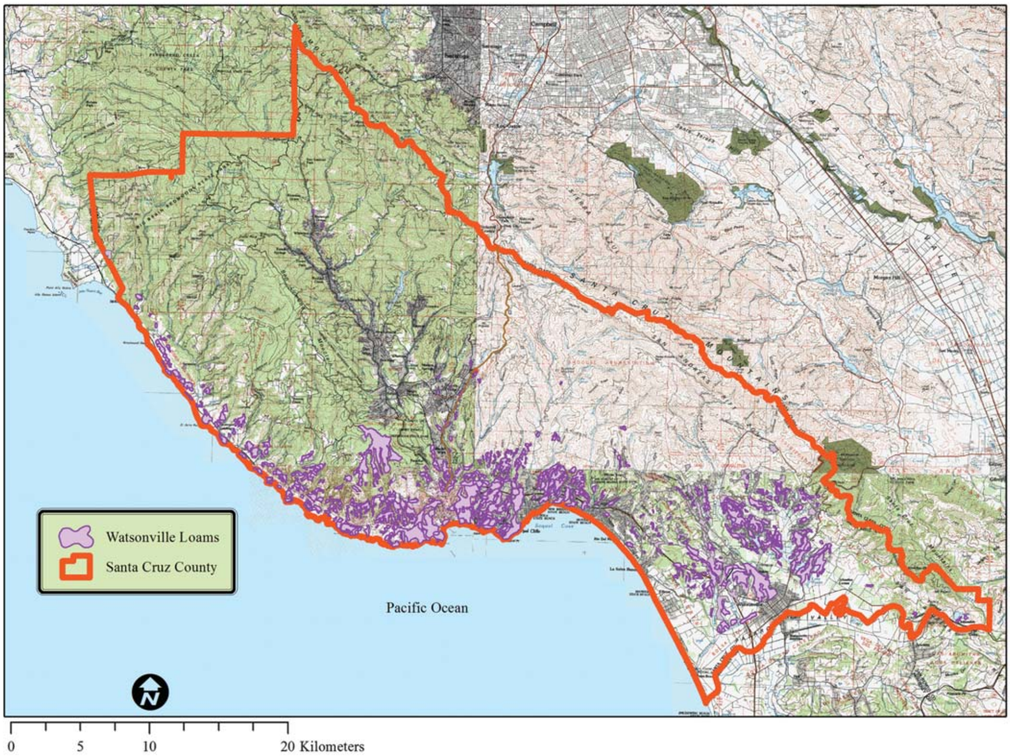

Fig. 2. Map showing the location of Watsonville loam soils in Santa Cruz County, California.

60–150 for *Cicindela scutellaris* Say. Hori (1982) reported as many as 300 eggs per female for *Cicindela japonica* Thunberg. Projecting fecundity of adults in the field on the basis of laboratory data is likely unreliable, but our results suggest that fecundity for females in the field could easily be 40–60 or more eggs during their adult life, if they obtain adequate food and other conditions for oviposition (*i.e.*, periodic rains to soften the soil and daytime temperatures conducive for adult activity) are favorable.

The respective mean longevities of laboratory-reared adults (from their dates of field collection) for the females collected on 7 March and kept without males, the females collected on 12 March and kept without males, and the females collected on 20 March and kept with males were 28, 47, and 27 days. The second group had much higher mean fecundity and longevity than the other two groups. This compares with a maximum observed longevity of 12 days for adults in the field, although the capture-recapture study was limited to only 12 days (R. A. Arnold, unpublished data). Longevity of adults in the laboratory is not especially relevant since in the field, exposure to predators, food limitation, cold temperatures, particularly in the earlier portion of the adult season, and other mortality factors will significantly reduce their survival times.

Durations of all three instars in the high feeding group were significantly shorter ($P<0.01$) than that of the corresponding stadia of the low feeding group (Table 4). Developmental time from eclosion from the egg to completion of the third instar (as indicated by burrow plugging) was highly variable, with a mean of 109 days (about 3 weeks

Table 3. Mean number of eggs produced per week, total eggs laid, and female survival time for three groups of female *Cicindela ohlone* collected on different dates in 2001. Number of females per group is in parentheses.

	March 7	March 12	March 20
Week	female only (2)	female only (4)	Female + male (4)
1	2	4	2
2	1	16	7
3	0	13	4
4	0	9	0
Total Eggs	**3**	**42**	**13**
Days Survived	**28**	**47**	**27**

Table 4. Mean and range of developmental time (days) of the three instars of *Cicindela ohlone* in low (one prey per two days) and high (1–2 prey per day) feeding groups.

	Low Feeding		High Feeding	
Stage	Mean	Range	Mean	Range
Hatching to 2nd instar	37	28–45	23	13–28
2nd instar plugging to 3rd instar	69	60–83	40	30–48
3rd instar to plugging	55	49–74	48	35–61
Total	**161**	**137–202**	**109**	**78–137**

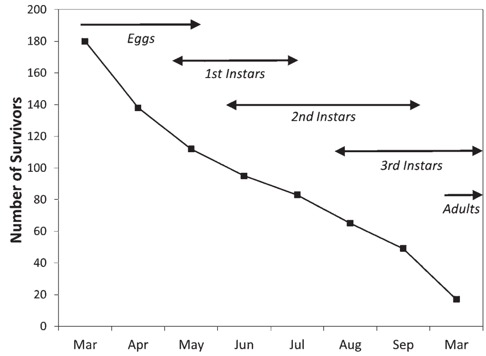

Fig. 3. Development and survival of *Cicindela ohlone* in 180 oviposition burrows marked in March 2004.

for first instars, 5 weeks for second instars, and 8 weeks for third instars) for individuals reared at a high feeding level (1–2 prey items per day) and a mean of 161 days for those reared at a low feeding rate (1 prey item every other day. Developmental times in the field study (see below) were most similar to those of the low feeding group. It is likely that many of the third instars did not complete development since none pupated. Mortality increased greatly during the third-instar plugging stage, apparently because of fungus contamination while they were inactive. This problem has been observed in developmental studies with other tiger beetles and is apparently due to a dormancy period (Knisley and Schultz 1997). Other studies have documented similar effects of food levels on developmental time (Palmer and Gorrick 1979; Pearson and Knisley 1985; Knisley and Juliano 1988; Brust *et al.* 2012).

In the field study of development, we found that of the 180 oviposition burrows marked in early March, eggs in 140 hatched by early April. Since tiger beetle females may not place an egg in all oviposition burrows (Shelford 1908), and because we could not easily determine which burrows had eggs, we based our survivorship calculations on the 140 first instars. Of these, 112 (62% survivorship, most second instars) continued development into May, and by September there were 49 survivors (27%, including 14 second instars and 35 third instars) (Fig. 3). Of the 17 (12%) that survived until the following year, 11 emerged as new adults in March and six continued development as third instars into June. Two of these six emerged as adults the following spring, after two years of development.

The low survivorship (first instar to adulthood) of developing OTB larvae that we recorded in the field is within the range of survivorship (0.5–11.0%) reported for seven Arizona species (Knisley 1987; Knisley and Juliano 1988). The causes of low mortality could not be determined, but food limitation and desiccation are likely important since these were found to be the main limiting factors for other tiger beetles (Palmer and Gorrick 1979; Knisley and Juliano 1988). Parasitism of larvae and predation on adults are important limiting factors for tiger beetles (Willis 1967; Pearson 1988; Knisley and Schultz 1997), but we found no evidence of these mortality factors for the OTB. We did find that grazing cattle and horses occasionally dislodged eggs and larvae (especially first instars) from their burrows, which resulted in mortality of these life stages. Similarly, adult beetles were occasionally crushed by the tires of mountain bikes, cattle, or service vehicles.

Discussion

Our field surveys reveal that OTB populations occur in limited areas of the coastal terrace prairie, even when bare or sparsely-vegetated ground is available. Soil moisture, shading, and degree of activity are factors that influence occupancy. Although coastal prairie habitat at these sites encompasses 201.40 ha (Table 1), oviposition and larval development has consistently been observed in about 10–15 ha and most recently in only about 6.88 ha, primarily on dirt trails and roads. As of 2012, dirt trails and roads collectively measured 16,725 m in length; historically, we found OTBs using about 10,164 m (60.8%) of these trails, but more recently, beetle life stages have been observed using only 2,336 m (13.9%) of these trails. Considerable annual variation in occupied areas occurs due to the amount and timing of rains which influence herbaceous vegetation growth. Off-trail habitat at most locations is even more limited, as herbaceous growth and thatch are often more dense and thick than the beetle can tolerate. Many areas have extended periods of saturated soils and ponded water and thus are not suitable for the OTB. Rather, adults and larvae are largely restricted to areas with bare to sparsely-vegetated patches of well-drained soil. These sites included cattle trails, where grazing has reduced vegetation height, biomass, and accumulated thatch, in the area of mima mounds, feral pig rooting sites, other lightly disturbed soil locations, and where cattle manure has recently decomposed. Such suitable patches of coastal prairie habitat are ephemeral and may be created, lost, or modified within a year or two.

We found that during the course of our studies the OTB has disappeared from eight of the 17 sites where it had been found and has declined in abundance at several others (Table 1). At two other sites (#12 and #17), we found them present in 2009, but since then the landowners have denied us access, so the status of the beetle there is uncertain. Among the factors we have identified as the cause of loss and decline are the following.

a) Deep ripping of the soil and installation of a vineyard at site #9 eliminated all apparent habitat, and the population was lost after 1999. Adult numbers were substantially reduced at adjacent site #10. Indeed, no beetles were observed at site #10 in a few subsequent years before being found later at lower numbers.
b) Several dirt trails formerly occupied by the OTB at sites #6, #7, #11, and #16 were covered with crushed rocks to make them passable during the rainy season, with the effect of reducing the area of suitable breeding habitat.
c) Development of a horse stable at site #8 extirpated the OTB, even though neighboring and nearby sites continued to support beetle populations.
d) Increased vegetation cover reduced the amount of bare or sparsely-vegetated ground, which, along with increased cover of thatch, extirpated populations at sites #1, #4, and #5 and greatly reduced numbers at #15, such that OTBs are only seen intermittently.
e) Small-scale excavations in the primary breeding habitat at #1 contributed to the loss of that population. This site was also well known to collectors who removed many specimens.
f) After grazing cattle were removed from site #13, invasive weeds became more prevalent, vegetation grew taller and more densely, thatch accumulated, and bare ground disappeared along with the beetle.
g) Populations at sites #12 and #17 are presumed to still be extant, but the property owners will not allow us access to confirm their status. Thus the OTB is now confirmed at only 9 of its historical 17 sites (Fig. 1, Table 1).

Even at sites where the beetle still persists, changes in land use activities have altered the grassland structure and reduced the amount of bare ground. For example, during the 1990s controlled burns occurred during several years at sites #6 and #16 as part of training for local fire departments. Controlled burns have also been conducted, albeit less frequently, at site #7. These burns ceased after it became too difficult for the fire departments to obtain all of the various permits needed. The controlled burns maintained a more open vegetation structure with bare or sparsely-vegetated patches of soil scattered throughout the coastal prairie, which provided additional areas for OTB adults and larvae.

Our finding that some larvae completed their development within one year and others in two years is common among tiger beetles and a result of variations in the time of adult emergence, oviposition, egg hatching, and the amount of food obtained as larvae (Knisley and Juliano 1988). The results of our monitoring and observations of marked larvae at several sites and adult seasonality suggest the following life history pattern for the OTB. Adults emerge, oviposit, and are active from mid- to late January to mid-May. First instars emerge from eggs and remain in this stadium from late spring until early summer, then progress to second instar, which usually occurs from late spring to early summer. Development to third instar may occur during summer (we have found them as early as June in some years) or be delayed until the following March to early April when they unplug their burrows after winter inactivity. These third instars complete development during the second spring and summer and emerge as new adults in the following year, thus completing a two-year life cycle. The one-year cycle could occur as a result of early oviposition and hatching, adequate food, and favorable climatic conditions. We have also observed a three-year life cycle in a small percentage of marked larvae.

Annual temperature and rainfall patterns in coastal Santa Cruz County influence the timing of adult emergence, duration of the adult season, and daily activity of the OTB. Collection records and our observations indicate that adult OTBs are generally active between mid-January through mid-May, although the duration and timing of the adult activity period can vary annually and between locations within a particular year. The earliest dates for observing adult in any particular year ranged from 17 January to 28 February, while the latest dates have generally ranged from 10 April to 13 May. A single adult was observed as late as early June (T. Cornelisse, personal communication).The mean duration of the adult activity period for several years was 87 days.

Coastal Santa Cruz County has a Mediterranean type climate, with a winter rainy season followed by a prolonged dry season. The OTB emerges and is active during the winter rainy season. The 30-year record of mean high temperatures for Santa Cruz, CA indicates a gradual increase during the period of adult activity, from 16°C in January to 17°C in February to 18°C in March, and 22°C in April (Fig. 4). The highest mean rainfall amounts are in the months before (16.5 mm in January, 15.6 mm in February) and during the usual time of peak adult activity in early March (12.1 mm). Rainfall declines significantly in April (5.0 mm), then declines further and continues very low through summer until late fall. In most years, adults were active from mid-February to mid-April, with peak abundance from late February to mid-March (Fig. 4), but first emergence and the duration of the adult season varied as a result of year-to-year differences in temperature and rainfall.

The number of adults active on a particular day was also affected by temperature and sky conditions. On sunny days, numbers of adults counted increased with increasing air temperatures from 16° to 24.5°C (bilinear regression $R^2 = 0.28$, df = 19, $p = 0.015$) (Fig. 5). We counted small numbers of adults on some survey days when it was sunny and temperatures were 1–3 degrees below 16°C, but none were active on cloudy days unless temperatures were over 23°C.

The winter seasonal activity pattern of adult *C. ohlone* is unusual and a pattern that rarely occurs among other North American tiger beetles. Other southern or coastal California species may exhibit similar patterns since collection records for January and February are known. This pattern is apparently a modification of the spring-fall life cycle that is typical of many USA species, includ-

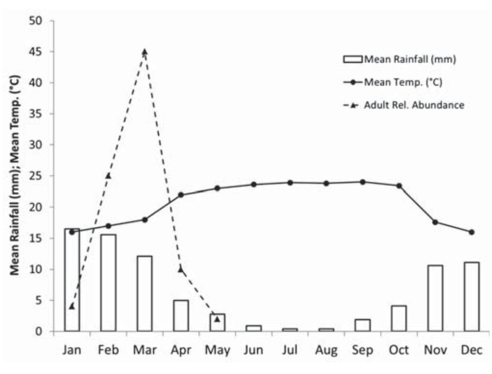

Fig. 4. Mean high monthly temperatures and total rainfall (30-year average) at Santa Cruz, California and seasonal abundance of adult *Cicindela ohlone*.

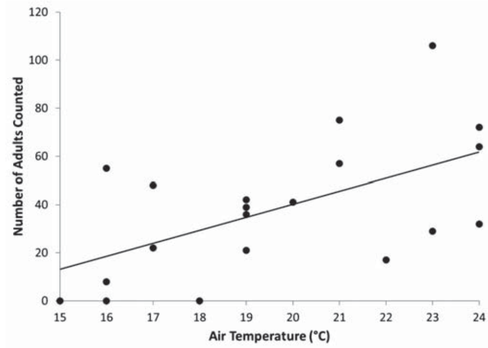

Fig. 5. Relationship of air temperature and number of adult *Cicindela ohlone* counted, based on surveys at six sites and 20 total days

ing all subspecies of *Cicindela purpurea* Olivier, the closest relative of *C. ohlone*. In the spring-fall pattern, one cohort of overwintered adults emerge, mate, and oviposit in spring (usually March-May), then die off while a co-occurring cohort of larvae mature to adulthood in late summer, pupate, and emerge as sexually immature adults for 4–6 weeks in September to early October before overwintering. The pattern of rainfall and temperature in Santa Cruz County apparently selected for an earlier emergence of adults and a suppression of fall emergence. The high rainfall during late winter period is ideal for adult oviposition, egg hatching, and early larval development, but by late March to mid-April rainfall declines, the soil begins to dry out, and conditions become unsuitable for oviposition and larval burrowing. There are many days and sometimes 1–2-week periods of cloudy, rainy, or cool weather when daily high temperatures are often too low or marginal for adult activity. During these periods, adults probably remain in grass clumps and do not emerge until sunny, mild conditions return. Some tiger beetles, including *C. purpurea,* may dig burrows to escape these unfavorable conditions, but that is unlikely for *C. ohlone* adults because the soil is too hard. While the daytime highs are often marginal for adult activity, there are enough sunny, warm days (>16°C) to allow adults to emerge, mate, and oviposit. Temperatures in April and May would be more favorable for adult activity, but by this time the clay soils in these coastal prairie habitats become dry and "rock-hard", making it impossible for females to oviposit, eggs to hatch, and firsts larvae to dig their burrows. It is also likely that because of these dry conditions food availability would decrease and adults could experience food-limitation which would further reduce recruitment.

Interestingly, there is a report of finding adults in closed larval burrows in October (U.S. Fish &

Wildlife Service 2001). This suggests that some adults may complete development by the fall but not emerge from the ground until late winter. Schultz (1998) reported a similar pattern for the spring active adults of *C. sexguttata* which complete development in the fall, and some may even emerge for a short period of activity.

Conservation Status and Management Needs

Like most native grasslands in California, coastal terrace prairie is a disturbance-dependent habitat. Examples of ecological disturbance processes include: periodic drought (Heady *et al.* 1988); wildfires due to lightning strikes (Greenlee and Langenheim 1990; Reiner 2007); annual fall burning by Native Americans to clear dead grass, stimulate new growth, and prevent brush encroachment (Jarrell 1982; Anderson 2007; Haff and Hayes 2008); as well as grazing and soil disturbance by native ungulates (Jackson and Bartolome 2007) and burrowing animals (Schiffman 2007). Mima mounds were likely created and maintained by gophers, which mixed the soils and altered plant species composition to favor forbs rather than dense grasses (Mielke 1977; Cox 1984). Collectively, these ecological disturbance factors maintained the bare ground patches utilized by the OTB and created new patches for colonization. However, with Spanish colonization and establishment of missions about 1769 (Burcham 1957), native ungulates were largely replaced by domesticated grazers such as cattle, sheep, and horses which may graze intensively and often on a year-round basis. Wildfire frequency decreased and burned smaller areas as they were detected and extinguished more quickly (Greenlee and Langenheim 1990). Exotic plants were introduced (D'Antonio *et al.* 2007), which rapidly colonized these grasslands and today predominate in many remnants of the coastal terrace prairie habitat. With these changes, plant species composition and vegetation structure of the coastal terrace prairies were altered, the amount and extent of bare ground likely declined, and new patches of bare ground were created less frequently. Reduction or absence of fire and native ungulates allowed thatch to accumulate, which further reduced the amount of bare or sparsely-vegetated soil. For these reasons, today the OTB is often restricted to dirt trails and road edges at some locations. Hikers, mountain bikers, vehicles, cattle, and horses limit the vegetative cover by crushing colonizing plants, compacting the soil, and minimizing accumulation of thatch. Compared to adjacent interior grasslands, the dirt trails and roads are characterized by lower canopy heights, reduced litter, and a lower proportion of cover by grasses and forbs, including native and non-native taxa (Knisley and Arnold 2004; Arnold *et al*. 2012). One approach we used to create new habitat was by scraping bare patches in densely vegetated areas (Knisley and Arnold 2004). This technique was expanded upon by Cornelisse *et al.* (2013).

Our studies with the OTB provide additional evidence of its rarity and substantiate it as endangered. Indeed, during our study, it became even more at risk due to the alteration or loss of habitat at eight historical OTB sites. Habitat quality declined at most sites as the bare ground required by both adults and larvae was lost or substantially reduced by vegetation encroachment as natural disturbance processes known to maintain and create bare ground ceased to operate. Tiger beetles need bare ground for adult foraging, thermoregulation, oviposition, and larval development (Knisley and Schultz 1997; Pearson and Vogler 2001). The loss of bare ground to encroaching vegetation has caused the decline or extirpation of other tiger beetle species in the USA. (Knisley and Hill 1992; Brust 2002; Cornelisse and Hafernik 2009; Knisley 2011). We will discuss various management options to combat the problem of increased vegetation in a forthcoming paper.

Since its discovery, the OTB has survived only at sites where anthropogenic disturbances have replaced natural disturbance processes to maintain and create open patches of bare soil needed by the beetle. Cattle and horse grazing and some recreational activities have replaced the natural disturbance processes and become the management tools useful for managing OTB habitat to maintain the beetle's populations. Management activities need to be implemented to maintain remaining OTB populations. Several of the historical OTB sites, where habitat quality has deteriorated and does not currently support the beetle, should be rehabilitated to provide more bare ground. Hopefully, the beetle will recolonize these locations or can be reintroduced as necessary to assist with the beetle's recovery and conservation (Cornelisse *et al.* 2013).

Acknowledgments

We greatly appreciate the assistance of Doug Cooper, David Pereksta, Roger Root, and Colleen Sculley of the U.S. Fish & Wildlife Service, who provided permits to conduct these studies, financial assistance, and field assistance. Randy Morgan kindly shared his knowledge of the OTB, while Grey Hayes provided insight about the coastal terrace prairie habitat. Robert Jensen assisted with field work, plus GPS and GIS mapping, and in 2003 Jim Hill assisted with field work. Tim Hyland and Kirk Lenington kindly shared results of their respective adult and other field surveys. We thank the NRCS staff who conducted the field and laboratory soil analyses and the various landowners for permission to work at their respective properties and their financial support.

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(Received 10 March 2013; accepted 25 August 2013. Publication date 20 December 2013.)