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BIOLOGY AND CONSERVATION OF THE CORAL PINK SAND DUNES TIGER BEETLE, *CICINDELA LIMBATA ALBISSIMA* RUMPP

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ABSTRACT.—This study investigated the distribution, abundance, and biology of *Cicindela limbata albissima* Rumpp, an endemic tiger beetle known only from the Coral Pink Sand Dunes (CPSD) in southwestern Utah. A recently implemented conservation agreement between BLM, USFWS, Utah State Parks, and Kane County protects most of the known habitat of this beetle from off-highway vehicle (OHV) use. A search of collection records and field surveys of 19 Great Basin sand dune sites indicated that this species occurs only at CPSD. Yearly index counts of adults (1992–1998) during peak season in May ranged from 331 in 1997 to 895 in 1993, but the actual population size is probably 2–3 times higher than the index counts. Nearly all of the population is found in the primary habitat, a 300-m-wide × 2.7-km-long area in the southern part of the dune field. Small numbers of adults and larvae have been found at the far north end of the dune field.

Mark-recapture studies indicated that most adults moved only short distances (<300 m), but a few moved 1000 m. This beetle has a 2-year, modified spring–fall life cycle. Adults are most abundant from April through early June, but some adults from the following year's adult cohort emerge and can be found from late August to early October. Adults are active on warm or sunny days, but they dig burrows which they use at night or during unfavorable weather. We observed little evidence of parasitism or predation of larvae or adults, but these limiting factors were not fully studied.

Surveys of dominant plant species, arthropod (potential tiger beetle prey) abundance, and OHV activity indicated that these vary throughout the dune field and may explain, in part, the distribution of *C. l. albissima.* The primary habitat is a transition area between the highly dynamic south end of the dune field and the more stabilized north end. *Psoralidium lanceolatum* Rybd., *Sophora stenophylla* Gray, and *Stipa hymenoides* R.&S. are the dominant plants in the interdunal swales of the primary habitat, but other species are dominant in other parts of the dune field. Numbers of arthropod individuals and taxa are greatest in the primary habitat. Off-highway vehicle activity was greatest at the south end of the dune field and lowest at the far north end. Run-over trials and observational data revealed that adult beetles are killed by OHVs, but more important impacts may be damage to vegetation, reduction of arthropod prey of *C. l. albissima,* and disturbance and increased desiccation of the larval microhabitat. We anticipate that the conservation agreement will provide long-term protection for this species at CPSD.

Key words: Cicindela limbata albissima, Coral Pink Sand Dunes, tiger beetle, conservation, off-highway vehicle impacts, population dynamics.

Tiger beetles of the genus *Cicindela* are predatory insects that prefer open, sparsely vegetated habitats. Adults are active, visual hunters that use their large mandibles to capture and eat small arthropods. Larvae are sedentary predators that live in permanent burrows in the ground. They also use large mandibles to capture small arthropods that pass near the mouth of their burrows. There is considerable interest in tiger beetle conservation. Two species (*Cicindela d. dorsalis* Say, *C. puritana* G. Horn) are listed as threatened by the U.S. Fish and Wildlife Service (USFWS). Several others are under consideration for listing. Among the 10+ *Cicindela* species occurring in sand dune habitats in the western United States are several endemic species or subspecies, including *Cicindela arenicola* Rumpp from the Bruneau and St. Anthony dunes of Idaho, *C. theatina* Rotger from the Great Sand Dunes of Colorado, *C. scutellaris yampae* Rumpp from northwestern Colorado, and *C. formosa rutilovirescens* Rumpp from the Mescelaro dunes of southeastern New Mexico. The only published study of these species is that of Bauer (1991) on *C. arenicola.*

Cicindela limbata albissima was described by Rumpp (1961) from specimens collected at the Coral Pink Sand Dunes in southwestern Utah. He distinguished it from other subspecies of *C. limbata* by the greatly reduced elytral pigmentation (the elytra are white except for a narrow medial line) and its disjunct geographic range in southern Utah, a distance of over 600

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km from other populations of the species. The other subspecies of *C. limbata* have separate, more northern geographic ranges, are east of the Continental Divide, and have more pigmentation on the lateral portions of their elytra. *Cicindela limbata limbata* occurs in the western Great Plains, *C. limbata nympha* occurs from North Dakota northwest into southern Canada, and *C. l. hyperborea* is found in northern Canada. Johnson (1989) recently described *C. l. labradorensis* from Goose Bay, Labrador, although Larson (1986) suggested this form was *C. l. hyperborea.* Rumpp (1961) believed that *C. l. albissima* was more closely related to *C. l. nympha* that, he said, followed a southward migration route during the Pleistocene when climatic conditions were more favorable. He suggested that the lack of elytral pigmentation may be a thermoregulatory adaptation to the warmer temperatures where *C. l. albissima* occurs. Acorn (1992) provided support of the relationship between coloration and thermoregulation in *C. limbata* and other dune *Cicindela.* He also reported on the ecology of *C. limbata nympha* and other sand dune *Cicindela* in the southern Canadian plains (Acorn 1991). A recently completed analysis of the mtDNA in *C. limbata* and its relatives found that *C. l. albissima* is genetically distinct from the other subspecies and that it should be given full species status (Morgan et al. 2000).

Cicindela l. albissima was first listed as a category II species in 1984 (Federal Register 49:21664). In 1994 the USFWS was petitioned by the Southern Utah Wilderness Alliance to list *C. l. albissima* as endangered and to designate critical habitat. The service's response (Federal Register 59[178]:47293–47294) indicated that the petition presented substantial information in support of listing, but progress toward its listing was interrupted by the listing moratorium in 1996. Currently, *C. l. albissima* is a candidate species. In 1997 a conservation agreement was signed by the USFWS, Bureau of Land Management (BLM), Utah State Parks and Recreation, and Kane County. The provisions of this agreement include the establishment of a 350-acre conservation area in the southern part of the dune field that is the primary beetle habitat (Fig. 1B). The western portion of this area is signed off to prevent vehicle access, while the eastern portion serves as a travel corridor for vehicles to move between the northern and southern portions of the dunes. An additional 370-acre conservation area at the northern part of the sand dunes has also been proposed. In this paper we present the results of our 1992–1999 studies of this rare insect, including information on distribution and abundance, seasonality, habitat, and possible OHV impacts.

METHODS

Geographic Distribution

Because tiger beetles are a popular, well-collected group of insects, our initial work in determining the distribution of *C. l. albissima* involved a compilation of collection records from various sources. We examined tiger beetle specimens in 23 museum and university collections that were rich in tiger beetle holdings or were likely to have many Utah records. Among the most important collections were those at Brigham Young University, California Academy of Sciences, Utah State University, U.S. National Museum, American Museum of Natural History, and Yale Peabody Museum. We also obtained label information from several individuals who had large cicindelid collections. We conducted field surveys of all major sand dunes and many other sandy areas in Utah and adjacent states where potential habitat for this species might occur (Fig. 2). All of these sites were visited 1 or 2 times in May 1993, 1994, and 1995. At each site we spent several hours to several days searching for tiger beetles in areas of suitable habitat. The searching method involved walking through the open areas of potential habitat and looking on the ground 5–10 m ahead for the adults to run or fly up as they were approached. This visual search method is commonly used to survey for tiger beetles (Knisley and Schultz 1997) and is effective when done during a species' peak activity period (warm, sunny days from mid-April to early June for *C. l. albissima*). At most of these sand dune sites we also surveyed dune arthropods using pitfall traps. We set out 20–32 sixteen-oz cup traps (Carolina Biological Supply Co., Burlington, NC) with approximately 100 mL of ethylene glycol (no longer recommended for this use) for 5- to 7-day periods in May 1993, 1994, and 1995.

Studies on Distribution, Abundance, and Biology

Much of our initial work at Coral Pink Sand Dunes (hereafter CPSD) in May 1992 involved
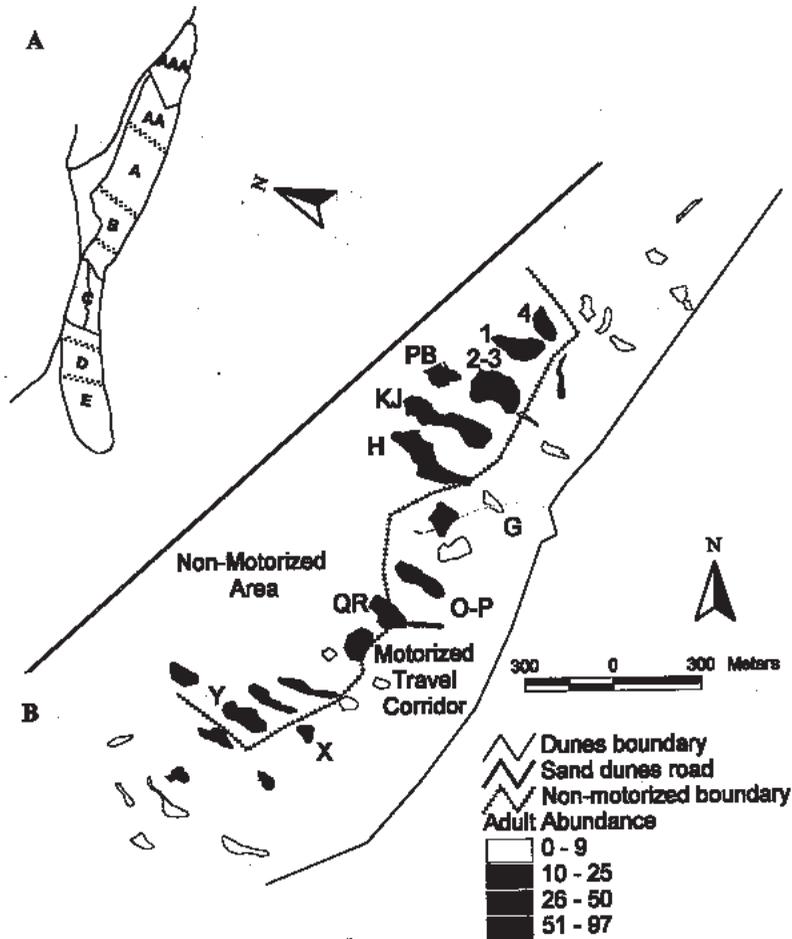
Fig. 1. A, Map of Coral Pink Sand Dunes showing different study areas; B, map of the primary habitat, area C, showing 6-year mean numbers of adults in different swales. The conservation area is divided into a non-motorized area and a travel corridor as indicated.

determining the distribution of adults and larvae within the dune field. We spent 4–6 hours per day for several days walking over all parts of the dune field and making preliminary counts of adults and larvae and recording their distribution relative to physical landmarks, Global Positioning System (GPS) readings, and wooden stakes which we placed in interdunal swales (see below). We separated the CPSD dune field into 7 areas, AAA at the north end to E at the south end (Fig. 1A). Our preliminary surveys indicated that adults and larvae were largely concentrated in an area ~300 m wide × 2.7 km long in the southern portion of the dune field (area C). Most of our studies were within this area, which we call the primary habitat (Fig. 1B).

Relative population size of adult *C. l. albissima* at the Coral Pink Sand Dunes was determined each year in May from 1992 to 1998 using index counts and mark-recapture. In this paper we include only the results of the index counts, which were conducted throughout the entire primary habitat during 2- to 3-day periods each year in mid-May from 0930 to 1230 hours on sunny, mild (>20°C) days. During this time of day, most beetles were active and primarily concentrated along the edges of the interdunal swales and on adjacent lower slopes. In making the counts, 2 individuals positioned themselves 20–25 m apart and walked back and forth across the width of the dune field, progressing from north to south and counting all observed beetles. We kept
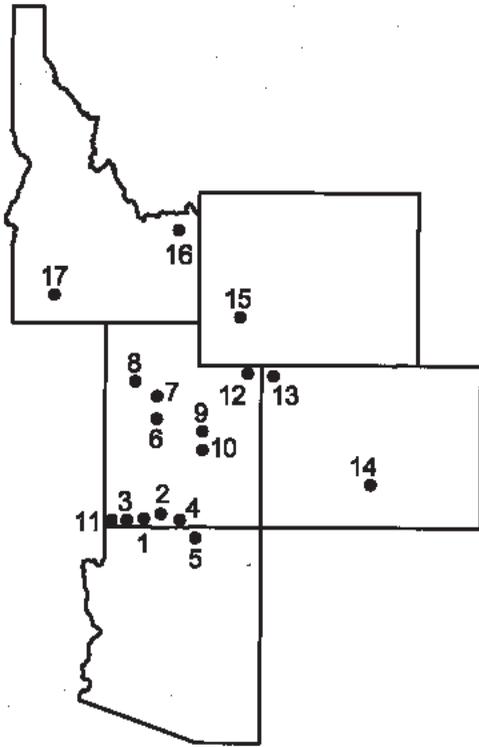
Fig. 2. Map of Great Basin sites surveyed for *Cicindela l. albissima* and other tiger beetles (see Table 1 for site information).

separate counts for each swale-slope area. We also counted adults of another tiger beetle, *Cicindela tranquebarica,* which co-occurred with *C. l. albissima* in some swales.

The distribution and abundance of tiger beetle larvae can be determined by searching the ground and counting numbers of burrows during times when larvae are active (Knisley 1987, Knisley and Schultz 1997). The 3 larval instars can be distinguished by differences in burrow diameter, which is fixed within an instar. Accurate estimates of larval numbers are difficult to obtain for sand dune species like *C. l. albissima* because their larval burrows may be plugged and thus unrecognizable during the day when the sand surface becomes warm and dry, and at other times when conditions are unfavorable (Knisley 1987). We surveyed larval burrows from 0700 to 1100 hours when a high percentage of larvae are active. Preliminary surveys in 1992 indicated that larvae were most abundant in open or sparsely vegetated edges of interdunal swales and low slopes.

To establish fixed survey points, we placed wooden stakes within these swales of the primary habitat near the centers of patches where larvae were aggregated and counted all larval burrows within a 10-m-diameter circle drawn in the sand around each stake. GPS readings were taken at each stake location so lost or vandalized stakes could be replaced. New stakes were added as we discovered new concentrations of larvae. Additionally, in 1996, 1997, and 1998 we also estimated total numbers of larval burrows in each swale (including those outside the fixed plots) by walking back and forth through the swale areas and counting all observed burrows. This number was added to plot counts to obtain a total count of larval burrows in each swale. We also compiled April–October rainfall records for Kanab, the nearest weather station to CPSD, because we hypothesized that rainfall might be an important factor affecting the population dynamics of *C. l. albissima.*

Movement of adults was determined by marking and releasing 200–400 adults each year during a 2–3 day period in mid-May. Beetles were marked by removing a 1-mm section from the tip of one of their elytra. By cutting at different angles, we had unique marks for many of the swale areas. Beetles were recaptured 3–10 days after marking, and distances between mark and recapture locations were measured. Seasonal activity, life cycle, and other natural history information of *C. l. albissima* were determined from our adult and larval surveys and field observations during our May and September visits to the Coral Pink Sand Dunes between 1992 and 1998. Feeding habits of adult *C. l. albissima* were determined by capturing individuals that were feeding and then examining their prey.

Habitat Characteristics and
OHV Impact Studies

We conducted surveys of dominant plant species and arthropod abundance in different areas of CPSD to determine if these might aid in explaining the distribution of *C. l. albissima* within the dune field and to characterize its habitat. Within each of the 7 areas of the dune field (Fig. 1A), we estimated the percentage cover of each plant species within 10-m-diameter circular plots located at 25-m intervals along a transect line running across the length

of each interdunal swale. A wire hoop subdivided into 4 quarters was placed on the ground at each sample point and the percentage cover of each species within each quarter estimated. The sum of the 4 quarters gave the total percent cover for a species. In the primary habitat we estimated the percent cover of plant species in most interdunal swales.

Surveys for swale arthropods (the prey resource base of adults and especially larvae of *C. l. albissima)* were conducted by placing 6 pitfall traps (see above) in 2 different swales in each of the 7 areas of the dune field for 6-day periods (9–15 July 1993, 5–11 September 1993, 21–27 May 1994, and 18–24 May 1996). Three traps were placed around the perimeter of the swale and 3 around the interior near the swale bottom. We transferred arthropods from each trap to separate plastic bags and later identified them to species (where possible). Mean numbers of individuals and taxa were determined from 12 traps (6 in each swale). Another pitfall trap survey from 16–22 May 1998 was designed to determine if there was a relationship between OHV activity and arthropod abundance. In this experiment we set 4 sets of 6 traps in each of 4 different areas of the dune field (AA, B, C, E). Two sets in each area were placed in 2 swales that were in areas of higher OHV activity (determined by higher numbers of OHVs and OHV roads), and 2 sets were placed nearby in 2 swales with lower OHV activity. A paired *t* test was used to compare means for low- versus high-use swales in each area.

Off-highway vehicle activity at CPSD was assessed on Memorial Day weekends in 1997 and 1998 and on Labor Day weekend in 1998. These holiday weekends are among the highest use times for OHV activity at CPSD. We counted the number of OHVs that crossed 8 transect lines (2 in area C and 1 in each of the other dune areas; Fig. 1A) across the width of the dune field during 4 one-hour periods, 2 on Saturday and 2 on Sunday, of each weekend. We also measured the width of all OHV paths or roads that crossed each of these 8 transect lines and summed them to obtain a total road width for each area. We determined the amount of motorized play, primarily the riding back and forth over the dunes, for the 8 areas of the dune field by obtaining the mean minutes per hour that all OHVs (vehicle minutes) were engaged in this activity.

Direct effects of OHVs on tiger beetles were determined from experimental run-over trials and by examination of individual beetles collected during mark-recapture studies. Run-over trials were performed at CPSD in May 1994 on 3 different substrates (dry sand, wet sand, mixed sand and stones). In preparation for the trials, we tied 1 end of a 50-cm length of thread around the thorax of a beetle and tied a piece of plastic surveyor flagging to the other end. The beetles were held in place on the sand surface by covering the middle portion of the string with a handful of sand. The groups of beetles were run over by 10 passes of a 1994 Honda 4-wheeled vehicle. They were examined after 1, 5, and 10 passes of the vehicle. Another indication of probable direct effects of OHVs was noted during our 1994 mark-recapture studies when we found adult beetles with injuries similar to those in the run-over trials. In 1994 and subsequent years, we examined all beetles captured during mark-recapture studies and recorded the numbers that were injured.

<center>RESULTS</center>

<center>Distribution and Abundance</center>

Only 1 of 65 locality records researched for the distribution of *C. l. albissima* was from a site other than CPSD. That record was of a specimen collected by H.P. Boyd (personal communication 1994) from a sandy floodplain of the Virgin River south of Mt. Carmel Junction (~15 km north of CPSD). We did not find *C. l. albissima* at any of the 19 sites that we surveyed (Fig. 2), although other *Cicindela* sp. were found at some sites (Table 1). Five sites (2, 4A, 4B, 4C, 5) seemed likely prospects for *C. l. albissima* because of their close proximity to CPSD and the presence of *Asclepias welchii,* a rare milkweed that may have similar habitat requirements because it occurs only at these sites and at CPSD.

The index counts in the primary habitat, where nearly all adults were found, ranged from 331 in 1997 to 895 in 1993 (Table 2). Most of these adults (60–79%) were in swale rows and low slopes in the northern part of the primary habitat, swales 4 through GH. Highest mean adult numbers (based on annual index counts from 1993 to 1999) were in swales KJ (97), 2–3 (85), 1 (73), and H (60; Fig. 1B). Numbers of adults in adjacent areas to the north and south

TABLE 1. Great Basin sand dunes sites surveyed for *Cicindela limbata albissima.*

Site	Location	Elevation (m)	Species found
1–UT, Coral Pink	15 km W Kanab	1830	*C. l. albissima*
			C. tranquebarica
2–UT, Sand Hills	14 km NNE Kanab	1830	none
3–UT, Sand Mountain	10 km SE Washington	1250	none
4A–AZ, Sand Cove	45 km E Kanab	1615	none
4B–UT, Coyote Buttes	45 km E Kanab	1740	none
4C–UT, AZ, state line	45 km E Kanab	1585	none
5–AZ, Thousand Pockets	12 km W Page	1540	none
6–UT, Holden Dunes	10 km WNW Holden	1430	*C. tranquebarica*
7–UT, Oak City	5 km W Oak City	1435	*C. lepida*
8–UT, Little Sahara	12 km W Jerico Junction	1640	*C. lepida*
9–UT, San Raphael Desert	Rt. 24, 12 km S I-70	1341	none
10–UT, Hanksville	22 km N Hanksville	1585	none
11–UT, Snow Canyon SP	12 km N Santa Clara	1310	none
12–UT, Green River	Green River at Utah Co. state line, Brown Park	1700	*C. formosa formosa*
			C. tranquebarica
13–CO, Maybell Dunes	2 km E Maybell	1835	*C. formosa formosa*
			C. scutellaris yampae
14–CO, Great Sand Dunes	Great Sand Dunes National Monument	2130	*C. theatina*
15–WY, Boars Tusk Dunes	43 km N Rock Springs	1890	*C. limbata limbata?*
			C. tranquebarica
16–ID, St. Anthony Dunes	11 km N St. Anthony	1524	*C. arenicola*
17–ID, Bruneau Dunes	Bruneau Dunes State Park	980	*C. arenicola*

TABLE 2. Index counts of adult *Cicindela l. albissima* in the primary habitat at Coral Pink Sand Dunes, 1992–1998.

	1992	1993	1994	1995	1996	1997	1998
Total for primary habitat	651	895	511	513	843	331	758
Swales north of swale 4	49	46	25	38	107	23	50
Swales south of GH	107	139	91	116	234	48	220
% of total north of 4 and south of GH	24	21	23	30	40	20	36

of the high-density area varied among years, but highest total percentages were in 1998 (36%) and 1996 (40%; Table 2). Adults were always more abundant in the adjacent area to the south, which extended for about 1300 m south of GH and included many swales having at least some adults (Fig. 1B). The adjacent area of primary habitat to the north extended only about 500 m beyond swale 4 and included only a few swales with adults. The only adults we found beyond the primary habitat were small numbers (<20 per year) of scattered individuals in 1994, 1996, and 1998 south of the primary habitat (areas D and E) or in the far northern end of the dune field (areas AAA and AA).

Total rainfall from April through October (the activity period for adults and larvae of *C. l. albissima*) varied greatly from 1991 to 1998. Totals for the last 3 years were higher than all other years. We found a significant positive correlation (Spearman rank correlation, $r = 0.036$, $P = 0.035$) between the total April–October rainfall in one year and adult numbers the following year (Fig. 3). For example, very low rainfall totals in 1993, 1994, and 1996 were associated with very low adult numbers the following years.

Checks of recaptured beetles during 6 years (1993–1998) of mark-recapture studies indicated that *C. l. albissima* adults moved very little throughout the dune field at CPSD. Of 275 adults recaptured, 205 did not move beyond the swale row (<200 m) in which they were marked, 34 moved 200–300 m, 16 moved 300–500 m, 14 moved 500–700 m, and 6 moved 700–1000 m.

Our initial observations and subsequent surveys indicated that larvae were most common in sparsely vegetated outer edges (away
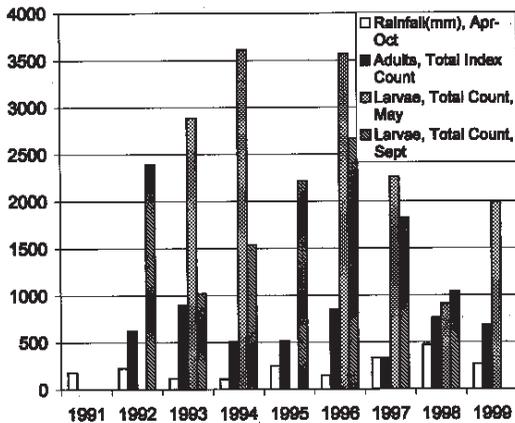
Fig. 3. Rainfall amounts and adult and larval numbers. Rainfall amounts are total mm from April through October each year at Kanab. Adult numbers are index counts in mid-May. Larval numbers are totals of all larval burrows counted in all swales of the primary habitat.

TABLE 3. Mean numbers of larvae in specific swale groups in the primary habitat at CPSD. Means are based on single counts in May and September 1993–1998 for individual swales listed in each row.

Swales	Mean number of larvae	
	May	September
5–9	76.8	97.9
4	193.4	189.8
1	247.8	227
PB,2,3	518.8	294.1
IJK	295.2	377.4
GH	244.4	129.1
LMN	78.8	69.6
OP	190.8	111.7
QR	414.4	281.2
ST	38.2	22.6
UVW	201	262.2
XYwY	46.3	29.4

from the slipface) of the interdunal swales and in nonvegetated adjacent low dune slopes. Some larvae were also found in the more densely vegetated interior of some swales, and small numbers were occasionally seen on mid- and upper slopes, especially after rains. We also noticed that on days after a substantial rainfall many larvae appeared at the base of some slipfaces. (Tiger beetle larvae frequently clear out their burrows after rains.) Total numbers of larval burrows counted (permanent plots and other areas within the swales) in the primary habitat during May and September varied more than threefold over the years. May counts ranged from 3567 in 1996 to 908 in 1998, while September counts ranged from 2830 in 1996 to 1880 in 1993 (Fig. 3). As with adults, highest numbers of larvae were in the area from swale 4 south to swale row GH (Table 3). Most swale rows in this area had means near or >250 larvae in both May and September survey dates. Other swales with similar high mean larval numbers were QR, UVW, and OP. However, larval numbers in QR and UVW declined to <100 in 1996, 1997, and 1998, while numbers in OP increased about twofold during this same period. Mean number of burrows for the 5 swales north of swale 4 (5 to 9) was <100 in both May and September counts. Small numbers of larvae were also found ~4 km from the primary habitat in 12 swales in the far northern end of the dune field (areas AAA, AA). Prior to 1996 we found only a few

scattered burrows in 1 or 2 swales in this area, but in 1996 we counted a total of 74 larvae in 5 swales, in 1997 we found 67 in 8 swales, and in 1998 we found 352 in 8 swales.

Seasonal Activity, Life Cycle and Behavior

We first saw adults of *C. l. albissima* on the dunes in late March or early April after they emerged from overwintering (Fig. 4). Emergence continues through May, with peak numbers occurring from early to mid-May. Numbers begin to decline in late May, and by late June most adults have died off. Few adults are found from July to mid-August. A small proportion of the previous year's larvae completes its development, pupates, and emerges in late August. These adults are active until late September or early October, then dig overwintering burrows. Our estimates of adult numbers during this period were ~300 in 1991, ~100 in 1993 and 1994, and 160 in 1998. These fall adults will reemerge in spring along with the larger proportion of the cohort, which develops more slowly and does not emerge in the late summer.

Mating and ovipositing were observed soon after spring adults emerged and continued throughout the adult activity period. First-instar larvae were first seen in late May, and by July most of the new larval cohort had progressed to the second instar (Fig. 4). Many second instars completed their development by October before overwintering as third instars, but slower developing individuals overwintered as second instars. Third instars had
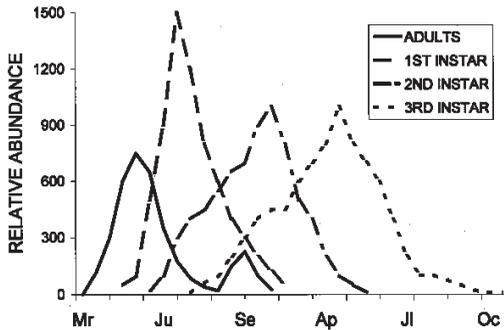
Fig. 4. Seasonal abundance of the life history stages of *Cicindela l. albissima.*
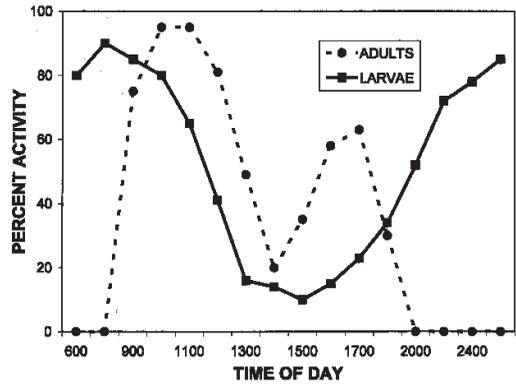

Fig. 5. Daily activity pattern for adults and larvae in May at CPSD.

the longest developmental period, and most of the larval cohort continued in this stage through most of the 2nd year before pupating and emerging as adults during the 2nd fall or the following spring. The rate of larval development is greatly influenced by climate, the amount of food obtained, and perhaps other factors that may cause the larvae in a cohort to develop asynchronously. In Manitoba the life cycle of *C. l. nympha* was 3 years (Criddle 1910), probably because lower temperatures in the spring and fall reduce seasonal activity of larvae.

Observations on warm, sunny days in May indicated that adults begin to emerge from their overnight burrows and appear in swales and low slopes at about 0830–0930 hours (Fig. 5). Numbers increase rapidly, with peak abundance from about 1000 to 1230 hours, and then decline from about 1300 to 1600 hours as many adults dig burrows in the dune slopes to avoid high surface temperatures. Some of these adults reemerge from their burrows about 1600 hours and remain active until 1700–1900 hours, when they again dig burrows on dune slopes or interdunal swales to spend the night. On cloudy or windy days when surface temperatures remain <35°C, adults may be active most of the day. For several years in May we made observations on adults digging burrows. Adult beetles used their mandibles and legs to dig the burrow and push out the sand with an alternating back-and-forth, sweeping movement of the meso- and metathoracic legs. These burrows were 4–9 cm deep, slightly angled, and 7–16 cm long. Fifty-two of 111 observations were of females, 37 were of males, and 22 were of mated pairs. Adult males of *C. l. albissima*, like those of many other species,

exhibit contact guarding (Knisley and Schultz 1997) and use the mandibles to grasp the female as she digs the burrow. Sixty-six percent of these burrows were within interdunal swales and low slopes, 24% in the mid-slope area, and 10% at or near the dune crest. The 85 prey items observed being eaten by adults included 27 ants, 21 already dead insects (mostly orthopterans and large ants), 11 flies, 9 homopterans, 7 beetles, and 10 unidentified insects.

Another tiger beetle, *Cicindela tranquebarica*, also common at CPSD, co-occurred (both adults and larvae) with *C. l. albissima* in some interdunal swales of the primary habitat where there was a layer of clay in the sand and/or presence of very moist soil (Romey and Knisley in preparation). Adults and larvae of *C. tranquebarica* were also common in similar types of swales outside the primary habitat (especially E, AA, A) where *C. l. albissima* was absent.

We observed little evidence of natural enemies attacking *C. l. albissima.* On 2 June 1994 we found an individual of the small, antlike parasitoid wasp, *Methocha* sp., entering a second-instar larval burrow. After the wasp exited the burrow, we dug out the larva and found it paralyzed and with an egg on it. In May 1995 we found 2 third-instar *C. l. albissima* larvae with larvae of the bee fly (possibly *Anthrax* sp.). Several days before, we observed an adult fly in the same area. None of the other 600+ larvae that we dug out between 1991 and 1998 were parasitized. Both parasitoids are specific to tiger beetle larvae, but their effects on tiger beetle populations are difficult to determine unless individual burrows are marked and

monitored. We frequently observed asilid flies on the dunes but did not see any instances of this known predator of adult tiger beetles attacking *C. l. albissima.*

Habitat Characteristics

Dominant plant species within the swales of the primary habitat (area C) were different from those in other dune areas (AAA, AA, A, B, D, E). *Psoralidium lanceolatum* Rydb. had the highest mean coverage percent in all but 1 of the swale rows of the primary habitat, while *Sophora stenophylla* Gray, *Stipa hymenoides* R. & S., and *Reverchonia arenaria* Gray were also abundant and widespread within this area (Table 4). These species were absent or much less common within swales of other dune areas. *Wyethia scabra* Hook. was absent or rare in primary habitat swales, but it was a dominant plant species in areas AAA, AA, A, B, and E, along with *Chrysothamnus* sp., *Eriogonum* spp., and several other species (*Gilia congesta* Hook, *Redfieldia flexosa*) included in the "other" category of Table 4. The northern half of the dune field (areas AAA to B) had a greater diversity of plant species and was dominated by *Wyethia scabra,* which also was the dominant plant species at the south end of the dune field (area E)*. Juncus arcticus* Willd., abundant in many of the wetter swales in the northern and southern parts of the dune field, was nearly absent from swales of the primary habitat. *Dicoria brandegei* was observed to be extremely abundant and widespread in primary habitat swales during September, but it was absent or present only as seedlings in May when vegetation surveys were conducted. Total percent vegetation cover was higher in all swales of the primary habitat (means of 23–57%) than in swales in other areas (means of 12–17%; Table 4).

Mean numbers of arthropod taxa and individuals per area (12 traps in 2 swales) from the 1993–1996 pitfall surveys were significantly different (Kruskal-Wallis ANOVA, $P < 0.05$) among the 7 areas surveyed. Highest means were in areas C and AAA (Table 5). Mean numbers of both taxa and individuals collected in the 1998 surveys were significantly higher in the low OHV-use swales than in the high-use swales (paired t test, $P < 0.05$). Importantly, the highest numbers of taxa and individuals were in the low-use swales of area C, and the greatest difference in numbers of individuals (1027 and 422) and taxa (51 and 39) between low- and high-use swales was also in area C. This great difference in area C probably reflects the greater difference in amount of OHV use in high- and low-use swales of this area.

OHV Activity and Impacts

Mean numbers of OHVs, mean play time, and total width of OHV roads were greatest in

TABLE 4. Mean percent cover of plant species in swales in different areas at CPSD. Plant species are: *S.s.* = *Sophora stenophylla* Gray, *P.l.* = *Psoralidium lanceolatum* Rybd., *S.h.* = *Stipa hymenoides* R.&S., *R.s.* = *Reverchonia arenaria* Gray, *D.b.* = *Dicoria brandegei* Gray, *W.s.* = *Wyethia scabra* Hook., *C.s.* = *Chrysothamnus* sp., *E.a.* = *Eriogonum.*

	Plant species								Other sp.	Total % cover
	S.s.	*P.l.*	*S.h.*	*R.s.*	*D.b.*	*W.s.*	*C.s.*	*E.a.*		
C (PRIMARY HABITAT OF *C. L. ALBISSIMA*)										
5–9	10	60	20	16	4	25			29	46
4	13	75	8	15	2				8	55
1	68	21	12	19	4				3	46
2,3	22	71	6	20	2					48
IJK	26	65	12	14		1			5	57
GH	23	64	9	11	1					45
L–P		32	21	9	4				5	32
QR	10	58	27	8	5	5			1	52
ST	18	70	9	34	6					28
U–Y	16	62	8	5	1				6	23
OTHER AREAS										
AAA	2	6	12			31	10	22	17	16
AA						17	33	3	47	15
A			2			12	12	9	57	12
B	12		4			19	30	9	31	16
E	8	12				40	15		25	17

TABLE 5. Mean numbers of arthropod taxa and individuals collected from pitfall traps in different areas of CPSD. Means for 1993–1996 are based on total numbers in 6 pitfall traps each in 2 different swales in each area averaged for 4 survey periods (see text). Numbers for 1998 are totals from 6 pitfall traps each in 2 low- versus 2 high-use OHV swales in each area.

Area	1993–1996		1998 low OHV		1998 high OHV	
	No. of taxa	No. of indiv.	No. of taxa	No. of indiv.	No. of taxa	No. of indiv.
AAA	43	285				
AA	18	124	27	194	22	90
A	24		139			
B	23	133	44	260	36	245
C	27	341	51	1027	39	422
D	22	222				
E	21	148	24	282	26	184
MEAN TOTALS			36.5	441	30.8[a]	235[a]

[a]Means are significantly different for low- versus high-OHV swales (paired t test, $P < 0.05$).

area E and lowest at the far northern end (area AAA; Table 6). Motorized vehicle play time was over 4 times higher in area E than in any other dune area. OHV activity parameters in the other dune areas were quite variable but indicated intermediate level of OHV activity between the 2 ends of the dune field. Areas E and A are major points of vehicle access to the dunes.

Numbers of injured adults of *C. l. albissima* found during our mark-recapture studies varied greatly among years. Numbers injured and total number captured and examined during Memorial Day periods were as follows: 1993, 14 of 179 injured in 1–2 days after Memorial Day; 1994, 0 of 363 injured before Memorial Day weekend, 6 of 125 after; 1996, 2 of 231 before and 41 of 287 after; 1997, 2 of 256 before and 6 of 64 after; and 1998, 1 of 168 before and 8 of 278 after. Results of run-over trials indicated that the type and/or condition of substrate and number of passes were important in the fate of beetles run over by an OHV. No beetles on dry sand were injured or killed when run over once, but a majority of those on either wet sand or gravel were injured or killed by a single vehicle pass (Table 7). Most or all beetles were killed or injured by 5 and 10 passes on all substrates.

DISCUSSION

Distribution, Abundance, and Biology

Our search of collection records and our field surveys indicate that *C. l. albissima* occurs only at CPSD. Its limited distribution in Utah

and surrounding areas may be due to the absence of other high-elevation sand dunes. The Great Sand Dunes of Colorado is the only similar high-elevation site, and the closely related species *C. theatina* occurs there. *Cicindela. l. albissima,* like its more northern relatives, is apparently restricted to habitats with cooler temperatures. Rumpp (1961) suggested that the distinct lack of elytra pigmentation in *C. l. albissima* may be a thermoregulatory adaptation to its presence in a more southern location than the other subspecies of this species. The single individual that was found north of CPSD may have been a dispersing individual since only one was encountered. Several searches of this area by us revealed no beetles or suitable habitat.

We believe that the index counts give an accurate representation of the year-to-year variation in numbers of adult *C. l. albissima,* but the counts clearly underestimate the actual population size at CPSD. Lincoln index values from mark-recapture studies that we conducted coincidentally with the 1993–1998 index counts (Knisley and Hill unpublished studies), other studies we have done with *Cicindela* (Knisley and Schultz 1997), and a study comparing different survey methods in 1999 (Gowan and Knisley in preparation) all suggest the actual population size may be 2–3 times higher than the index counts. The underestimate is probably the result of some beetles flying off before they are counted or occurring in patches of overlooked habitat or in burrows.

The significant year-to-year variation in *C. l. albissima* numbers is typical of many desert arthropods that are greatly affected by climatic

TABLE 6. OHV activity throughout different areas of CPSD. OHV numbers are means of two 1-hour counts each on Saturday and Sunday of Memorial Day weekends in 1997 and 1998 and Labor Day 1998. Vehicle play time is the mean number of OHVs multiplied by minutes per hour averaged for the 3 weekends (Cn is the northern part of C, Cs the southern part).

	Area of dune field							
	AAA	AA	A	B	Cn	Cs	D	E
Mean number of OHVs per hour	3	19	69	60	67	70	51	94
Mean vehicle play (vehicle minutes per hour)	22	62	138	161	50	92	138	771
Total width of OHV roads (m)	75	125	188	181	122	108	226	230

TABLE 7. Effects of OHV run-over trials on adults of *Cicindela l. albissima* on 31 May 1994.

Substrate type	No. in trial	No. of passes	Effect on beetles		
			No effect	Injured	Killed
Dry	5	1	5	0	0
Dry	5	5	2	1	2
Dry	5	10	0	0	5
Wet	15	1	5	7	3
Wet	15	5	2	0	13
Wet	15	10	1	0	14
Gravel	5	1	2	3	0
Gravel	5	5	2	1	2
Gravel	5	10	0	1	4

factors, especially rainfall (Seely 1991). The positive correlation we found between April–October rainfall amounts one year and adult numbers the following year suggests rainfall may be one of the key factors affecting population dynamics of *C. l. albissima.* Studies with other desert tiger beetle species in Arizona demonstrated that higher rainfall increases survivorship of larvae by reducing mortality from desiccation and starvation, especially of first instars (Knisley 1987, Knisley and Juliano 1988). Prey was more abundant during wet years, and this not only reduced the effects of starvation but also decreased development time and increased fecundity. We expected that these effects and the importance of soil moisture for oviposition and egg hatch should similarly result in higher larval numbers in September counts in years with high rainfall, but our data do not show this. Obviously, other factors are important in population dynamics of this species, and clear patterns of cause and effect are difficult to determine without more detailed studies. Our study does provide some evidence that larval survivorship is very low for this insect. Total adult numbers are consistently much lower than larval numbers, and larval numbers in September counts are lower

than those in May. We also found survivorship was <20% for several patches of larvae that were marked as first instars in May 1996 and monitored through part of the third instar (Knisley unpublished study).

Much of what we learned about the biology of *C. l. albissima* was similar to that of other tiger beetles that have been studied. Its biology is especially similar to that of *C. l. nympha* in Canada (Acorn 1991) and *C. arenicola* from the St. Anthony Sand Dunes in Idaho (Anderson 1988, 1989, Bauer 1991). The amount of movement of marked individuals of *C. l. albissima* was, like *C. arenicola,* quite limited compared to many tiger beetle species. Anderson (1989) found that most marked adults of *C. arenicola* remained in the same general area where they were marked and only a few dispersed (in a "step-stone" manner) >500 m. The *C. l. albissima* found near Mt. Carmel Junction suggests that, at times, adults may disperse much greater distances than what we observed. The adults and larvae found at the far northern end of the dune field probably represent a colonizing event by adults that dispersed from the primary habitat. Dispersal may be greater during times of high density, as is common in many other animals. For example, we found that

highest proportions of adults in areas adjacent to the swale 4 to GH concentration area were in 1996 and 1998, 2 of the years of greatest adult abundance.

The seasonal pattern we observed for *C. l. albissima* represents a variation of the typical spring–fall life cycle common in many *Cicindela* sp. In this pattern most larvae complete their development in the summer, pupate, and emerge as sexually immature adults in late August and September. They dig burrows in October to overwinter and then reemerge in the spring. The very low counts of adult *C. l. albissima* in September suggest that most of the maturing larval cohort do not emerge in the fall, although they may molt into the adult stage and remain in their pupal burrows (Schultz 1998). Acorn (1991) found that numbers of adults of *C. l. nympha* in the Canadian dunes peak in June and September. This is the typical spring–fall pattern and similar to what Bauer (1991) found for *Cicindela arenicola.* The pattern of adult burrowing during midday to escape heat or unfavorable weather conditions and at night is similar to that of *C. arenicola* (Anderson 1988) and other *Cicindela* (Willis 1967, Knisley and Schultz 1997). Our finding of more females and mated pairs digging burrows may indicate that females could be using burrows to oviposit and thus position eggs deeper into the soil where more moisture is present. Such behavior has been observed in other species in the laboratory and in the field (Anderson 1989, Knisley and Schultz 1997). Our observations of predation and potential predators on adults indicate that predation may not be a major limiting factor for adults. Interestingly, Acorn (1991) found evidence that adults of *Cicindela formosa* are an important predator of adult *C. l. nympha.* More studies are needed to determine the importance of parasitism and predation for *C. l. albissima.*

What Factors Explain the Distribution of *C. l. albissima* at CPSD?

Results of this study provide some insight but do not fully explain the localized distribution of *C. l. albissima* within the CPSD dune field. The concentration of adults and larvae within the primary habitat and the presence of very few adults with moderate numbers of larvae in swales at the far north end of the dune field are puzzling. There is significant variation in

the geology, vegetation, prey arthropods, and OHV activity throughout the CPSD dune field, and all of these could significantly affect the distribution and abundance of *C. l. albissima.* Importantly, the primary habitat is very closely associated with distribution of the transverse type of sand dunes at CPSD, while other dune types are present north and south of the transverse dunes where *C. l. albissima* occurs (Ford and Gillman 2000). There is also a distinct transition in the dynamics, physical characteristics, and elevation of the dune field progressing from southwest to northeast. The south end of the dune field (area E) is lowest in elevation (<1800 m) and nearest the sand source that feeds the dunes. It is the most dynamic area with the least vegetated interdunal swales (with little *P. lanceolatum* and *S. stenophylla*) and the best developed and most active dunes. *Wyethia scabra* is the dominant cover plant in this sparsely vegetated part of the dune field. This is also the part of the dune field with the highest level (by far) of OHV activity (a primary vehicle play area) and relatively low numbers of arthropods. The high OHV use probably contributes to the low vegetation cover, an effect that is well documented (Vollmer et al. 1976, Hosier and Eaton 1980, Luckenbaugh and Bury 1983). We have observed that many interdunal swales in this area had OHV tracks indicative of heavy use and were nearly devoid of vegetation. We cannot determine which of these differences in this part of the dune field explains the absence of *C. l. albissima.* Adults and larvae of *C. tranquebarica* were mostly found in swales with damp soils and lower OHV activity.

The northern half of the dune field (areas A to AAA) is the highest in elevation (>1900 m) and the least dynamic area, with large numbers of ponderosa pine stabilizing the dunes. Most of the swales, however, are sparsely vegetated, similar to that at the south end, and dominated by *Wyethia scabra* and a greater variety of plant species. Arthropod abundance is low and OHV activity moderate to heavy in areas B and A, but in the far north end (AAA) this pattern is reversed. Low OHV activity and high numbers of arthropods in AAA may partly explain the presence of *C. l. albissima* there and its absence in areas A and B. The increase in numbers of larvae in the past 3 years may be due partially to the exceptionally high rainfall and its effect on larval recruitment

and survival (see above). However, the very low adult numbers here suggest that this north end of the dune field may be unfavorable for complete development and successful emergence of adults.

The primary habitat of *C. l. albissima* (area C) has some distinctive features that may contribute to the beetle's predominance there. This area is a transitional zone between the highly dynamic south end and the stabilized dunes north of area B. Dune slopes and ridges are open and very active, but interdunal swales have higher percent vegetation cover relative to other areas. The dominance of *Psoralidium, Sophora,* and *Stipa* in these swales may provide a different and more favorable habitat for larvae by supporting a greater abundance of arthropods as a food source for larvae and adults. The level of OHV activity in this area is moderate, but numbers of OHV roads are fewer, play time less, and apparent OHV damage to swales more limited than in adjacent areas to the north and south. We have also observed during the years of our study that swales in the northwestern part of the primary habitat supporting most of the adults and larvae have received less OHV use than swales along the eastern side of the primary habitat.

Our studies show that some adults are killed each year from run-overs by OHVs, but it is not certain if this significantly impacts the population. A greater effect may occur when adults are run over and crushed in their shallow adult burrows on the dune slopes. We have not observed this effect. Low levels of OHV activity may not impact larvae because their burrows are deep enough (>20 cm) for them to avoid being crushed. In experimental run-over trials, Anderson (1989) found no effects to larvae of *C. arenicola* after 10 OHV passes. Heavy OHV activity, such as seen at some areas of CPSD, may impact the population through other direct or indirect effects on adults and larvae. Adult feeding, oviposition, and mating may be disrupted by OHVs, and this effect could reduce recruitment, as was reported for *C. dorsalis* on Virginia's coastal beaches (Knisley and Hill 1992). The reduction of swale vegetation may coincidentally reduce prey arthropod abundance and negatively affect larval survival. Off-highway vehicles may cause a mixing of the upper sand layers, which can increase desiccation (Webb et al. 1978) or alter the soil moisture gradient of the larval micro-

habitat (Schultz 1988). Soil moisture measurements taken in 1996 in different portions of the CPSD dune field indicated that areas in and near heavy-use OHV roads had significantly lower soil moisture readings than undisturbed areas nearby (Gwilliam, Hill, and Knisley unpublished study). Although it cannot be concluded from our study, it is possible that high levels of OHV activity in area E and parts of areas B and A, just north of the primary habitat, prevent the successful colonization of *C. l. albissima.*

Despite the potential negative impacts from OHV activity, there is no evidence of a progressive decline of the population of *C. l. albissima* at CPSD. There are no records of this species' abundance prior to the beginning of OHV activity >20 years ago, and so it is unknown whether the population was historically larger. Year-to-year fluctuations in adult population size have been significant, but declines have been followed by a rebound in abundance. It is believed that implementation of the conservation plan in 1998, which prevents or reduces vehicle activity in most of the primary habitat, will provide long-term protection for this species at CPSD. Continued monitoring and study of the *C. l. albissima* population will help to determine this.

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