

BIOLOGY AND DISTRIBUTION OF A RECENTLY REDISCOVERED ENDEMIC HAWAIIAN
LEAFROLLER MOTH, *OMIODES CONTINUATALIS* (CRAMBIDAE)

CYNTHIA KING

University of Hawaii, Dept. of Plant and Environmental Protection Sciences, 3050 Maile Way, Gilmore Hall 310, Honolulu, HI 96822
e-mail: cbaking@hawaii.edu

DANIEL RUBINOFF

University of Hawaii, Dept. of Plant and Environmental Protection Sciences, 3050 Maile Way, Gilmore Hall 310, Honolulu, HI 96822
e-mail: rubinoff@hawaii.edu

and

WILLIAM HAINES

University of Hawaii, Dept. of Plant and Environmental Protection Sciences, 3050 Maile Way, Gilmore Hall 310, Honolulu, HI 96822
e-mail: whaines@hawaii.edu

ABSTRACT. The endemic Hawaiian leafroller moth *Omiodes continuatalis* was documented by early entomologists to be one of the most common species encountered during initial collecting trips in the Hawaiian Islands at the end of the 19th century. The species was declared extinct in 1982, and while subsequent surveys have resulted in their “rediscovery”, it is evident that *O. continuatalis* populations have experienced declines and localized extinctions throughout their historical range. The objective of our research was to document the life history, biology, general morphology, and behavior of this little studied species. To complete the investigation, we observed both wild caught and laboratory reared *O. continuatalis*. We also conducted light trap surveys to document the current distribution of *O. continuatalis* across the Hawaiian Islands. We have integrated our findings from this study with all available historical data on *O. continuatalis*, to create a document which can be referenced for future research relating to the biology or conservation of this species.

Additional Key words: pyraloid, light trap, fossorial, development, extinction

The genus *Omiodes* Guenée, 1854 (Lepidoptera: Crambidae) occurs in tropical and subtropical regions of Oceania, Southeast Asia and the Americas, and contains over 100 species, including 23 species endemic to the Hawaiian Islands. The subject of this research, *Omiodes continuatalis* (Wallengren, 1860), is a generalist grass-feeding species, originally documented from all of the high Hawaiian Islands, with the exception of Kahoolawe (Zimmerman 1958). The Reverend Thomas Blackburn found *O. continuatalis* to be one of the most common moths encountered during collecting trips in Hawaii prior to 1880 (Zimmerman 1958). Swezey reported the species from “drier, lower” habitats, but does not provide specific collection localities beyond a single reference to a population in Olinda, Maui (Swezey 1907; Zimmerman 1958). Despite their early documented widespread abundance, 100 years later the species was declared extinct by the U.S. Fish and Wildlife service, and other agencies (Gagné & Howarth 1982; IUCN 2007). *Omiodes continuatalis* and 13 other *Omiodes* species were listed as “extinct or possibly extinct” based on reviews of museum collections which indicated that specimens had not been collected for

several decades. Non-target impacts of the biological control agents introduced for the coconut and sugar cane leafroller pest species were blamed for the extinctions (Gagné & Howarth 1982). However, data from surveys of more recent museum collections completed in 2003 revealed extant *O. continuatalis* populations (Haines *et al.* 2004). Specimens were identified from light trap samples collected at five mesic forest study sites on both the leeward and windward sides of Hawaii Island (Haines *et al.* 2004). In addition, field collections completed in 2003 confirmed *O. continuatalis* to be abundant at several localities on East Maui (Haines unpublished data).

In the past, *O. continuatalis* larvae have been collected from native pili grass *Heteropogon contortus* (L.), as well as introduced species such as kikuyu grass *Pennisetum clandestinum* (Hochst. ex Chiov.) and Hilo grass *Paspalum conjugatum* Berg. (Zimmerman 1958). Like other species in the group, *O. continuatalis* larvae are leaf-rollers, and use silk to bind plant foliage together to create a refuge in which they feed and take shelter. Early observations by Swezey describe how *O. continuatalis* larvae typically feed near the base of their

host plants, within the grass matrix or in leaf litter at the soil surface (Zimmerman 1958). This behavior is uncharacteristic of other Hawaiian *Omiodes* larvae, which generally feed higher on host plant foliage, fastening or rolling the tips of leaves together (Swezey 1907). *Omiodes continuatalis* larvae were also noted to be physically distinct from larvae of other *Omiodes* species, in that they attain a greater body width and often exhibit pinkish-green coloration in contrast to the monochromatic green coloration displayed by larvae of other *Omiodes* species (Zimmerman 1958).

Unlike the sugarcane leafroller *O. accepta* (Butler, 1877), *O. continuatalis* is not considered a pest and consequently few data have been collected to document its life history. *Omiodes continuatalis* appear to share similar habitat requirements, feeding habits and physical characteristics with *O. accepta* (Zimmerman 1958), and initially seemed likely to have comparable biology and development. The objective of this chapter is to describe the complete life history of *O. continuatalis*, providing new information on its biology, ecology, general morphology and life history, and to integrate recent findings with information gathered by early naturalists, to create a document that can serve as a reference for future research on the biology and conservation of *O. continuatalis*.

MATERIALS AND METHODS

We collected data for this laboratory and field study from February 2005 to March 2008.

Insect rearing. We established laboratory colonies of *O. continuatalis* using wild female moths captured from UV light traps set on Kailiili Road in Kokomo, Maui (484m) and at the University of Hawaii Kula Agricultural Research Station (975m), Maui. Moths were collected alive in plastic specimen vials, and held at ambient temperature until being transferred into rearing cages. Moths were easily identified using the key to *Omiodes* species in Zimmerman (1958), as *O. continuatalis* is a very distinctive species. Rearing cages were composed of hand-made 61cm×46cm×31cm PVC-framed sleeve cages covered with fine insect mesh sleeves. Moths were fed a 30% honey/70% water solution, and were provided potted sugarcane, pili grass and/or Hilo grass, on which to oviposit. We obtained young sugarcane starts from Hawaii Commercial and Sugar (HCS) and Hawaii Agricultural Research Center (HARC) fields, while pili grass and Hilo grass were propagated from seed. These plants provided food and served as host plants for colony larvae. The substrate in each host plant pot consisted of a 50/50 blend of Sunshine Mix 5® potting soil and vermiculite. All moth colonies and host plants were housed in the University

of Hawaii at Manoa, Gilmore Hall greenhouses, and University of Hawaii, Kula Agriculture Research Station greenhouses. In Manoa, temperatures ranged seasonally from a mean low of 18.7°C in the winter to a mean high of 24.3°C during the summer (Manoa Lyon Arboretum weather station), and plants were watered three times each day. In Kula, temperatures ranged from a mean low of 11.1°C in the winter 2006, to a mean high of 24.4°C during the summer 2006 (UH Kula weather station), and plants were watered twice daily. We collected additional wild *O. continuatalis* moths and integrated them into laboratory colonies periodically to replenish adult stock and maintain genetic diversity.

Biology and morphology. To elicit oviposition, we isolated female moths in vials lined with wax-paper and temporarily denied them access to a food source. These stressful conditions commonly stimulate female moths to oviposit. Eggs deposited in each egg mass were then counted under a Leica dissecting microscope to determine the total number present, and the minimum and maximum number of eggs per mass. In order to quantify mean egg size, we selected 50 eggs randomly from 50 *O. continuatalis* egg masses, and measured them at the widest point using an ocular micrometer in a Wild Heerbrugg microscope.

We obtained data on *O. continuatalis* larval development and morphology by observing 100 individual larvae develop from egg to pupal stage. Larvae were stored in individual 2-oz Solo® cups (ventilated with 3–6 holes in the lid). Cups were cleaned and larvae provided with fresh sugarcane foliage every 2–3 days. We measured the head capsule width of each larva daily to document larval growth; head capsule widths were measured at their widest point, as above for eggs. We also recorded changes in larval morphology following each larval molt. Only head capsule widths of larvae which survived from egg to pupal stage ($n = 52$) were used to assess instar duration and size ranges. We completed a one-way analysis of variance to document variation in head capsule width by instar.

Behavior. Data relating to *O. continuatalis* larval behavior were collected based on observations of individual larvae contained in laboratory colonies, or from colony larvae deployed on potted host plants at selected Maui field sites. We collected data opportunistically, observing behaviors in the field during larval deployment and retrieval, and in the laboratory during daily colony maintenance and larval feedings. Adult *O. continuatalis* were isolated and observed individually to assess adult lifespan under laboratory colony conditions.

Distribution. Field sites were selected to be surveyed based on accessibility and the presence of *O.*

continuatalis host plants. We collected *Omiodes continuatalis* adults using two types of UV light traps: sheet light traps and bucket light traps. Sheet light traps consisted of an 18" UV light bulb placed in front of a large, white bed sheet suspended vertically. Bucket light traps were constructed with an 18" UV light bulb attached to three 10.2cm×25.4cm clear plastic flight intercept vanes, and secured on top of an 8 liter bucket with bungee cords. Each bucket trap was baited with a killing agent such as cyanide or a Hot Shot No-Pest Strip®. Individual moths landing on sheet light traps were collected alive, however insects collected from bucket traps were always dead. We set at least one of the two trap types at each field site to survey for *O. continuatalis* adults. When an initial survey yielded numerous *O. continuatalis* specimens, we revisited sites to replenish and diversify laboratory colonies. Visual surveys of and sweep netting for adult *O. continuatalis* were also completed at field sites to complement data collected from light trapping. To quantify total survey effort, the number of nights and the number of traps that were used, were multiplied to obtain the total number of "trap nights" completed at each survey location.

RESULTS AND DISCUSSION

Biology. *Omiodes continuatalis* are highly attracted to UV light, and both male and female moths were regularly collected from light traps. In addition, *O. continuatalis* appeared to be more attracted to UV light traps than other *Omiodes* species. Once drawn to a light, *O. continuatalis* adults frequently remained around the light for long periods of time, in contrast to the sedge-feeding species *O. anastrepta* Meyrick, 1899, which are not as readily attracted to light traps, even when adults are observed flying in close proximity to a trap. Over the course of one year, adult *O. continuatalis* were collected, on multiple occasions, from light traps at Kokomo, Makawao, and Kula, on Maui (Table 1). Data from these surveys indicate that *O. continuatalis* is multivoltine, with more than three generations per year. Considerable climatic seasonal variation exists at mid-high elevation localities, so if *O. continuatalis* populations are multivoltine at these three mid-high elevation field sites, it is likely that populations are also multivoltine and not seasonal at low elevation sites, where seasonal changes in temperature and rainfall may be even less restrictive to *O. continuatalis* development. Based on mitochondrial genetic data, *O. continuatalis* populations do not exhibit much structure, either within or among islands (Haines, unpublished data), suggesting that moths are strong dispersers. Because of this, we do not suspect that populations on islands other than Maui

exhibit very different morphology or life history characteristics from those observed in our colonies.

Laboratory colonies of *O. continuatalis* were maintained continuously from July 2005–December 2005, and from March 2006–March 2008. In laboratory colonies, the moths were most successfully reared on sugarcane host plants, as compared with pili grass and hilo grass, which the moths were previously documented feeding on in the field. At one point during rearing of the colony, some larvae escaped from cages and were discovered feeding on *Canavalia pubescens*, Hook. & Arn. (Fabaceae) an endemic Hawaiian legume which was being grown in the same greenhouse as food for another caterpillar species (*O. monogona* Meyrick, 1888). The *O. continuatalis* larvae were caged with *C. pubescens*, and surprisingly, multiple generations were reared on the plant. There are no previous records of this grass-feeding species surviving on a dicot host, yet it survived through four generations on *C. pubescens* with no obvious morphological or reproductive disadvantages. The success of the moth on this host plant over multiple generations indicates that its host range in the wild might be broader than previously expected, although oviposition preference may be more important than nutritional suitability as a determinant of host range. While the utilization of this host plant was unexpected given the documented life history of the species, it may be explained by recent molecular analysis of the genus. Phylogenetic analysis based on mitochondrial DNA shows that *O. continuatalis* is the sister species, and the closest relative, of *O. monogona*, the sole Hawaiian *Omiodes* species which feeds on fabaceous host plants (Haines unpublished data). Other tropical *Omiodes* species are documented to feed on Fabaceae, thus this dietary shift may reflect a reversion to an ancestral host plant retained in the evolutionary 'memory' of some Hawaiian *Omiodes*. Evolutionary memory is the idea that larvae may retain an ability to feed on ancestral hostplants on which they are no longer found in nature (Janz & Nylin 1998). This discovery has important implications not only for the conservation of the species, but also for the evolution of host plant shifts in the genus.

Adult *O. continuatalis* (Fig. 1) lived a maximum of 18 days under laboratory conditions. In cages, *O. continuatalis* females were observed ovipositing on both the upper and lower surfaces of host plant vegetation, and females did not avoid ovipositing on material such as wood, plastic, wax paper and screen mesh. Egg masses ranged in size from a single egg, to a maximum of 73 eggs, with a mean of 7.25 (\pm 0.81 S.E.) per individual egg mass ($n = 115$). A limited survey of *O. continuatalis* females ($n = 33$) indicated that gravid



FIG. 1. Adult *Omiodes continuatalis* moth.

females can lay more than 400 eggs over their lifetime, and up to 122 eggs in a 24 hour period. Egg masses are composed of even rows or clusters of flattened eggs, slightly overlapping one another (Fig. 2). Eggs have a mean width of 1.22mm (± 0.025) ($n = 50$), are light yellow in color, and exhibit fine surface reticulations and an iridescent sheen. *Omiodes continuatalis* eggs took four days to hatch at 32°C, and eight days to hatch 22°C.

Morphology. Swezey broadly described the life history and physiology of *O. continuatalis* (summarized by Zimmerman 1958). Zimmerman (1978) later provided limited descriptions and illustrations of larval morphology, including a larval key to most Hawaiian *Omiodes* spp. However, no detailed research has been reported that fully characterizes the life history and larval stages of *O. continuatalis*.

Based on head capsule width measurements from 52 individuals, we observed *O. continuatalis* larvae transitioning through seven to nine developmental instars (Fig. 2). In a previous study, *O. continuatalis* larvae were observed transitioning through as many as 10 instars prior to pupation (King & Rubinoff 2008). Analyses of variance of head capsule widths by instar indicates that mean head capsule widths for instars 1 through 9 are significantly different from one another (Figure 2; $df = 8$; $F = 1823.68$; $P = <0.001$). Due to considerable overlap in head capsule widths in each instar (Fig. 3), it is difficult to distinguish discrete larval instars at any stage of development based on measurements alone.

Upon eclosion, larval head capsules are reddish-

brown in color and have a mean width of 0.35mm (range: 0.32–0.38). The reddish-brown coloration persists throughout the entire larval stage. Unlike the larvae of other Hawaiian *Omiodes* species which maintain bright green body coloration (Swezey 1907), *O. continuatalis* larval coloration is comparatively less vivid. The abdomen is a gradient of off-white to light olive, and once larvae begin feeding they acquire the approximate pigment of the vegetation they are digesting. Larvae may molt to the second instar (mean: 0.45mm, range: 0.40–0.50) and the third instar (0.64mm, 0.50–0.74mm) after three to five days. In the third instar, larvae develop a single black head spot on each of the head capsule lobes, as well as two black spots on the prothoracic shield. *O. continuatalis* larvae continue to molt every three to five days (4th: 0.92mm, 0.66–1.10mm; 5th: 1.28mm, 0.90–1.42mm; 6th: 1.78mm, 1.3–1.96mm), growing in size and developing more intricate patterns of melanization on the prothoracic shield, as well as tubercles on the 2nd and 3rd thoracic segments and the 7th–10th abdominal segments. During the penultimate instar (6th; 7th: 2.32mm, 1.8–2.52mm; 8th: 2.84mm, 2.34–3.56mm), *O. continuatalis* larvae acquire a faint pink tint, while the

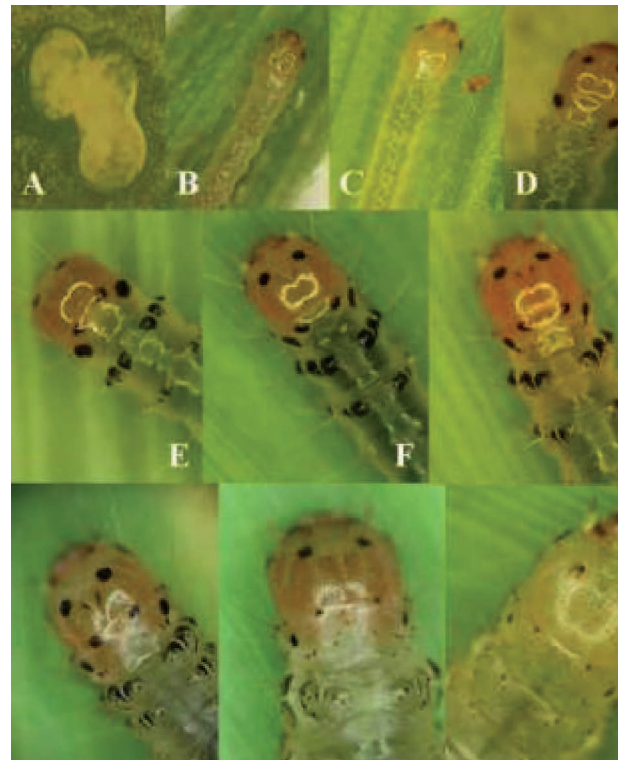


FIG. 2. *Omiodes continuatalis* larvae exhibit changing patterns of melanization on the prothoracic shield during nine developmental instars. A. Cluster of eggs. B. First instar. C. Second instar. D. Third instar. E. Fourth instar. F. Fifth instar. G. Sixth instar. H. Seventh instar. I. Eighth instar. J. Ninth instar.

head, thoracic and abdominal spots are reduced. Molts to the final instar (7th; 8th; or 9th: 3.19mm, 2.86–3.50mm) also occur in three to five days. At this stage, head spots disappear completely, and the thoracic and abdominal segments become very pink. Immediately prior to pupation, *O. continuatalis* larvae become pale and begin to shrink in size to form pre-pupae. It is common for lepidopterous larvae to change color prior to pupation, when the procuticle increases in area in the cuticle column above the epidermal cells (Chapman 1998). Pre-pupae develop into pupae over 1–2 days, and remain as pupa for 13–17 days. In total, immature *O. continuatalis* development was 36–57 days.

Behavior. Early instar larvae feed on the surface and inner tissue of host plant foliage, often near the midrib of the leaves. *Omiodes continuatalis* larvae cannot be characterized as gregarious, like the larvae of *O. blackburni* (Butler, 1877) which share the same shelters throughout most of their development, however early instar *O. continuatalis* larvae often feed in close proximity to one another. Aggregations of larvae on host plants especially in the first and second instars are a natural result of larvae emerging from eggs laid in clusters. General observations from this research suggest that first instar *O. continuatalis* larvae are more likely to survive when feeding together. First instar larvae that were separated, and made to feed independently, frequently failed to feed successfully and progress to the subsequent instar. The reasons for this increased mortality are not clear, but may involve the cumulative benefit of aggregated larvae feeding cooperatively during early instars. Research indicates that cooperative feeding behavior has many advantages for lepidopterous larvae, including increasing feeding efficiency on physically tough host plant material (Clark & Faeth 1997). It is possible that *O. continuatalis* larvae exhibit this type of cooperative feeding due in part to the fact that they have evolved on grasses, which are tougher than many dicot host plants and contain higher concentrations of silica (Fahn 1982). When *O. continuatalis* larvae reach the third instar they continue to consume the surface and inner tissue of host plant leaves, but fed independently from other larvae more frequently than in the early stages. Third instar larvae began to fasten silk threads across the foliage and/or roll-up foliage to create a protected shelter in which to retreat. During the fourth instar and/or when larvae attain a head capsule width of 1mm, they begin to feed on the entire leaf structure. Some larvae were observed to feed predominantly inside their shelters, while others migrated back and forth between their shelter and feeding areas elsewhere on the host plant. Late instar

larvae primarily feed outside the shelters they construct. Feeding patterns were easily discerned based on areas of feeding damage on field deployed host plants, and host plant material provided to isolated *O. continuatalis* larvae.

In colony, *O. continuatalis* larvae occupied all available space on the host plants provided, from the sheaths at the very base of the sugarcane, to the top of each blade. In contrast, when placed at lower densities on host plants in the field, larvae generally stayed on the green sugarcane foliage on the mid to upper portion of the plant. When foliage was available at the base of the plant, larvae often constructed shelters there, using both fresh and dead vegetation as materials. This behavior is consistent with early observations of larval feeding habits made by Swezey (Zimmerman 1958). Additional observations by King & Rubinoff (2008) indicate that some *O. continuatalis* larvae display a more unusual habit, burrowing beneath the soil surface at the base of their host plants for shelter. In some cases, larvae were recovered up to 14cm below the soil surface. This fossorial behavior was observed in early, middle and late instar larvae, and is not pupation behavior.

Another behavior we observed during laboratory colony rearing was larval cannibalism. *O. continuatalis* larvae, specifically late instars, were observed feeding on other live *O. continuatalis* larvae. This behavior was more common on occasions when larval density was high and host plant resources were decreasing, but still available. Most frequently, late instar larvae were observed feeding on middle instar larvae. In one case a ninth instar larva was found feeding on another ninth instar larva. In all cases, the larvae being consumed did not appear to fight or try to avoid the predation, but remained stationary during the attack. The cannibalistic

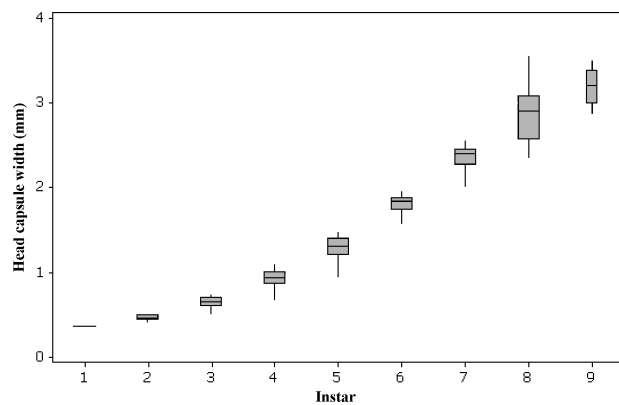


FIG. 3. Boxplot of headcapsule widths of *Omiodes continuatalis* larvae by instar. Medians and inter-quartile ranges are represented for each instar, and box widths are proportional to sample size.

TABLE 1. Locations surveyed for *O. continuatalis* on the main Hawaiian Islands.

Island	Location	Elevation (m)	Method	Date	Trap nights	<i>O. continuatalis</i> present	Surveyor(s)
Kauai	Pu'u Ka Pele Forest Reserve	855	light trap	8/6/08	1	No	W. Haines
	Koke'e State Park, Camp Sloggett	1060	light trap	5/16/05, 10/6/07	3	No	W. Haines, C. King
	Mohihi Road, Koke'e State Park	1110	light trap	6/2/04	2	No	W. Haines
	Koke'e State Park, Koke'e Museum	1130	light trap	8/7/07	2	No	W. Haines
	Na Pali Kona FR, Pihea trail	1140	light trap	8/7/07	1	No	W. Haines
	Koke'e State Park, Nualolo Trail	1170	light trap	8/8/07	1	No	W. Haines, M. Medeiros
	Na Pali Kona FR, Alakai Swamp Trail	1180	light trap	8/7/07	3	No	King, Haines, Rubinoff
	Na Pali Kona FR, Pihea trail	1200	light trap	5/18/05, 7/23/06, 8/18/06	4	No	Eiben, Haines, Rubinoff
	Koke'e State Park, Near Awaawapuhi Trail	1245	light trap	6/3/04	1	No	W. Haines
	Na Pali Kona FR, Kalalau Lookout	1255	light trap	8/17/06	2	No	J. Eiben, D. Rubinoff
Oahu	Aina Haina, Niuiki Circle	2	light trap	3/24/05	1	No	C. King
	Mokuleia Beach	2	light trap	5/1/05	1	No	W. Haines, C. King
	Sandy Beach	3	light trap	3/6/05, 6/20/05	2	No	W. Haines, C. King
	Ewa, open grass lot	15	light trap	5/21/05	1	No	C. King
	Diamond Head Crater, wetland	80	light trap	4/3/05, 2/15/08	4	No	W. Haines
	Palolo Valley	80	light trap	2/25/08, 2/26/08, 2/27/08, 2/28/08	4	No	W. Haines
	HARC Maunawili	160	light trap	5/26/05, 6/22/05	3	No	C. King
	Lyon Arboretum, sugarcane patch	228	light trap	1/27/07	2	No	C. King
	Lanipo Trail	240	light trap	5/29/05	1	No	W. Haines, C. King
	Dole pineapple field	256	light trap	3/12/05	1	No	Haines, King, Vorsino
	Hawaiiolo Ridge Trail	425	light trap	6/14/06	1	No	J. Eiben, W. Haines
	Wiliwilinui Trail, access	440	light trap	6/6/06	1	No	W. Haines
	Wa'ahila Ridge	475	light trap	6/8/06	1	No	W. Haines
	Kahanahaiki Valley	605	light trap	2/24/07	1	No	C. King
	Mt. Tantalus	613	light trap	6/3/05, 6/22/05	2	No	W. Haines, C. King
	Wiliwilinui Trail, Summit	731	light trap	6/24/06	1	No	W. Haines
	Ko'olanu Moutains, Konahuanui Trail	762	light trap	6/1/06	1	No	W. Haines
	Palikea Trail	777	light trap	5/15/06	1	No	W. Haines
	Mokuleia FR, along Mt. Kaala Road	1100	light trap	6/15/07	2	No	W. Haines
	Waiaiae-Kai FR, near Kaala NAR boundary	1190	light trap	6/15/07	1	No	W. Haines
Ka'ala NAR, bog	1200	light trap	6/15/07	1	No	W. Haines	
Ka'ala NAR, DOFAW shed	1210	light trap	6/15/07	1	No	W. Haines	
Maui	Kanaha Beach Park	3	light trap	3/20/05	1	No	C. King
	Maliko Gulch sugarcane field	76	light trap	6/1/05, 7/13/06	2	No	C. King
	West HCS sugarcane field	137	light trap	6/6/06	1	No	C. King
	Iao Valley	183	light trap	6/5/06	1	No	C. King
	Waiehu Valley Trail	183	light trap	7/6/06	1	No	C. King
	Haliimaile sugarcane field	274	light trap	6/1/05	1	Yes	C. King
	University of Hawaii Agricultural Park	305	light trap	6/1/06	1	No	C. King
	Waihe'e Ridge Trail	305	visual survey	6/8/05	0	Yes	W. Haines
	2955B Kaili'ili Rd, Kokomo	484	light trap	3/19/05 ^a	15	Yes	W. Haines, C. King
	Pu'u Kukui Watershed, Kaluanui Valley	485	light trap	4/5/06	2	No	W. Haines
Waihe'e Ridge Trail	670	light trap	6/8/05	1	No	W. Haines	

^a dates = 3/19/05, 5/25/05, 6/1/05, 7/19/05, 9/3/05, 9/23/05, 2/8/06, 3/7/06, 4/18/06, 7/8/06, 3/9/07, 4/19/07, 5/18/07, 8/17/07, 2/6/08

TABLE 1. Continued

Island	Location	Elevation (m)	Method	Date	Trap nights	<i>O. continuatalis</i> present	Surveyor(s)
Maui	Makawao Forest Reserve, Site 1	750	light trap	3/23/05	1	No	W. Haines
	Makawao Forest Reserve, banana patch	762	light trap	6/19/06, 7/14/06, 7/15/06	8	Yes	W. Haines
	Makawao Forest Reserve, Site 5	825	light trap	3/23/05	1	Yes	W. Haines
	Kipahulu Valley Delta Camp, HALE	860	light trap	1/15/04, 9/14/04	4	No	W. Haines, D. Rubinoff
	Makawao Forest Reserve	914	light trap	3/19/05, 5/25/05, 6/1/05	4	Yes	W. Haines, C. King
	Makawao Forest Reserve, Site 2	915	light trap	3/23/05	1	Yes	W. Haines
	Makawao Forest Reserve, Site 6	930	light trap	3/23/05	1	Yes	W. Haines
	UH Kula Field Station	975	light trap	3/9/07*	5	Yes	C. King
	Makawao Forest Reserve, Site 4	1050	light trap	3/23/05	1	No	W. Haines
	Waipoli Road, Kula	1065	light trap	6/20/04	2	Yes	W. Haines
	Haleakala Ranch	1280	visual survey	6/23/06	0	Yes	C. King
	Makawao Forest Reserve	1280	light trap	6/3/06, 8/17/07	2	Yes	W. Haines, C. King
	Makawao Forest Reserve, Site 3	1330	light trap	3/23/05	1	Yes	W. Haines
	Kula FR	2073	light trap	6/4/06	1	No	C. King
Molokai	Moomomi Preserve	10	light trap	7/5/05	1	No	W. Haines
	Molokai Forest Reserve, TNC Barracks	915	light trap	7/7/05, 12/30/05	3	No	W. Haines
	Kamakou Preserve, Kamakou Flats	1105	light trap	5/18/04	2	No	W. Haines
	Kamakou Preserve, Puu Kolekole	1130	light trap	5/19/04, 7/7/05	2	No	W. Haines
	Kamakou Preserve, Pepeopae Bog	1240	light trap	5/19/04, 7/6/05	2	No	W. Haines, D. Rubinoff
Lanai	Lanai Game Management Area	365	light trap	7/3/05	1	No	W. Haines
	Kanepuu Preserve	520	light trap	7/2/05	1	No	W. Haines
	Kanepuu Preserve	544	light trap	3/6/08	2	Yes	D. Rubinoff, P. Schmitz
	Munroe Trail	1000	light trap	7/3/05	1	No	W. Haines
Kahoolawe	Base Camp, south of Kanapou Bay	5	light trap	1/14/06	1	Yes	S. Meyers
Big Island	Pahala sugarcane field	292	light trap	6/10/05	1	No	C. King
	Honokaa sugarcane field	303	light trap	6/9/05	2	Yes	C. King
	Glenwood, Omega Rd.	700	light trap	2/6/05	2	No	W. Haines
Big Island	Glenwood, Near Kahaualea NAR	700	light trap	2/6/05, 7/30/06	6	No	W. Haines
	Ka'u, Kaiholena	770	light trap	7/31/06	2	No	W. Haines, J. Giffin
	Ola'a FR	822	light trap	2/5/05	1	No	W. Haines
	Ola'a FR	975	light trap	2/5/05	1	No	W. Haines
	Ka'u, Kaiholena	975	light trap	7/31/06	1	No	W. Haines, J. Giffin
	Kahuku Ranch, HAVO	1005	light trap	5/18/06	3	No	W. Haines, D. Rubinoff
	Volcano Village	1128	light trap	6/8/05, 11/26/05	2	No	C. King
	Ola'a Tract, HAVO	1150	light trap	5/17/06	4	No	W. Haines
	Escape Rd./Thurston, HAVO	1158	light trap	4/16/05, 6/29/05, 5/18/06	3	No	W. Haines, C. King
	Kilauea Field Station, HAVO	1158	light trap	2/5/05	1	No	W. Haines
	Kipuka Puaulu, HAVO	1200	light trap	10/15/04	1	Yes	W. Haines
	Ola'a Tract, Pu'u Unit	1300	light trap	5/17/06	1	No	W. Haines, D. Rubinoff
	Waikii	1432	light trap	6/11/05	1	No	C. King
	Mauna Loa Strip Road, HAVO	1500	light trap	10/14/04	1	Yes	W. Haines
Kona Forest Unit, Hakalau Nat'l Wildlife Refuge	1615	light trap	4/12/05	2	No	C. King	
Keamoku flow, HAVO	1707	light trap	4/15/05, 6/28/05	3	No	C. King	

* dates = 3/9/07, 4/7/07, 4/19/07, 5/10/07, 5/18/07

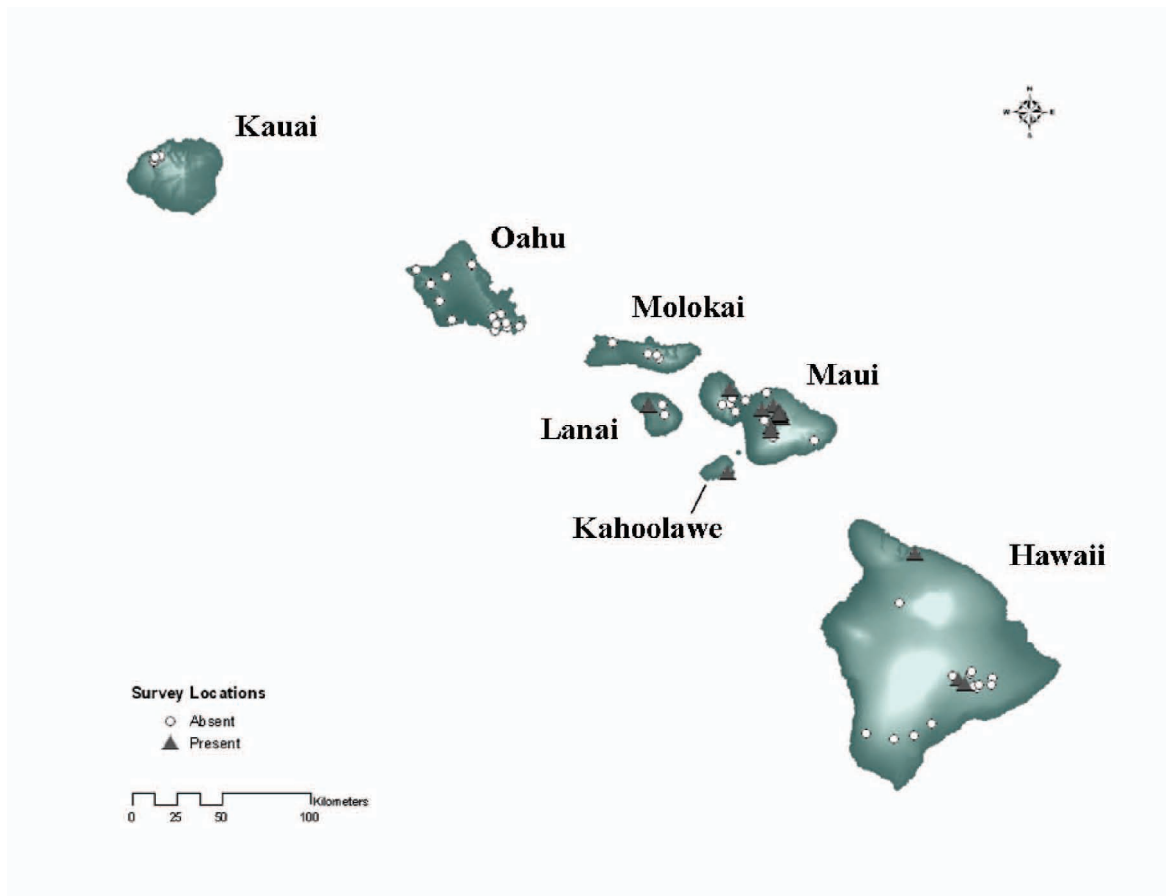


FIG. 4. Map of current distribution of *Omiodes continuatalis* in the Hawaiian Islands, based on recent field survey data.

larvae began their attacks at the tenth abdominal segment, working forward and consuming the entire contents of the abdomen. The only structures not consumed by the cannibalistic larvae were the head capsule and the cuticle. Thus, the end product of such an encounter resembled a shed head capsule and cuticle following a developmental molt. Perhaps the behavior has never been documented in *Omiodes* larvae because Hawaiian *Omiodes* species have not been reared in colony prior to this investigation. Cannibalism, prompted by competition for limited resources such as host plant resources and over-wintering sites, has been documented in non-Hawaiian crambid species (Baskauf 2003), so it is possible that *O. continuatalis* larvae may exhibit the behavior in the natural environment under high density conditions.

Distribution. We completed more than 166 trap nights of surveys at 85 field sites for populations of *O. continuatalis* across the Hawaiian Islands (Table 1). While previous collecting records show *O. continuatalis* to be present in mostly dry or mesic habitats (Zimmerman 1958; Haines *et al.* 2004), our surveys

show that *O. continuatalis* populations are present in dry, mesic and also wet habitat types (Table 1) (Fig. 4). On Hawaii Island, *O. continuatalis* was collected from three mesic habitats: Kipuka Puau (1195m) and Mauna Loa Strip Road (1492m) on Mauna Loa in Hawaii Volcanoes National Park, and a remnant sugarcane field near the town of Honokaa (303m). All of these sites receive a mean annual rainfall (MAR) of 1500–2000mm. On Maui, *O. continuatalis* were collected from seven distinct field sites: Waihee Ridge trail (305m), Haliimaile/Haleakala Hwy sugarcane field (274m), Kokomo (484m), UH Kula field station (975m), Makawao Forest Reserve (914m, 1280m), and Haleakala Ranch (1280m). With the exception of Waihee Ridge, which is located on West Maui, all of the field sites are located on East Maui. The two Makawao Forest Reserve sites and the Haleakala Ranch site are wet habitats (2000–3000mm MAR). Waihee is a mesic habitat (1500mm MAR), as is Kokomo (1500–2000mm MAR), while Haliimaile/Haleakala Hwy sugarcane field and the UH Kula field station are dry habitats, due to their position in the rain shadow of East Maui (MAR

<750mm). *O. continuatalis* were also collected on the islands of Kahoolawe and Lanai. Both of these islands are exceedingly dry (630mm MAR) as they are also located in the rain shadows of Maui and Molokai.

Based on survey data of *O. continuatalis*, it is clear that this species can persist in diverse habitat types ranging from dry to wet. *O. continuatalis* also occurs in habitats exhibiting varying levels of alteration and disturbance. The species is present in predominantly native forest habitat (e.g. Mauna Loa, Makawao Forest Reserve), as well as areas where native habitat has been converted to pastureland (e.g. Haleakala Ranch), and/or agricultural land (e.g. Honokaa and Haliimaile sugarcane fields). Their persistence appears possible so long as the habitat contains sufficient host plant resources, in the form of native or introduced grasses, to support larval development. Given their widespread distribution, their palpable ability to adapt to significant changes in habitat, and their ability to utilize invasive grasses as host plants, *O. continuatalis* would seem an unlikely candidate to face high risk of declines and/or extinction. Nevertheless, the current distribution of *O. continuatalis* on the islands of Maui, Kahoolawe, Lanai and Hawaii represents a significant range reduction for a species which was previously common, but is now extirpated from, Kauai, Oahu, and Molokai.

It is possible that the reduction in distribution is not as great as these survey data might indicate. Even small variations in season, moon phase, air temperature, precipitation and wind speed can affect light trap catch on a given day. Therefore, it is possible that *O. continuatalis* may have gone undetected at sites where light trapping occurred on only one occasion. The Kailiili Road study site in Kokomo, Maui was surveyed frequently due to the consistent *O. continuatalis* trap catch. Even so, there were at least two occasions where *O. continuatalis* adults were not observed. Furthermore, during surveys on Hawaii Island, *O. continuatalis* was not collected from light traps at the Keamoku flow on Mauna Loa, where the species has been previously recorded (Haines *et al.* 2004). Thus, it is possible, that *O. continuatalis* are present at additional field sites on Maui, Kahoolawe, and Hawaii Island. Accordingly, the species may remain undetected on other islands despite extensive negative data from these survey efforts. This hypothesis seems more plausible at sites where traps were only set-up for 1–2 trap nights, as opposed to field sites like Kokee State Park or the Alakai Swamp on Kauai where more than 18 trap nights have cumulatively been completed, and no *O. continuatalis* have yet been detected.

Potential factors influencing the decline and restricted distribution of *O. continuatalis* were not

quantified under the scope of this research. Given the persistence of the moth in severely degraded habitats, it seems unlikely that habitat destruction or habitat alteration alone could be significant limiting factors for the species. There are habitats on the islands of Kauai, Oahu and Molokai, both pristine and disturbed, which we presume contain suitable resources to support *O. continuatalis*, and yet the species has still not been “rediscovered” on these islands. If habitat destruction and alteration are not consistently affecting the persistence of this species across the Hawaiian Islands, then what other factors may be contributing to their declines? The intentional and accidental introduction of natural enemies into the Hawaiian Islands has been viewed suspiciously by entomologists for over a century (Perkins 1897; Zimmerman 1958; Howarth 1983; Henneman & Memmott 2001), and some of these parasitoids and predators appear to suppress populations of other *Omiodes* species (Zimmerman 1958; Bess 1974). Additional research is currently underway to examine the mortality factors, specifically parasitism, which may be affecting *O. continuatalis* populations. However, the individual and compound effects of introduced predators, such as ants and spiders, are also likely mortality factors, and their effects on *Omiodes* species remain to be investigated.

ACKNOWLEDGEMENTS

We thank A. Arcinas (Hawaii Agricultural Research Center) and M. Nakahata (Hawaii Commercial & Sugar Company) for providing plant material, and D. Oka and G. Otani (University of Hawaii Kula Agricultural Research Station) for field preparation and greenhouse assistance. J. Patu provided essential laboratory assistance. Access permits were granted by S. Meidel (Haleakala Ranch), G. Shishido and B. Gagne (Department of Land and Natural Resources, Division of Forestry and Wildlife), and C. Haines and G. Haines (Pacific Produce). Special thanks to M. Wright, C. Hooks, J. Eiben, L. Leblanc and L. Kaufman (University of Hawai'i, Department of Plant and Environmental Protection Sciences) for valuable input on research methods, and also W. Haines (University of Hawai'i, Department of Plant and Environmental Protection Sciences) for access to unpublished data. Anonymous reviewers provided valuable feedback on this publication.

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Received for publication 23 May 2008; revised and accepted 9 Dec 2008.

