

Rediscovery and Uncertain Future of High-Elevation Haleakalā Carabid Beetles (Coleoptera)¹

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Abstract: Recent biotic surveys in subalpine shrubland on Haleakalā Volcano, Maui, Hawai'i, have resulted in rediscovery of several species of carabid beetles previously known only from their nineteenth-century type specimens. *Blackburnia lenta* (Sharp), described from specimens collected just below Haleakalā summit in 1894, was found at lower elevational sites ranging from 2,400 to 2,750 m. *Mecyclothorax rusticus* Sharp, last seen in 1896, and *M. nubicola* (Blackburn), collected only in 1878, were also rediscovered in that vicinity. Recent collections of *B. lenta* contradict the U.S. Fish and Wildlife Service's previous classification of this species as one likely to be extinct. Nevertheless, *B. lenta*'s known distribution comprises only 145 ha within an elevational zone that is bounded above and below by unicolonial populations of the invasive alien Argentine ant, *Linepithema humile* (Mayr). The known recent collections of *M. rusticus* and *M. nubicola* also occurred outside the distributional range of the Argentine ant. Mature eggs held in the lateral oviducts of *B. lenta* females averaged 1.4× the volume of the largest eggs previously reported among 13 species of *Blackburnia*. We hypothesize that the giant eggs of *B. lenta* result from selective forces favoring large, well-nourished developing and hatched first-instar larvae, consistent with a patchy distribution of suitable microhabitat and prey in the subalpine Haleakalā landscape. The specialized life history of *B. lenta*, and coincidence of distributional limits of the three rediscovered carabid species with range limits of the Argentine ant populations suggest that all would be jeopardized by future distributional expansion of Argentine ant. These intersecting phenomena compel us to conclude that *B. lenta*, *M. nubicola*, and *M. rusticus* are appropriate candidates for I.U.C.N. threatened species designation, pending further studies of their geographic ranges and historical trends in abundance.

BIOLOGICAL EXPLORATION of the Hawaiian Islands achieved a marked maturity during the end of the nineteenth century due to the extensive biotic survey activities of R. C. L. Perkins that formed the core of the *Fauna Hawaiiensis* (Sharp 1913, Manning 1986).

From our vantage point near the beginning of the twenty-first century, we can assess the impact of human activities on the Islands through our ability to observe in nature those species collected by Perkins and his associates. Species not recovered in recent times may have been rare 100 yr ago, or they may

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represent species relatively common then but now seen rarely or not at all. The latter instances represent the criteria used to list species as threatened or endangered (I.U.C.N. 2001), but the former situations by necessity remain ambiguous due to the lack of field observations for extremely rare, long-missing taxa and our resultant inability to reach informed conclusions concerning their conservation status. In this paper we report recent discoveries of three long-missing ground beetle species (Carabidae) from the northwestern upper slope of Haleakalā Volcano, East Maui, Hawaiian Islands. In all three instances, previous collections were limited in frequency, numbers of specimens, and geographic scope, making these species symptomatic of the most difficult situations for conservation status assessment.

Hawaiian carabid beetles are represented by over 300 described and undescribed species, most of which belong to two remarkable evolutionary radiations—classified as member taxa of the genera *Mecyclothorax* Sharp and *Blackburnia* Sharp—that evolved from a pair of original founder species (Britton 1948, Liebherr and Zimmerman 2000). As a group, Hawaiian carabids occupy a tremendous range of habitats, including wet, mesic, and dry forest; savanna; shrubland; riparian corridors; and even lava tube caves (Liebherr and Zimmerman 2000). Nearly all species in these radiations are restricted to single volcanoes or even portions of volcanoes. On Haleakalā Volcano, which forms East Maui, 10 carabid species are associated with shrubland and aeolian habitats at elevations from 2,000 m to the summit at 3,055 m. Until recently, six of these species had not knowingly been observed since their original discoveries over 100 yr ago (Liebherr 2004). In the course of work addressing the spread and impact of the Argentine ant, *Linepithema humile* (Mayr), in Haleakalā National Park, we have rediscovered three of them: (1), *Mecyclothorax nubicola* (Blackburn), formerly known from a single specimen collected by Thomas Blackburn (1878); (2), *M. rusticus* Sharp, (1903), previously known from 81 specimens collected by Perkins in 1894 and 1896; and (3), *Blackburnia lenta* (Sharp), described from five

specimens collected by Perkins in 1894 (Liebherr and Zimmerman 2000). Our recent work provides considerable new information for *B. lenta* in particular, based on numerous specimens collected at multiple sites. As a result, in this report we focus on initial findings regarding biology and ecology of this species and evaluate the threat to high-elevation Haleakalā carabid beetles posed by the invasive Argentine ant.

MATERIALS AND METHODS

Nearly all specimens of the three carabid species were collected through two different pursuits. First, a comprehensive study investigating the impacts of invasive ants on arthropod faunas in high-elevation Hawaiian habitats yielded numerous carabid specimens. As part of this study, we implemented pitfall trapping, leaf litter sampling, and vegetation beating within multiple plots on the upper west slope of Haleakalā Volcano within Haleakalā National Park during 2001–2003. These plots were distributed in two main geographic areas associated with two large unicolonial populations of Argentine ants in the national park: one area spanned the southeastern boundary of the lower ant population at about 2,250–2,425 m elevation (lower area), and the other spanned the western boundary of the upper ant population at about 2,675–2,850 m elevation (upper area) (Figure 1). During a 2001 localized pilot study, we established four 4 by 8 m plots in the lower area only, with two plots inside the lower ant population and two plots outside the lower ant population. Each plot contained 15 pitfall traps (300-ml [10-oz], 80-mm-diameter cups) spaced every 2 m, for a total of 60 pitfall traps during 2001. All traps contained a 50:50 propylene glycol:water solution as preservative and were left open for 2 weeks. Pitfalls in two of the plots (one plot inside plus one plot outside the ant population) were baited around the rim with blended fermented fish (monamon). During 2002 and 2003, we used 48 5 by 5 m plots each year, split evenly between the lower and upper areas and spread more broadly across the study site (Figure 1). Each year, two-thirds

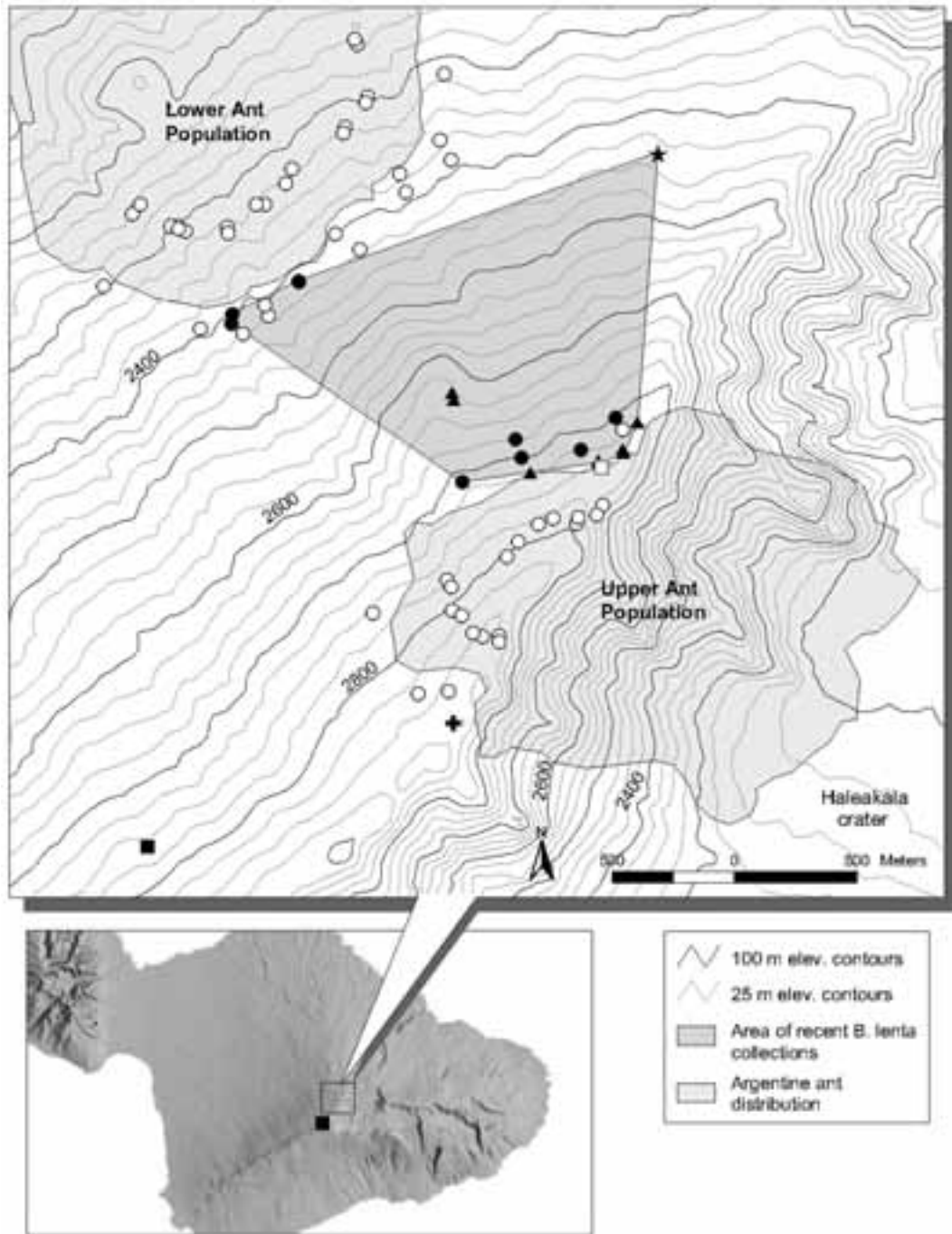


FIGURE 1. Distribution map of collection and sampling localities for reported Carabidae in Haleakalā National Park: two Argentine ant populations (stippled); *Blackburnia lenta* pitfall trap adult collection localities, 2001–2003 (●); *B. lenta* localities found while mapping ant population boundaries in 2003 and during additional searches in 2004 (▲); *B. lenta* pitfall collection locality, 1975 (★); *Mecyclothorax nubicola* collection locality, 1996 (□); *M. rusticus* pitfall collection locality, 2002 (⊕); pitfall, leaf litter, and vegetation beating sampling localities where no rare native Carabidae were captured, 2001–2003 (○); two estimated sites of Perkins' 1894 *B. lenta* collections (■) are located, respectively, in the southwest corner of the expanded map and to the southwest on the map of Maui.

(32) of these plots were located within the ant populations, and one-third (16) were located outside the ant populations. Each 5 m by 5 m plot contained three pitfall traps, separated from each other by at least 2 m, for a total of 144 pitfall traps per year. One pitfall in each plot was baited with blended fish, and the other two were unbaited. In each plot, from 2001 to 2003, we collected leaf litter from three areas, mixed it together, and removed 1 liter; this was placed in a Berlese funnel extractor for 24 hr (we previously determined that 99% of the leaf litter catch exited the litter within the first 24 hr in this mesic habitat). Shrub vegetation within each plot was also beaten between 1000 and 1600 hours. Each focal shrub species received five beats (spread among multiple individuals of each species within each plot, if possible) onto a 1-m² nylon beating sheet, from which we aspirated all arthropods. Focal shrub species were *Sophora chrysophylla* (Salisb.), *Dubautia menziesii* (A. Gray), *Vaccinium reticulatum* (Sm.), and *Styphelia tameiameia* (Cham. & Schlechtend.) in the lower area and *S. tameiameia* and *D. menziesii* in the upper area. Sampling periods were as follows: 9–23 August 2001; 17 September–1 October 2002 for lower-area plots, 18 September–2 October 2002 for upper-area plots; 6–20 July 2003 for lower-area plots, 14–28 June 2003 for upper-area plots.

Our second source of carabid beetle specimens consisted of beetles encountered while mapping Argentine ant population boundaries. Argentine ant queens disperse by budding, and as a result this species forms large, contiguous unicolonial populations that are composed of numerous mutually tolerant nests (Passera 1994). We mapped the boundaries of the two ant populations by searching on the ground, under rocks, and on vegetation for the presence of ants at stations that were spaced at 30- to 110-m intervals along the population perimeters. We typically searched 50 to 75 m beyond the farthest location at which ants were found at these stations, resulting in numerous 50- to 75-m-long corridors of habitat searched around the southeast boundary of the lower ant population and around the entire perimeter of the upper ant population. In June and July of

2003, we collected any native carabid beetles encountered during this process. In addition, one specimen was found while mapping the upper ant population boundary on 16 February 1996, and two specimens were found while searching between the two ant populations on 6 March 2004. For the purposes of ant population mapping, we supplemented the visual searching technique just described with honeypot traps: small 118-ml (4-oz) plastic containers with snap-top lids and four 8-mm-diameter holes punched in the sides approximately 20 mm from the bottom, filled partially with honey-water solution and placed directly on the soil surface. These traps were meant to capture ants, if present, over a period of a week and were placed on short transects spaced irregularly around the ant population perimeters. On several occasions these traps captured carabid beetles.

Considerable habitat variation is represented in the total study area encompassed by the two described activities. The lower sampling area sits within the atmospheric inversion layer that forms on Haleakalā Volcano (Giambelluca and Nullet 1991). As a result, ground-level clouds frequently sweep across the mountain at this elevation. This entire area is characterized by native shrubland vegetation, and tradewind-generated moisture decreases from the windward (northeast) to the leeward (southwest) portions of this flank of the mountain, causing change in vegetation density and soil characteristics. As the habitat becomes drier, shrub density drops, groundcover vegetation between shrubs decreases, and the soil is more poorly developed, with a higher cinder composition. Common shrubs throughout this elevational zone include *S. tameiameia*, *V. reticulatum*, *S. chrysophylla*, *D. menziesii*, *Coprosma montana* Hillebr., and *Dodonaea viscosa* Jacq.

Additional habitat variation exists in the areas surrounding the upper Argentine ant population. The upper sampling area is perched on or near the crater rim, at elevations above 2,675 m. This area sits above the inversion layer and as a consequence tends to be drier than lower-elevation areas. A windward-leeward moisture gradient re-

mains, however, with the higher and drier southern portions of the crater rim being characterized by poor soil development, large expanses of cinder and rock, and very sparse vegetation (mostly small *S. tameiameiae* and *D. menziesii* shrubs). In contrast, the northern, windward portions of the crater rim within our study area support moderate densities of bunchgrass as well as more abundant and larger shrubs, and have more advanced soil development. In addition to *S. tameiameiae* and *D. menziesii*, *V. reticulatum* and *S. chrysophylla* shrubs occur in this area. To the east, the crater wall drops to the crater floor some 600 m below. The crater walls support bunchgrass and intermediate shrub densities, whereas the crater floor in the vicinity of the upper ant population boundary is dominated by largely barren rock scree and relatively young lava flows. Soil development there is generally poor.

Beetle specimens collected in this study were removed from the various traps or their positions in the field and preserved in 95% ethanol. *Blackburnia lenta* was identified using Liebherr and Zimmerman (2000) and by direct comparison with specimens in the Bernice P. Bishop Museum, Honolulu, Hawai'i (BPBM). Specimens of *Mecyclothorax* were identified using Britton (1948) and by direct comparison with type specimens (or specimens compared with primary types) held in The Natural History Museum, London (J.K.L., unpubl. data).

Eggs of *B. lenta* were initially discovered during female dissection made to confirm species-level identification using the methodology of Liebherr (1992). Subsequently, females were dissected under 70% ethanol, with mature eggs removed from the abdomen for measurement. Eggs were measured both while in 70% ethanol and again for comparison after several of the eggs were soaked in distilled water for 3 hr.

RESULTS

Field Collections

We collected 32 specimens of *Blackburnia lenta* (Figure 2) at 14 collection sites from



FIGURE 2. Dorsal habitus of *Blackburnia lenta* (Sharp) male; scale bar 1.0 mm.

2001 to 2003 (Figure 1) through the combined methods of pitfall trapping, honeypot trapping, and visual searching on the ground and under rocks (Table 1). We found an additional two individuals (the only live *B. lenta* specimens captured) while searching between the two Argentine ant populations on 6 March 2004 at approximately 1400 hours (Figure 1). One of these individuals was inactive deep in the litter beneath a clump of bunchgrass; the other was inactive, together with a *B. rupicola* individual, at the interface of rock and litter beneath bunchgrass. After all the field collections reported here were completed, we discovered one specimen of *B. lenta* in the collections of the BPBM. This specimen, hidden among unsorted carabid beetles and misidentified as the sympatric *B. frigida*, was collected on 13 June 1975 in a pitfall trap at the Halemau'u trailhead by R. Burkhart. The

TABLE 1
Numbers of *Blackburnia lenta* Specimens Collected during 2001–2003 by Sampling Method and Location

Sampling Method	2001		2002		2003	
	Upper Area ^a	Lower Area ^b	Upper Area	Lower Area	Upper Area	Lower Area
Pitfalls	—	11	3	0	10	1
Honeytrap	—	—	—	—	3	0
Found while ant mapping	—	—	—	—	4	0
Vegetation beating	—	0	0	0	0	0
Leaf litter extraction	—	0	0	0	0	0

^a Upper area refers to the area around the western boundary of the upper ant population (2,675–2,875 m) where pitfalls, honeytrap, vegetation beating, and leaf litter extraction (in Berlese funnels) were employed. In the case of specimens found while mapping ant boundaries, the upper area refers to the entire boundary of the upper ant population.

^b Lower area refers to the area around the southeastern boundary of the lower ant population (2,250–2,425 m) for all sampling methods listed.

unambiguous location of this site allowed us to map the collection locality of this specimen with certainty (Figure 1).

All *B. lenta* specimens were found between 2,400 and 2,750 m elevation, and the total area encompassed by the recent collections for this species (including the 1975 specimen) amounts to 145 ha. We found no specimens while mapping ant population boundaries within Haleakalā Crater. Our collection localities lie from the lower edge to 500 m lower in elevation than the estimated collection localities of Perkins (1894 [Liebherr and Zimmerman 2000]). Perkins collected two specimens of *B. lenta* on 9 April 1894, when he “Worked from 9000 ft. [2,743 m] to the summit” (Perkins 1894:16). He collected three more specimens on 11 April 1894, when he collected “Coleoptera, which I found most plentiful from 9,500 [2,895 m] to the top [3,055 m], or within 100 or 200 ft. short of the top” (Perkins 1894:16). We acquired no specimens via leaf litter sampling or shrub beating. In addition, no specimens were collected within either Argentine ant population, despite the fact that we employed twice as many sampling plots within ant-invaded habitat compared with ant-free habitat in 2002 and 2003.

We collected one live specimen of *Mecyclothorax nubicola* from under a rock just outside the upper Argentine ant population in February 1996 while mapping the population boundary. Figure 1 appears to show this col-

lection site as located within Argentine ant-invaded habitat, but this is because the upper ant population has spread outward since 1996. We also captured one specimen of *Mecyclothorax rusticus* in a pitfall trap outside the upper Argentine ant population in June 2003 (Figure 1).

Records for *Blackburnia lenta* collections are as follows (all Hawai‘i, Maui I., Haleakalā National Park): west slope, 20° 44.8′ N, 156° 14.7′ W, 2,405 m el., 23 August 2001, P. Krushelnycky, pitfall traps (4 males, 7 females); Kalahaku, 20° 44.5′ N, 156° 13.9′ W, 2,725 m el., 2 October 2002, P. Krushelnycky, pitfall trap (1 female); Kalahaku, 20° 44.5′ N, 156° 14.1′ W, 2,700 m el., 2 October 2002, P. Krushelnycky, pitfall trap (1 male); Kalahaku, 20° 44.4′ N, 156° 14.2′ W, 2,715 m el., 2 October 2002, P. Krushelnycky, pitfall trap (1 female); nr. Leleiwi Overlook, 20° 44.5′ N, 156° 13.8′ W, 2,745 m el., 30 May 2003, P. Krushelnycky, dead on cinder (1 female); nr. Leleiwi Overlook, 20° 44.5′ N, 156° 13.9′ W, 2,745 m el., 6 June 2003, J. Van DeMark, pterothorax and abdominal carcass under rock (1 male); nr. Leleiwi Overlook, 20° 44.5′ N, 156° 13.9′ W, 2,740 m el., 6 June 2003, P. Krushelnycky, dead under rock (1 female); nr. Leleiwi Overlook, 20° 44.6′ N, 156° 13.8′ W, 2,720 m el., 6 June 2003, P. Krushelnycky, dead in leaf litter under *Styphelia* shrub (1 female); nr. Leleiwi Overlook, 20° 44.5′ N, 156° 13.8′ W, 2,740 m el., 6 June 2003, P. Krushelnycky, dead in

honey trap (1 female); nr. Leleiwi Overlook, 20° 44.5' N, 156° 14.0' W, 2,725 m el., 6 June 2003, P. Krushelnicky, dead in honey trap (1 female); nr. Leleiwi Overlook, 20° 44.5' N, 156° 13.8' W, 2,740 m el., 6 June 2003, P. Krushelnicky, dead in honey trap (1 female); Kalahaku, 20° 44.6' N, 156° 13.8' W, 2,705 m el., 28 June 2003, P. Krushelnicky, pitfall trap (1 male); Kalahaku, 20° 44.5' N, 156° 13.9' W, 2,725 m el., 28 June 2003, P. Krushelnicky, pitfall trap (1 male); Kalahaku, 20° 44.5' N, 156° 14.1' W, 2,675 m el., 28 June 2003, P. Krushelnicky, pitfall traps (2 male, 6 females); above Pu'u 'Ō'ili, 20° 44.9' N, 156° 14.6' W, 2,415 m el., 28 June 2003, P. Krushelnicky, pitfall trap (1 female); west slope, 20° 44.6' N, 156° 14.2' W, 2,640 m el., 6 March 2004, P. Krushelnicky, live in litter beneath bunchgrass (1 male); west slope, 20° 44.6' N, 156° 14.2' W, 2,640 m el., 6 March 2004, P. Krushelnicky, live between rock and bunchgrass litter (1 male); Halemau'u trailhead, 2,440 m el., 13 June 1975, R. Burkhart, pitfall trap (BPBM accession no. 1990.009). Specimens are vouchered in BPBM; the Cornell University Insect Collection (CUIC); the Essig Museum of Entomology, University of California, Berkeley; and Haleakalā National Park insect collection.

The recent distributional record for *Mecyclothorax nubicola* is: Hawai'i, Maui I., Haleakalā National Park, Leleiwi Overlook, 20° 44.5' N, 156° 13.9' W, 2,750 m el., 16 February 1996, P. Krushelnicky (1 female, CUIC).

The new distributional record for *Mecyclothorax rusticus* is: Hawai'i, Maui I., Haleakalā National Park Kalahaku, 20° 43.9' N, 156° 14.2' W, 2,870 m el., 28 June 2003, P. Krushelnicky, pitfall trap (1 female, BPBM).

Blackburnia lenta Egg Size

To confirm the identification of *B. lenta*, an initial female was dissected to allow examination of the gonocoxal ovipositor apparatus and the female reproductive tract (Liebherr 1992). The cleared specimen exhibited one mature oocyte each lodged near the bases of the lateral oviducts (Figure 3). The eggs had been cleared by the KOH treatment, but

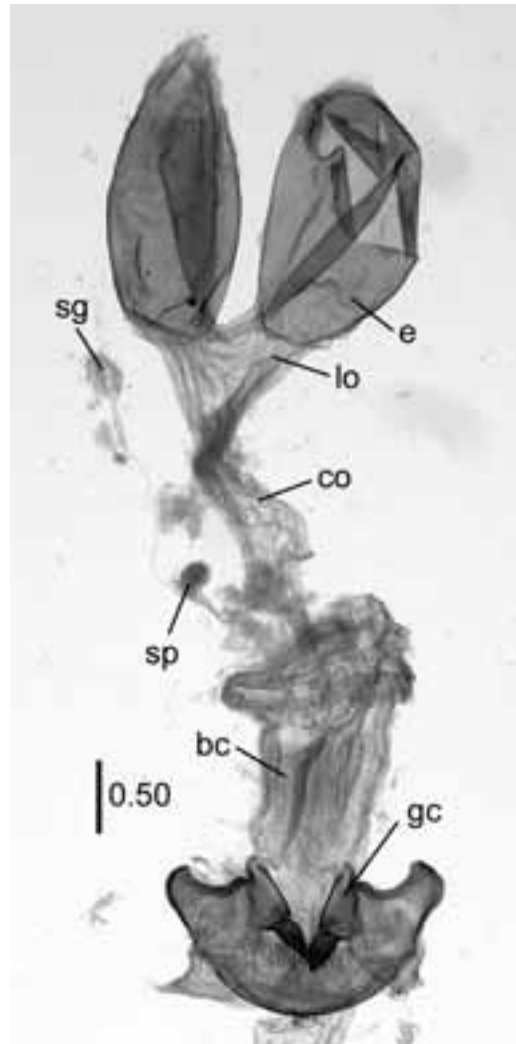


FIGURE 3. Female reproductive tract and ovipositors (gonocoxae) of *Blackburnia lenta* (ventral view). Eggs are held in the lower reaches of lateral oviducts, and eggshells (i.e., hard chorionic layer) remain after clearing of preparation in aqueous 10% KOH solution. bc, bursa copulatrix; co, common oviduct; e, chorionic layer of cleared egg; gc, gonocoxa; lo, lateral oviduct; sg, spermathecal gland; sp, spermatheca. Scale bar 0.50 mm.

the hardened chorion remained, upon which lenticular-shaped microsculpture could be observed.

As a result of this finding, four other females were dissected and found to hold ma-

TABLE 2
Dimensions (mm) of Eggs Held in Lateral Oviducts of Field-Collected Specimens of *Blackburnia lenta*

Date/Locality of Female	No. Eggs	Range		
		Egg Length (L)	Egg Breadth (B)	Volume (mm ³)
23 Aug. 2001/West slope, 2,300 m	1	1.92	1.10	1.13
23 Aug. 2001/West slope, 2,300 m	13	1.60–2.00	0.90–1.06	0.77–1.18
6 June 2003/Lelewi Overlook ^a	2	1.60–1.90	0.85–1.00	0.71–0.84
28 June 2003/Kalahaku	4	1.60–2.12	0.87–1.12	0.63–1.51
28 June 2003/Kalahaku	1	1.60	0.87	0.63
Average (SD)	21	1.84 (0.16)	1.00 (0.08)	0.98 (0.22)

^a Eggs measured were cleared in KOH while held in lateral oviducts of female reproductive tract (Figure 3).

ture oocytes in their lateral oviducts (Table 2). In one instance, two groups of six and seven eggs were found lodged together in greatly distended oviducts. There was no evidence of embryonic development such as pharate larval mandibular sclerotization in these eggs, which were examined without clearing, so it is not known whether they had been fertilized. By their position lodged in the lateral oviducts, basad (i.e., upstream from) the spermathecal duct entrance to the female tract (Figure 3), it is presumed that they were mature but unfertilized eggs.

The eggs observed within the five *B. lenta* females ranged in size from 1.60 to 1.92 mm long and 0.85–1.10 mm broad (Table 2), on average larger than other eggs reported for Hawaiian *Blackburnia* (Figure 4). The eggs were nearly regular ovoid solids in females holding only 1 egg in the oviduct, and more irregularly shaped in the female holding 13 eggs. In this instance, packing of eggs in the lateral oviducts was associated with their distortion, resulting in flattened surfaces where eggs were pressed together. All eggs were covered with a hardened, removable coating of unknown origin; possibly the remains of follicular cells fixed during preservation. The egg chorion was complete within this removable encrusting layer. Maximum body length observed among female *B. lenta* was 11.1 mm, 6–12% longer than observed in species with next-largest eggs (Figure 4) (e.g., *B. molokaiensis* (Sharp) at 10.5 mm, and *B. fracta* (Sharp) at 9.9 mm).

DISCUSSION

Blackburnia lenta was listed as one of six Hawaiian carabid beetle species of concern likely to be extinct (Beattie 1994). Our intensive sampling near its type locality has yielded 34 new specimens, and a misidentified specimen discovered in museum collections indicates that an additional individual was collected in 1975. This represents a substantial increase over the original type series of five specimens. At the same time, we uncovered one new specimen each of *Mecyclothorax nubicola* and *M. rusticus*, both of which were last seen over 100 yr ago. We have no evidence that *M. nubicola* has ever been common, because both collections (Blackburn's and ours) are single specimens. However, *M. rusticus* was much more commonly encountered by Perkins in the 1890s, with his collections amounting to over 80 specimens, all but one collected during his two trips to Haleakalā summit when he collected his specimens of *B. lenta* (Perkins 1894; J.K.L., unpubl. data). From available evidence, we can conclude either that we have not yet rediscovered the optimal habitat for *M. rusticus* or that this species has diminished in relative abundance since Perkins' time. Expanded survey of high-elevation habitats adjacent to those described herein remains the most direct way to determine which conclusion is warranted.

Conversely, the recovery of multiple *B. lenta* individuals allows us to begin forming a picture of the biology and ecology of this

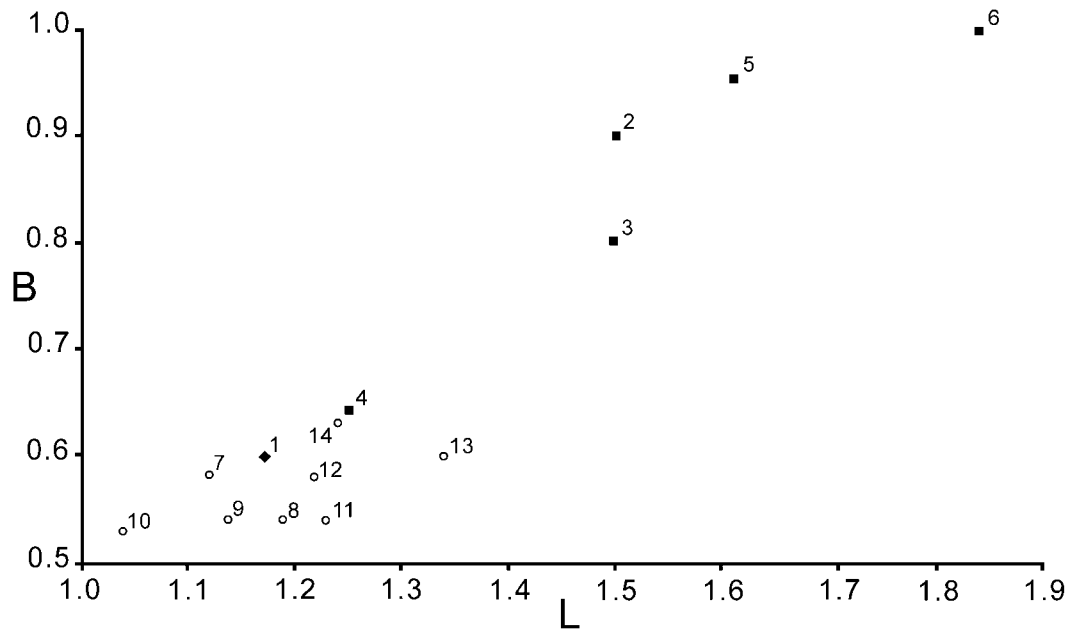


FIGURE 4. Average egg dimensions (length and breadth in mm) for 14 *Blackburnia* species (Liebherr 2000 and herein), representing Division 0 (◆), Division 1 (■), and Division 2 (○) (Liebherr and Zimmerman 2000). Species include 1, *B. posticata* (Sharp); 2, *B. molokaiensis* (Sharp); 3, *B. aterrima* (Sharp); 4, *B. optata* (Sharp); 5, *B. fracta* (Sharp); 6, *B. lenta* (Sharp); 7, *B. fossipennis* (Blackburn); 8, *B. caliginosa* (Blackburn); 9, *B. fractistriata* (Perkins); 10, *B. pavidata* (Sharp); 11, *B. erro* (Blackburn); 12, *B. longula* (Sharp); 13, *B. palmae* (Blackburn); 14, *B. fraudator* (Sharp).

beetle on the upper slopes of Haleakalā Volcano. The distribution of recent *B. lenta* collections, including the single specimen collected in 1975, only covers an area of 145 ha. Because our sampling locations were limited to areas proximate to the two Argentine ant populations, we believe the actual range of this species is almost certainly larger. Even so, the distribution of specimens captured relative to sampling locations in 2002 and 2003 suggests that *B. lenta* has a naturally small range. Specifically, it was absent from the northeastern, windward areas around the lower ant population, where moisture, vegetation density, and soil development increases. We also found no specimens in the southwestern, leeward areas of the crater rim around the upper ant population, where moisture decreases and vegetation density, plant diversity, and soil development also decline. Nor did we encounter any individuals within Haleakalā Crater. It is therefore possi-

ble that *B. lenta* is restricted to a relatively narrow band of suitable habitat delimited by upper and lower rainfall or soil moisture tolerances. This zone appears to be characterized by the presence, but not complete dominance, of grass and sedge groundcover, an intermediate level of soil development, and a shrub component of moderate density and diversity. The 1975 Halemau'u trailhead collection site also fits this habitat description. The two live specimens we found appeared to be using the moist microsites beneath and adjacent to clumps of bunchgrass as daytime refugia, suggesting a potential explanation for the putative narrow habitat affinity. If our inferences about habitat requirements are correct, we estimate that the total actual range of *B. lenta* may only be several times larger than the currently known range.

The previously estimated locations of Perkins' two 1894 collection sites (Liebherr and Zimmerman 2000), however, sit 2 and 3.6 km

away from the nearest recent collection, toward the drier summit of Haleakalā. These locales, if accurately estimated, could substantially extend our concept of this species' habitat tolerances to include cinder and rock-dominated landscapes sparsely populated by herbs and small shrubs. Alternatively, these sites may have been considerably moister in the 1890s: a large winter snowcap during 1894 persisted in lower-elevation gulches up to the time of Perkins' 9–11 April summit ascents (Perkins 1894:2). Because we cannot determine Perkins' precise collection locations from his limited site descriptions, we suggest additional survey work to clarify the range of *B. lenta* in the summit area of Haleakalā and to seek other populations in similar habitat patches on other parts of the mountain.

Blackburnia lenta is a member of the "big-head carabid" clade that was first identified by Sharp (1900, 1903). Polhemus et al. (2003) noted that species for which we have ecological information, including the basally divergent species, exhibit vegetation-climbing behavior. They hypothesized that the propensity to climb might be an ancestral trait within this clade, suggesting that all member species might be found to use arboreal microhabitats. We beat all of the dominant shrub species in our plots but failed to uncover any specimens of *B. lenta* through these means. Because we only sampled on vegetation during daylight hours, however, additional nighttime sampling is needed to determine whether *B. lenta*, unlike its nearest relatives, is restricted to ground-level microhabitats.

Previous analysis of egg size among *Blackburnia* beetles showed that species of Sharp's Division 1 clade exhibited cladistically derived, larger eggs relative to other *Blackburnia* species (Liebherr 2000). The results reported above for *B. lenta*, a member taxon of Division 1 (Liebherr and Zimmerman 2000), corroborate this finding (Figure 4). Eggs of several Division 1 species are also the largest observed for the tribe Platynini; larger than those reported for the genera *Agonum* Bonelli, *Calathus* Bonelli, *Laemostenus* Bonelli, *Platynus* Bonelli, or *Synuchus* Gyllenhal (1.03–1.61 mm length) (Levesque et al. 1980, Luff

1981). Compared across Platynini, Hawai'i's Division 1 species are characterized by larger eggs even though their body size maximums are smaller than those of the *Platynus* or *Laemostenus* species for which egg sizes have been reported. This loose association of egg and adult body size is also observed when comparing across all Hawaiian *Blackburnia*, because several non-Division 1 species comprise larger adult females laying much smaller eggs than observed among the Division 1 species *B. optata* (Figure 4). Comparing within Division 1 Hawaiian *Blackburnia*, however, the larger egg size of *B. lenta* is associated with larger maximum female adult size (Figure 4) (Liebherr 2000).

Based on evidence from reared *Blackburnia* larvae, larger egg size in Division 1 species is evolutionarily associated with an extended first instar larval period, as well as an increase in the summed developmental time of the three larval instars occurring before pupation. Such an extended larval life, especially of the first instar, increases the amount of time a larva can search for prey before obtaining its first meal; generally only one meal is taken before molting to the second instar (J.K.L., unpubl. data). An extended search time may be important in the high-elevation shrubland of Haleakalā, where available prey items are likely to be limited. In the presence of adventive ants, however, an extended development time could increase the risk of predation.

Because Perkins only collected in the habitat zone of *B. lenta* for a limited time period on two dates, it is difficult to judge whether the five specimens he collected in 1894 derived from a species abundance that was higher than, lower than, or similar to the one that currently exists. During the 107 intervening years, apparently only one specimen has been collected (in 1975). Yet examination of museum collections indicates that at least nine collectors collected carabids from in and around *B. lenta*'s known current range during that period, and substantial pitfall sampling and under-rock surveying was conducted during the 1980s and 1990s (data for *Blackburnia* summarized in Liebherr and Zimmerman 2000). Our collections from 2001–2003 suggest substantial fluctuations in

the abundance of this species. In our lower-elevation sampling zone (2,250–2,425 m elevation), we caught 0.37 *B. lenta* individuals per pitfall trap outside Argentine ant-invaded habitat in 2001, compared with 0 individuals per trap in 2002 and 0.04 individuals per trap in 2003. By a second line of evidence, *B. lenta* specimens composed 50% and 83.3% of all native Carabidae caught in pitfalls in our upper-elevation sampling zone (2,675–2,850 m elevation) during 2002 and 2003, respectively. It seems unlikely that this species would have been collected so rarely had its relative abundance consistently been this high.

At the moment *B. lenta* is relatively common within its limited range, however this can be expected to change dramatically as the invasive Argentine ant continues to spread. Based on recent rates of invasion, we estimate that without management intervention the two ant populations will merge in less than 20 yr (P.D.K., unpubl. data). When this happens, the available habitat that is suitable for *B. lenta*, as we currently understand it, will disappear, despite its location within the protected lands of Haleakalā National Park. Similarly, whereas rediscovery of *M. nubicola* and *M. rusticus* provides hope that other long-missing carabid species from the top of Haleakalā—i.e., *M. apicalis* Sharp, *M. pusillus* Sharp, and *M. subconstrictus* (Sharp) (Liebherr 2004)—may still be extant, it is clear that these latter species will also suffer from continued Argentine ant invasion to the degree that their distributional ranges coincide with habitat favored by the ant. We have collected no individuals of any native carabid species in ant-invaded areas, with the exception of *Mecyclothorax* undescribed sp. “montivagus,” which can apparently coexist with ants in certain habitat patches. These results are consistent with those of Cole et al. (1992), who also found native carabid beetles to be negatively impacted by Argentine ants. For this reason, we propose *B. lenta*, *M. nubicola*, and *M. rusticus* as threatened species whose long-term persistence appears tenuous. More precise categorization within the I.U.C.N. (2001) threatened categories (i.e., vulnerable, endangered, or critically endangered) will require more detailed assessment

of the historical trends in the species’ distributional extent and relative abundance. In the meantime, our findings in this report highlight the importance of current efforts aimed at slowing the ongoing spread of the two Argentine ant populations in the National Park (Krushelnycky et al. 2004) and impart a sense of urgency to the twin goals of increasing surveys for rare native species and improving techniques for invasive species eradication.

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