Conservation Status of the Endemic Bees of Hawai'i, *Hylaeus* (*Nesoprosopis*) (Hymenoptera: Colletidae)[1]

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Abstract: The 60 species of native *Hylaeus* bees in the Hawaiian Islands are important pollinators in native ecosystems, but they have been almost completely ignored in conservation studies. The only previous assessment of the conservation status of the individual species was not based on recent collections. Here I report on conservation status of all known species, based on collections made from 1999 to 2002. Species are arranged into six categories according to degree of threat, and species considered to be threatened are discussed individually. Five species have not been collected recently from one or more islands from which they are historically known, seven are restricted to endangered habitat, 10 are considered to be very rare and potentially endangered, and 10 have not been collected recently and could be extinct. With such a high proportion of rare species and the importance of *Hylaeus* species as pollinators, further work on their ecology is needed.

The Hawaiian Islands are famous for their numerous evolutionary radiations. A large number of species derived from a relatively small number of introductions is the rule for both plants and insects, due to extreme isolation from continents and other high islands (Zimmerman 1948, 1970, Wagner et al. 1990). The result is a fauna in which many higher taxa are absent, including some that dominate continental areas. The aculeate (stinging) Hymenoptera are a striking example. The native fauna contains 404 described endemic species, nearly 90% of which are derived from only three introductions: *Hylaeus* (*Nesoprosopis*) bees (Colletidae, 60 species), the "*Nesodynerus*" group of eumenine wasps (Vespidae, 112 species), and *Sierola* bethylid wasps (Bethylidae, 180 species with many more undescribed). The remainder includes a second small group of eumenines (the *Odynerus nigripennis* group, probably belonging in *Euodynerus*, three species), another group of bethylids (*Sclerodermus*, 17 species), and two Crabronidae: one group of crabronines (*Ectemnius*, 20 species) and two sister genera of pemphredonines, *Deinomimesa* and *Nesomimesa* (five and six species, respectively, derived from a single introduction [Nishida 2002, Daly and Magnacca 2003]). Entirely lacking are ants, social vespids, and the enormous array of other solitary hunting wasps and bees. The groups that are native to Hawai'i make up a small fraction of the fauna in continental areas, in terms of both numbers of species and numbers of individuals. For example, of the more than 3,000 species of bees in North America, there are only 48 *Hylaeus* species (fewer than occur in Hawai'i), distributed among seven subgenera. Moreover, the radiation in Hawai'i is extraordinary for the genus; with the inclusion of the eight known Japanese species, *Nesoprosopis* is the second largest subgenus of *Hylaeus* (Michener 2000) (the Australian subgenus *Prosopisteron* is also larger when undescribed species are included, but it is highly polyphyletic [unpubl. data]).

The 60 Hawaiian *Hylaeus* species arose from a single introduction, probably from Ja-

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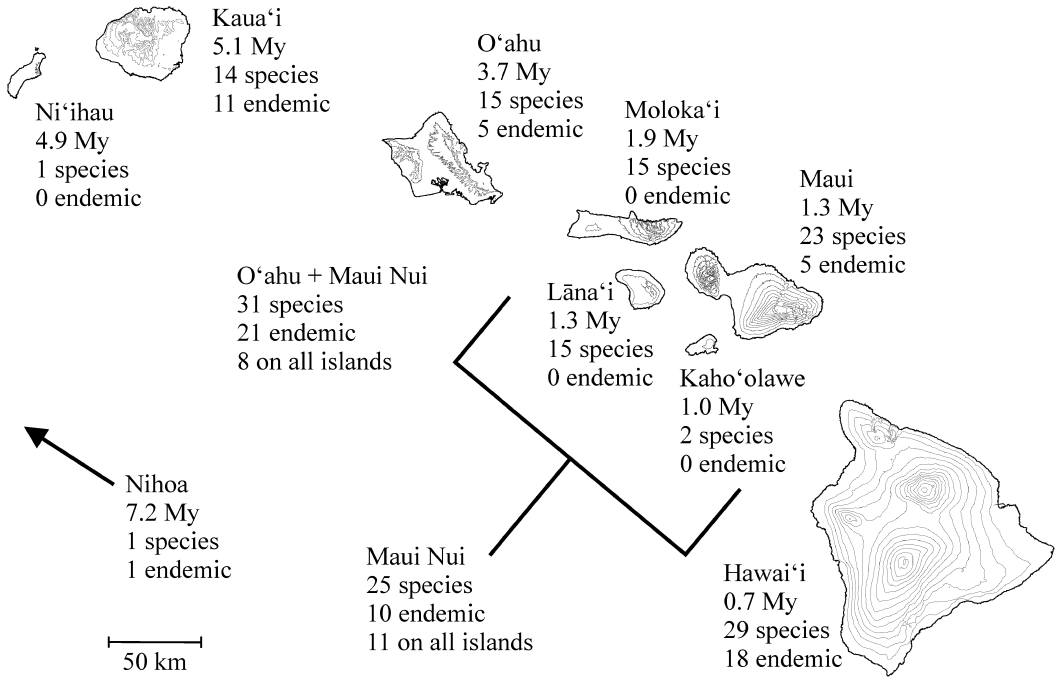

FIGURE 1. The main islands of the Hawaiian chain, with 300-m contours. Under the name of each island is its approximate age in millions of years (Moore and Clague 1992, Carson and Clague 1995). Numbers for species occurring on "all islands" of Maui Nui do not include Kaho'olawe, which has a much more depauperate fauna.

pan or East Asia where other species of the subgenus live (Hirashima 1977). Being strong fliers, they have a lower rate of endemism than most Hawaiian groups; only 40 of the species are single-island endemics, and many species found on Maui Nui are shared among two or more islands (Figure 1). Nevertheless, they form one of the larger Hawaiian insect radiations (Liebherr 2001). They were considered by Perkins (1913:lxxix) to be "almost the most ubiquitous of any Hawaiian insects." Unlike nearly all other native groups, they can be found across virtually the entire range of rainfall and elevation in the Islands and in all vegetation types (Figures 1 and 2). Yet despite the widely recognized importance of bees as pollinators (Proctor et al. 1996), their role in maintaining the health of Hawaiian forests and other ecosystems has not been investigated. Only recently has the basic taxonomy been revised for the first time in over 100 yr (Daly and Magnacca 2003).

Very little has been done on conservation assessment for these bees. Information is so scattered that a paper recently appeared in a major journal stating that almost the entire group was extinct (Cox and Elmqvist 2000). Thirty-four currently recognized species were listed en masse as Category 2 candidate endangered species in 1984 (see Table 1) (U.S. Fish and Wildlife Service 1984), meaning that they are likely to be endangered but that not enough information was available to justify listing as endangered. This candidate listing was based on a very preliminary assessment of conservation needs (Gagné 1982), and further determinations of listing status were made with little solid information. Eight names now considered synonyms were also included in the Category 2 list, and 17 species were listed as Category 3A (probably extinct). Five of the latter group are now considered synonyms of species known to be extant and eight have been recollected recently, but four

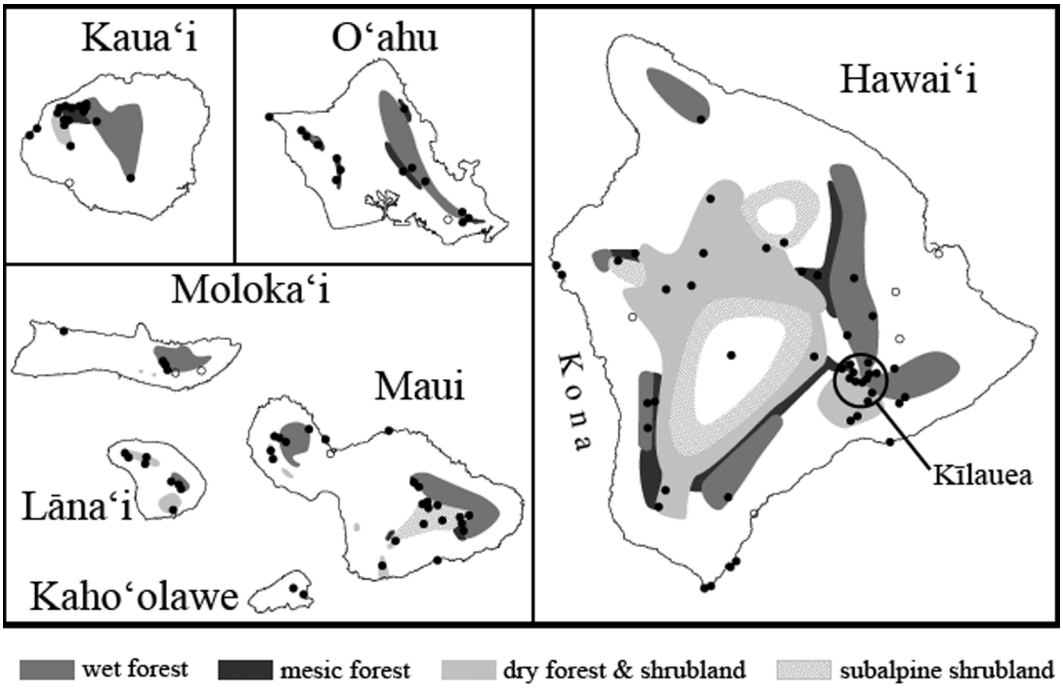

FIGURE 2. Approximate extent of native habitat suitable for bees (adapted from Juvik and Juvik [1998]; see Results). For coastal habitat, see Figure 3. Closed circles denote recent collection sites; open circles are historic collection sites now dominated by nonnative vegetation.

(*H. finitimus*, *H. mauiensis*, *H. melanothrix*, and *H. perspicuus*) have still not been recovered (Daly and Magnacca 2003). Since that original listing, virtually no follow-up work has been done to ascertain the true status of the Hawaiian bees. The impetus to do so has declined even further since the Category 2 candidate list was eliminated and its members reclassified as "species of concern," with no official federal status (U.S. Fish and Wildlife Service 1996).

In this paper, I present a summary of the distribution and abundance of Hawaiian *Hylaeus* species, based on recent and historic collections. Rare species are considered individually, followed by discussion of factors influencing their distribution and abundance. It is intended as a first step toward assessment of the state of Hawaiian bee populations and cannot be regarded as comprehensive while several large areas of the Islands remain unsurveyed. Nevertheless, it is the first report of threats to *Hylaeus* species to be based on recent field data.

MATERIALS AND METHODS

Bees were collected from all main islands during the summers of 1999–2002. Collecting was done primarily with a net at flowers or over ground; at some localities yellow pan traps were used. An attempt was made to collect from all ecosystems where *Hylaeus* species are likely to occur. Due to a number of restrictions, collections could not be made at some sites. These restrictions included physical access, land ownership, weather, and time. Bees are also capable of maintaining populations in small areas, and sites that are largely dominated by exotic vegetation may still harbor *Hylaeus* species in pockets of native habitat. No collections have been made on Ni'ihau (except the islet of Lehua), offshore islets, or the Northwestern Hawaiian

Islands for several decades; among the latter, *Hylaeus* species are recorded only from Nīhoa. Additional records from other collectors were also examined; details of collection records used in this study can be found in Daly and Magnacca (2003). Unless otherwise cited, factual references here are from that reference or from personal experience.

For the purpose of conservation status analysis, the species were sorted into six categories. Placing species into discrete categories as done here is somewhat subjective but is necessary as a first step in assigning priorities. Because there is a gap of approximately 70 yr in regular collections of *Hylaeus* species in Hawai'i and much is still unknown about their distribution and abundance, it is difficult to use more objective categories such as those used by the IUCN (2001). The categories are (in order of increasing threat): (1) uncommon to abundant, widespread, habitat relatively safe; (2) generally found in low numbers but widespread, with a large potential habitat; (3) abundant in some areas, but some populations threatened; (4) abundant where found but habitat restricted and/or threatened; (5) very rare, potentially endangered; (6) not recently collected, probably endangered or extinct. Species in category 1 are considered to be safe, barring a dramatic increase in habitat destruction, and are not discussed. Those in categories 2 and 3 are probably safe, at least as a species, and are covered briefly. Category 4 species are discussed in the context of their habitats, which also include some category 5 species. The remainder of the category 5 and 6 species are considered individually.

RESULTS

The distributions and conservation status of *Hylaeus* species are listed in Tables 1 and 2. In addition to those shown, *H. flavifrons* is known from Ni'ihau (including the islet of Lehua), and *H. anthracinus* and *H. assimulans* are known from Kaho'olawe (all recent collections). The only species recorded from the Northwestern Hawaiian Islands, *H. perkinsianus*, is endemic to Nīhoa. Little collecting has been done there, and the most recent specimens date from 1964 (Beardsley 1966). The island's vegetation appears to be largely intact, including as major components several plant species that are rare on the main islands (Conant 1985), and *H. perkinsianus* is probably safe. No bees were collected during a recent trip to Nīhoa to assess the impact of an outbreak of *Schistocerca* locusts (S. Montgomery, pers. comm.), but bees in other localities have been observed to go through boom-and-bust cycles. Although the locusts had a severe impact on the island's vegetation, a later trip found a low population of them and the vegetation recovering.

Figure 2 shows recent collection sites and approximate extent of habitat; empty areas of native habitat indicate regions that have been searched inadequately or not at all. Native habitat is generally patchier in reality than depicted on the map. This is particularly the case for regions on the island of Hawai'i such as South Kona where ranch land alternates with state forest reserves in mauka-makai strips, and upper areas of Mauna Loa that are largely bare rock but contain numerous kīpukas, "islands" of older substrate with more-developed vegetation than the surrounding, newer lava flows. On older islands, high ridges with native vegetation alternate with valleys that are often dominated by exotic plants.

Rare but Widespread

The species in this category have been collected only in low numbers and could potentially be threatened but due to the relatively large available habitat probably occur in much larger populations than collections indicate.

Hylaeus hirsutulus from Kaua'i; *H. angustulus* from Maui Nui; *H. kukui* from Maui and Hawai'i; *H. crabronoides*, *H. filicum*, *H. muranus* (= *insignis*), and *H. rugulosus* from Hawai'i; and *H. specularis* from Hawai'i, Moloka'i, O'ahu, and Kaua'i (and probably Maui) have all been collected only sporadically. All are found in wet forest (several also occur in mesic areas), and all except *H. muranus* are known from widely separated locales.

These species are found in habitat that is

TABLE 1

Island Distribution, Habitat Preference, Currently Assessed Conservation Status (See Text and Table 2 for Details), and U.S. Fish and Wildlife Service (1984) Candidate Listings for All Hawaiian *Hylaeus* (*Nesoprosopis*) Species

Species	FWS (1984)	Status	Habitat[a]					Island[b]					
			c	d	m	w	s	K	O	Mo	L	Ma	H
akoko Magnacca & Daly, 2003	n[c]	5			●								●
andrenoides (Perkins, 1899)	2	1			●	●		●					
angustulus (Perkins, 1899)	3A	2				●				●	○	●	
anomalus (Perkins, 1899)	2	6			●	●			○				
anthracinus (F. Smith, 1853)	2	4	●	●					●	●	○	●	●
assimulans (Perkins, 1899)	2	5	●	●					○		●	●	
chlorostictus (Perkins, 1899)	2	1	●	●	●			●					
coniceps (Blackburn, 1886)	2	1			●	●	●					●	●
connectens (Perkins, 1899)	3A[d]	3	●	●	●	●		●	●	○	●	●	●
crabronoides (Perkins, 1899)	2	2				●							●
difficilis (Perkins, 1899)	2	1	●	●	●	●	●			●	●	●	●
dimidiatus (Perkins, 1899)	2	4		●	●								●
dumetorum (Perkins, 1899)		1			●	●							●
facilis (F. Smith, 1879)	2	5	●	●	●	●			○	●	○	●	
filicum (Perkins, 1911)	2	2			●	●							●
finitimus (Perkins, 1899)	3A	6	●					○					
flavifrons (Kirby, 1880)	2	4	●					●					
flavipes (F. Smith, 1853)	2	3	●	●							●	○	●
fuscipennis (F. Smith, 1879)	2	3			●	●			○	●	●	●	
gliddenae Magnacca & Daly, 2003	n	6			●								○
haleakalae (Perkins, 1899)	2	1				●				●		●	
hilaris (F. Smith, 1879)	3A	5	●							●	○	○	
hirsutulus (Perkins, 1899)	2	2		●	●	●		●					
hostilis (Perkins, 1899)	2	1	●	●	●			●					
hula (Perkins, 1911)	2	5			●								●
inquilina (Perkins, 1899)		1		●									●
kauaiensis (Perkins, 1899)	2	1			●	●		●					
kokeensis Magnacca & Daly, 2003	n	2			●			●					
kona (Blackburn, 1886)	2	4		●									●
kuakea Magnacca & Daly, 2003	n	5			●				●				
kukui Magnacca & Daly, 2003	n	2				●						●	●
laetus (Perkins, 1899)	2	3		●	●	●		●	●	○	●	●	●
longiceps (Perkins, 1899)	2	4	●	●					●	●	●	●	
mana Magnacca & Daly, 2003	n	5			●				●				
mauiensis (Perkins, 1899)	3A	6				●						○	
melanothrix (Perkins, 1899)	3A	6				●						○	
mimicus Magnacca & Daly, 2003	n	1			●	●			●				
muranus (Warncke, 1970)	2	2				●							●
mutatus (Perkins, 1899)	3A	1			●	●		●					
nalo Magnacca & Daly, 2003	n	6							○				
niloticus (Warncke, 1970)	2	6	●	●						○	○		○
nivicola Meade-Waldo, 1923	3A	1					●					●	
ombrias (Perkins, 1910)	2	4	●	●									●
paradoxicus (Perkins, 1899)		5		●	●								●
pele (Perkins, 1911)	3A	1		●	●								●
perkinsianus (Timberlake, 1926)	2	1	●	●									
perspicuus (Perkins, 1899)	3A	6			●	●		○					
psammobius (Perkins, 1911)	3A	4	●									●	○
pubescens (Perkins, 1899)	2	1			●	●							●
rugulosus (Perkins, 1899)	3A	2		●	●	●							●
satelles (Blackburn, 1886)	2	6				●				○	○	○	
setosifrons (Perkins, 1899)		1			●	●							●
simplex (Perkins, 1899)	2	6		●	●								○

TABLE 1 (continued)

Species	FWS (1984)	Status	Habitat[a]					Island[b]					
			c	d	m	w	s	K	O	Mo	L	Ma	H
solaris Magnacca & Daly, 2003	n	4	●					●					
specularis (Perkins, 1899)	2	1			●	●		●	●	●			●
sphecodoides (Perkins, 1899)	2	1	●	●	●	●							●
takumiae Magnacca & Daly, 2003	n	1					●					●	
unicus (Perkins, 1899)	2	1			●	●			●	●	●	●	
volatilis (F. Smith, 1879)	2	3	●	●			●		○	○	○	●	
volcanicus (Perkins, 1899)		1		●	●		●					●	●
Collected								12	9	10	8	18	25
Missing								2	6	5	7	5	4
Proportion collected								0.86	0.60	0.67	0.53	0.78	0.86

[a] c, coastal; d, dry forest and shrubland; m, mesic forest; w, wet forest; s, subalpine shrubland. Open circles indicate only historical collections.

[b] K, Kaua'i; O, O'ahu; Mo, Moloka'i; L, Lāna'i; Ma, Maui; H, Hawai'i.

[c] n, new species described in Daly and Magnacca (2003).

[d] Although *H. connectens* was listed as 3A, two junior synonyms (*H. koae* and *H. vicina*) were listed as category 2.

difficult to access as well as difficult to collect bees in; wet forest makes up the bulk of the areas that have not been surveyed (aside from vast areas of montane shrubland on the island of Hawai'i [Figure 2]). Because *Hylaeus* species typically forage only during sunny weather, the chances of successfully collecting them in these almost perpetually cloudy regions are low, and it is a testament to their adaptability that they are able to persist in

TABLE 2

Hylaeus Species Listed by Conservation Category

1	2	3	4	5	6
Uncommon to abundant, habitat safe	Rare but widespread, habitat safe	Missing from one or more islands	Restricted to endangered habitat	Very rare, probably endangered	No recent collections, endangered
andrenoides	*angustulus*	*connectens*	*anthracinus*	*akoko*	*anomalus*
chlorostictus	*crabronoides*	*flavipes*	*dimidiatus*	*assimulans*	*finitimus*
coniceps	*filicum*	*fuscipennis*	*flavifrons*	*facilis*	*gliddenae*
difficilis	*hirsutulus*	*laetus*	*longiceps*	*hilaris*	*mauiensis*
dumetorum	*kokeensis*	*volatilis*	*ombrias*	*hula*	*melanothrix*
haleakalae	*kukui*		*psammobius*	*kona*	*nalo*
hostilis	*muranus*		*solaris*	*kuakea*	*niloticus*
inquilina	*rugulosus*			*mana*	*perspicuus*
kauaiensis	*specularis*			*paradoxicus*	*satelles*
mimicus					*simplex*
mutatus					
nivicola					
pele					
perkinsianus					
pubescens					
setosifrons					
sphecodoides					
takumiae					
unicus					
volcanicus					

such places. Thus, although they have been collected only rarely, the fact that their habitat is largely unsurveyed and is relatively pristine over large expanses (Cuddihy and Stone 1990) suggests that they may be much more abundant than their collection records imply. Although *H. angustulus* has not been found recently on Lāna'i, that is probably due to poor weather during collecting trips and it likely persists on the island.

Hylaeus kokeensis, a newly described species from Kaua'i, appears to be restricted to mesic and dry forest. Both of these area types are generally under greater threat from development, agriculture, and invasive plants than are wet areas. However, the species occurs in a protected area (Kōke'e State Park/Nāpali-Kona Forest Reserve), and the habitat is intact over relatively large areas. Although it has been collected only twice, it was found in high numbers. Invasive exotic plants are probably the greatest threat to this species.

Some Populations Threatened

Hylaeus connectens, though usually not greatly abundant, is the most widespread species in the Islands. It occurs on all the main islands and in all habitats except subalpine shrubland, though it seems to prefer mesic forest. Nevertheless, it has not been collected recently from Moloka'i. The habitat it is typically found in on Maui—open 'ōhi'a-uluhe wet forest, with abundant *Scaevola gaudichaudiana* shrubs—is relatively common on Moloka'i. On other islands (Hawai'i and Kaua'i, in particular) it tends to be collected as scattered individuals, so it is not entirely surprising that it has not been found on Moloka'i. Only one collection is known from the island, so it may never have been abundant there. It is unusual, however, that it is quite abundant on O'ahu, where many other bee populations are depleted. Unknown species-specific factors are also likely at work: *H. fuscipennis* is abundant on Moloka'i but is now absent from O'ahu (see later in this section), although *H. unicus* is common on both islands, and all three occur sympatrically on Maui.

Hylaeus flavipes is the only coastal species with large, widespread populations, particularly on Hawai'i. At least in part this is because it can also be found in some upland areas; the largest known population is at the coast at South Point, but it is relatively abundant at Kīpuka Nēnē in Hawai'i Volcanoes National Park, at approximately 900 m, and on the western slope of Mauna Kea at 1,700–2,800 m. The Maui and Lāna'i populations were originally described as *H. blackburni* and can usually be distinguished from the Hawai'i populations by their smaller size and more extensive coloration. The initial Maui site was the Wailuku sandhills (see discussion of coastal areas in the next section); it has not been collected on Maui since 1912. It was recently rediscovered on Lāna'i at an elevation of about 450 m, but the size and stability of the population there is not known. The Lāna'i site is in a heavily eroded, largely barren area on the windward side of the island, in a small patch of *Myoporum* trees. Although other such patches presumably occur, the bees were not found on other *Myoporum* nearby. The coast of Lāna'i has not been adequately explored for bees, but *H. flavipes* was not found in a small area of native vegetation at the coast where *H. longiceps* was present.

Hylaeus fuscipennis, like its close relative *H. pubescens* of Hawai'i, is one of the most common wet-forest bees of Maui Nui. It can be found there in mesic forest and even in relatively marginal habitat at the edge of native forest but has not been collected recently on O'ahu. Why this should be, when several other wet-forest species (*H. connectens*, *H. mimicus*, and *H. unicus*) have been collected in good habitat there, is not clear.

Hylaeus laetus is a dryland species and is also very abundant on some islands but rare on others. The only species besides *H. connectens* to occur on all the main islands, it is common on Hawai'i, Lāna'i, and Kaua'i, even in relatively poor habitat (i.e., low plant diversity, high cover of invasive exotics, few other *Hylaeus* species). On Maui it has been collected recently only from a few lowland areas of West Maui, and on O'ahu from a single locality in the northern Wai'anae Range; no recent collections have come from Moloka'i. Unlike its close relatives *H. difficilis* and *H. hirsutulus*, it is almost never found in

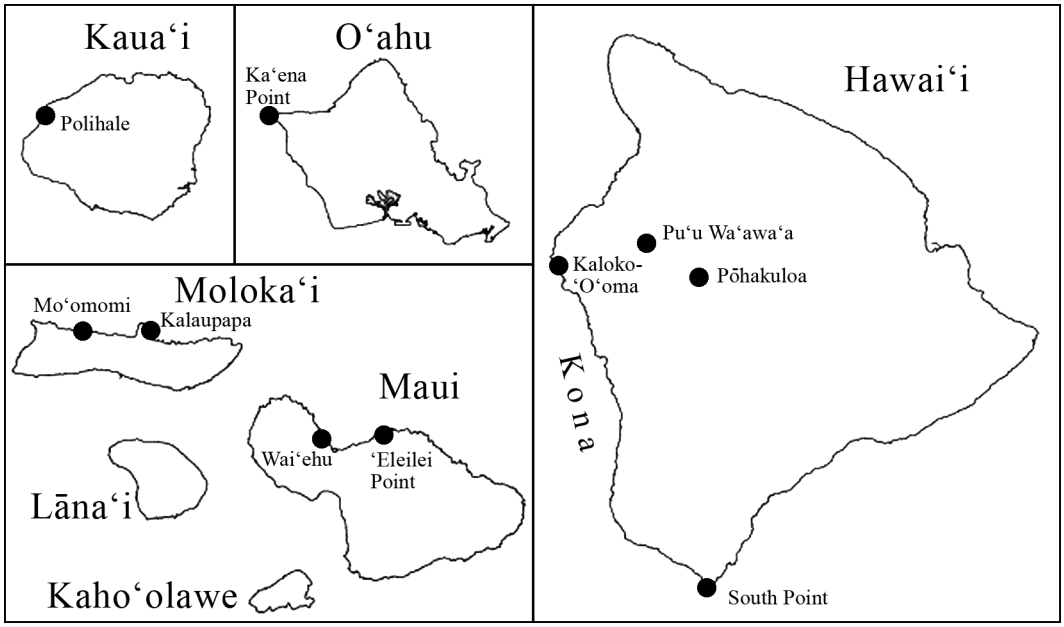

FIGURE 3. Rare habitats (primarily coastal), described in Results.

wet or even mesic forest, and this may be a primary reason for its rarity on Maui, Moloka'i, and O'ahu, where intact native dry forest and shrubland are scarce. However, all three islands have unsurveyed areas that may support larger populations of *H. laetus*.

Hylaeus volatilis is one of the five cleptoparasitic species of Hawaiian *Hylaeus*, the only known cleptoparasitic colletids (Michener 2000). It is fairly common in the subalpine shrubland in and around Haleakalā National Park, where its presumed hosts, *H. difficilis* and *H. nivicola*, form extremely dense populations. Although it has historically been recorded from various parts of all the islands of Maui Nui and from O'ahu (Perkins 1899), the only other recent collection is from West Maui, above Lahaina at about 600 m. As noted earlier, other dry areas are highly degraded, although some of those that remain have not been surveyed.

Restricted to Rare Habitats

Coastal strand habitat (Figure 3) is the most endangered in Hawai'i for a number of reasons: it is highly valued for development, popular for recreation, typically dry and therefore vulnerable to fire, susceptible to invasion by exotic plants, and it covers a small area by definition. On most of the Islands, only one coastal site with diverse native vegetation is protected, making the bees that inhabit them vulnerable to single catastrophes. As a result, they make up the bulk of the areas of concern for species in this category.

At Polihale, a state park on the western coast of Kaua'i, the vegetation is almost all native along the first few banks of dunes before changing to mostly exotic trees about 100 m back from the water. The bee fauna consists of *H. chlorostictus*, *H. connectens*, *H. hostilis*, *H. flavifrons*, and *H. solaris*. The first three are also found in montane areas, but the last two are apparently restricted to the coast. The site is open to the public for camping and other recreational activities, making it vulnerable to physical destruction of plants by people and vehicles. However, the Pacific Missile Range Facility at Barking Sands is directly to the south and probably also includes intact habitat. There are also areas

on the southeastern coast where native vegetation persists, but these are threatened by development.

Ka‘ena Point, on the western tip of O‘ahu, is a state Natural Area Reserve. The bee fauna includes *H. anthracinus* and *H. longiceps;* this is the only known locality for these species on O‘ahu. However, *H. assimulans* and *H. volatilis*, both previously recorded from the leeward coast of O‘ahu, are notable in their absence from such prime habitat. Illegal off-road driving has long been a problem there, but the site is now blocked off, and the diverse vegetation is recovering and being restored (B. Gagné, pers. comm.).

South Point (Ka Lae) is the best coastal site for bees on Hawai‘i. Most of the species found there—*H. anthracinus*, *H. difficilis*, *H. flavipes*, *H. ombrias*, and *H. sphecodoides*—can also be found at other sites, either farther east along the coast or at higher elevations, but South Point is the only place where all the coastal species on the island (with the exception of *H. psammobius*) are found together. Much of the area is under the jurisdiction of the Department of Hawaiian Home Lands, but access is largely unregulated. Although driving may injure vegetation, the native plants extend over a wide enough area that the bee populations there are probably not threatened. However, *H. anthracinus* appears to be restricted to regions of more-recent lava flows east of the point, on flowers of *Scaevola* and the introduced *Tournefortia*. It is not clear why this should be when the other species are abundant on the carpet of *Sida* (‘ilima) and *Jacquemontia* (pā‘ū o Hi‘iaka) growing on the older substrates and *H. anthracinus* is found at these plants on other islands. However, the high degree of genetic divergence between island populations of *H. anthracinus* (Magnacca and Danforth 2006) may point to behavioral differences between them.

A second population of *H. anthracinus* was recently discovered at Pūhili Point on the Kona coast of Hawai‘i, also on *Tournefortia*. Although the extent has not been fully investigated, it appears to live in a narrow area between a population of *Anoplolepis gracilipes* ants to the south and barren lava to the north. In addition, this area may be developed in the near future. *Hylaeus difficilis*, but apparently not *H. anthracinus*, can be found in the protected Kaloko-Honokōhau National Historic Park just to the south. The difference in distribution between the two species may be related to greater ant tolerance by *H. difficilis.*

Mo‘omomi, on the northwestern coast of Moloka‘i, is a Nature Conservancy of Hawai‘i preserve. Like Polihale, it consists of a native beach flora backed by mostly exotic trees. The bee fauna includes *H. anthracinus* and *H. longiceps*, as well as the extremely rare cleptoparasite *H. hilaris.* The latter has been collected only twice in recent years (with only a single specimen each time), and its apparent extirpation from Maui and Lāna‘i leaves this as the only known site for it. Based on the few visits I have made, it is difficult to estimate numbers of the other two species, its presumed hosts. However, I have never caught more than 10 bees in an hour, a much lower rate than at most other sites. The population of *H. hilaris* must therefore be extremely small, and among species that have been collected recently it is probably the most endangered. It is the most colorful of the Hawaiian bees: the abdomen is largely red, with unusual white hair bands, and the front of the male’s head is almost entirely yellow. As one of only five species of parasitic Colletidae in the world (the others are also Hawaiian but are not threatened), it would be a particularly tragic loss if it were to become extinct. Even with a well-protected site, the apparent lack of a second population (it is unknown how far *H. hilaris* and its hosts extend along the coast) makes the known population highly vulnerable to fluctuations in host numbers, which can drop very low during periods of drought or other poor flowering periods.

The Kalaupapa peninsula on the northern coast of Moloka‘i has an extensive area of native coastal vegetation on its east side. It is similar to the site at South Point, with prostrate, windswept plants including *Chamaesyce degeneri* (‘akoko), *Heliotropium* spp. (hinahina), *Jacquemontia*, and *Sida*, as well as *Tournefortia* in places. *Hylaeus anthracinus* and *H. facilis* have been collected there on the latter;

H. longiceps and possibly *H. hilaris* are probably also present on the native species during flowering season but were absent when I visited during a dry period.

There are few coastal sites of the quality of those just described on the island of Maui. Areas of native vegetation exist on the northern coast of West Maui (F. Warshauer, pers. comm.) but have not been investigated. Perkins' primary site for coastal bees on Maui was the Wailuku sandhills, which once supported a diverse bee fauna: *H. anthracinus*, *H. assimulans*, *H. facilis*, *H. flavipes*, *H. hilaris*, *H. laetus*, *H. longiceps*, and *H. volatilis* (Perkins 1899). These dunes are now built upon or covered with the exotic tree *Prosopis pallida* (kiawe); native plants are scarce, and bees are absent. *Hylaeus flavipes* and *H. hilaris* have not been collected on Maui since 1912; their absence from areas where other coastal or lowland species have been collected suggests that they may have been extirpated.

Two of the species listed above, *H. facilis* and *H. volatilis*, are (or were) commonly found at higher elevations. The other more strictly coastal species, *H. anthracinus*, *H. assimulans*, and *H. longiceps*, have been found recently at a few scattered sites around the island. The first has been collected at Kanaio at 600 m on the lower southern slopes of Haleakalā, an unusual location for this otherwise exclusively coastal species (it was also found at the coast nearby, at Manawainui). *Hylaeus assimulans* was found in dry forest at 600 m on the western side of the island, together with *H. laetus* and *H. volatilis*. A small population of *H. longiceps* occurs at Waiehu, on a very small (<1 ha) patch of relictual native dune vegetation near a golf course. A few additional specimens have been collected from elsewhere on West Maui, but that area is largely dominated by exotic plants and has not been adequately searched for patches of native vegetation.

Hylaeus psammobius, known historically from Maui and Hawai'i, is the only native bee to inhabit windward coastal regions. It lives in *Sesuvium* ('ākulikuli) herbland (Gagné and Cuddihy 1990), where it collects pollen of *Sesuvium*, *Bacopa*, and *Lycium* (unpubl. data). This is a unique habitat for a Hawaiian *Hylaeus* species, very different from that of other coastal species. Phylogenetic data (Magnacca and Danforth 2006) show that it is sister to *H. anthracinus* + *H. flavifrons*. Very few historic collections are known, and it has been found recently at only one site, at 'Eleilei Point on the northern coast of East Maui (similar sites exist elsewhere along the coast but have not been surveyed). Although it is reasonably abundant there, the area is so small and close to the shoreline—the plants grow on rocks barely above the spray zone, in an area ~10 m wide between the ocean and cliffs—that a single large storm could seriously damage or destroy the site as habitat for the bees. The species has not been collected on Hawai'i since 1908, but the windward coast there should be checked for intact habitat of this type.

Coastal habitat is even scarcer on Lāna'i. Two of the typical coastal species, *H. flavipes* and *H. longiceps*, are primarily found at middle elevations (around 300–450 m); *H. anthracinus* has not been collected there recently.

A number of other potential coastal sites that have not been investigated should be checked for *Hylaeus* populations. These include Keoneloa on Kaua'i, Kahuku on O'ahu, and the northeastern coasts of Maui and Hawai'i. Bees have also been collected on Kaho'olawe (*H. assimulans* in 1997 and *H. anthracinus* in 2002), but the island has not been searched widely.

The most notable threatened habitat in montane regions is *Chamaesyce olowaluana* ('akoko) trees in mesic or dry forest in western Hawai'i. At both Pōhakuloa Training Area and Pu'u Wa'awa'a Wildlife Sanctuary, isolated trees of this species appear to support large populations of a diverse group of bees rarely found elsewhere. These include *H. akoko*, *H. dimidiatus*, *H. filicum*, *H. hula*, *H. kona*, and *H. paradoxicus*, along with more common species such as *H. coniceps*, *H. difficilis*, *H. laetus*, and *H. pele*. The species of the first group were not found at nearby, more common flowering plants, such as *Bidens*, *Myoporum*, and *Styphelia*, where those of the second group were collected. Moreover, of the first group, only *H. dimidiatus* and *H. paradoxicus* were found at both sites, and none was

found in the Mauna Loa–Mauna Kea saddle or Mauna Kea north slope regions, where *C. olowaluana* is more abundant. This suggests that conservation of *C. olowaluana* in the Pu'u Wa'awa'a and Pōhakuloa areas is important for the survival of the bees, even if other populations of the tree remain. Despite abundant seed set and germination, reproduction of *C. olowaluana* is impeded by sheep, which devour the seedlings before they have a chance to grow.

In addition to the presence of *C. olowaluana*, Pōhakuloa and the adjoining western slope of Mauna Kea are unique upland sites for *H. flavipes* and *H. ombrias*. Most of the other sites for the former are below 400 m, and all (except the Halepōhaku record) are below 1,000 m; the only other recent collections of the latter are from South Point, at the coast. Why both species should occur there, at over 1,700 m and on an entirely different set of host plants, but not in other upland areas is unknown. It may be that the "coastal" species also formerly inhabited all areas of upland dry forest but not the shrubland that makes up most of the dry habitat that remains today. This would also explain the presence of *H. anthracinus* in dry forest at over 600 m at Kanaio on Maui, when it is otherwise strictly coastal. A single *H. anthracinus* was recently collected at Pōhakuloa, but the existence of a viable population there still needs to be verified.

Rare Species

Hylaeus akoko, *H. hula*, *H. kona*, and *H. paradoxicus* were discussed earlier. All four might be found farther south in the uplands of the Kona and Ka'ū Districts, but much of that area has been heavily grazed and has not been searched for bees since Perkins at the turn of the last century. Aside from Pu'u Wa'awa'a, *H. hula* is known from a small area of mesic forest at Kīlauea but is rare there as well; the other species have been collected recently only on *C. olowaluana* at Pōhakuloa or Pu'u Wa'awa'a.

Hylaeus assimulans is a large coastal and lowland species, known historically from O'ahu, Maui, Kaho'olawe, and Lāna'i. It is strange that it does not seem to occur at Ka'ena Point, the best coastal site on these islands. Recent collections have been sporadic and few, from West Maui, Lāna'i, and Kaho'olawe. Like its sister species, *H. ombrias* of Hawai'i, it appears to be more closely associated with *Sida* than other species are, visiting it for both nectar and pollen. Thus, it may be more common in areas with large amounts of *Sida*, for example, the *Prosopis* (kiawe) forests of southern Lāna'i. Unfortunately, I visited this area during a prolonged drought during which nearly all of the *Sida* had died. I collected only a few *H. assimulans*, but it may be more common under favorable conditions.

The closely related *H. facilis* and *H. simplex* present a striking case. According to Perkins (1899), they were among the most common and widespread species on O'ahu/Maui Nui and Hawai'i, respectively. Dozens of specimens in the Bishop Museum collection attest to this. But between the 1930s, when collecting of *Hylaeus* species tapered off, and recent years, when it picked up again, the species virtually disappeared. Only three specimens of *H. facilis* have been taken in the last 30 yr: one from O'ahu in 1975, one from Maui in 1993, and one from Moloka'i in 2005. I was unable to recover either species during extensive searches in areas where they had previously been recorded. It is a mystery why these two formerly abundant species should have decreased to the point of near extinction while substantial habitat remains and other similar, closely related species, such as *H. chlorostictus* and *H. difficilis*, are still very abundant.

The answer may be complex. It may be that *H. simplex* was never as common as it was thought to be. The expansion of the male gonocoxae is the primary character that unites *H. simplex* and *H. facilis*, and it is the only reliable means of distinguishing them from *H. difficilis* (females of the three species cannot be separated at all). The genital capsule is usually retracted within the abdomen, and the gonocoxae are not visible in most of the museum specimens labeled as *H. simplex* that I have examined. This makes their determinations questionable, especially in light

of the current great abundance of *H. difficilis*. It is still strange that it should have disappeared while its habitat seems to remain but perhaps not as much so as if it had been very abundant.

The gonocoxae of *H. facilis* are usually visible externally even without being extracted, and there is no question that it was formerly quite common. However, all dry- and mesic-forest species are now rare on Maui Nui and O'ahu. Even *H. laetus*, one of the most common species in drier areas of Kaua'i and Hawai'i, is difficult to find on Maui and O'ahu, and has not been recently collected on Moloka'i. Native dry and mesic habitats have been decimated on the latter three islands (Mueller-Dombois 1973, Medeiros et al. 1986); much of what remains is in very small patches that may be incapable of supporting a population of bees. It may be that if *H. facilis* still survives on Maui and O'ahu, it is in small remnant patches of mesic or dry forest that have yet to be searched for bees.

Two recently described O'ahu species, *H. kuakea* and *H. mana*, are also inhabitants of mesic forests. Each is known from a single collection record, with two and four specimens, respectively. The former is from a Nature Conservancy preserve in the Wai'anae Range (Honouliuli); this region contains a relatively large amount of potential habitat, and current protection and restoration efforts may help maintain it there. It is not known what its specific habitat requirements are. *Hylaeus mana* was collected in mesic forest on *Santalum* at a relatively low elevation (430 m) in the leeward Ko'olau Range. Although there is a considerable amount of native wet forest above 500 m, at lower elevations and rainfall levels the vegetation is largely alien on most of the ridges with trails. That no other species were found with either *H. kuakea* or *H. mana*, and both were collected more or less by accident, suggests that more intensive and systematic searching will turn up more specimens and possibly even more species. Nevertheless, the fact that it has taken so long for them to be discovered, coupled with the general scarcity of their habitat, means they are likely to remain rare.

Uncollected Species

Ten species have not been collected recently, including the previously mentioned *H. simplex*. Most are known from very few specimens.

Hylaeus anomalus occurred on southern leeward Ko'olau ridges on O'ahu. Although apparently never highly abundant, it was not uncommon during the early collecting period through the 1930s. Like *H. fuscipennis*, which lived in the same area, it has not been collected in decades. In light of the apparent disappearance of these two species from the area, it is particularly strange that the newly described *H. mimicus* had not been collected before. Even on the ridges directly above Honolulu, I found the latter species in sufficient numbers that a collector could hardly fail to recover it; yet in the Bishop Museum collection (which contains dozens of *H. facilis* from this area) only a single specimen was found, and that was from the northern Ko'olau Range where little collecting was done. Clearly a shift in species composition has occurred in the area despite the apparently good quality of the vegetation.

Hylaeus finitimus is known from two specimens collected by Perkins (1899) on the coast at Makaweli (probably in the vicinity of Ho'ānuanu Bay, east of Waimea) on Kaua'i. Although there are patches of *Scaevola* at the coast in that area, there do not appear to be any intact coastal communities there. Perkins (1899) stated that he searched there and in other places for more specimens and did not find any, and the species was not found at Polihale. Whether it is phylogenetically closer to *H. longiceps* or *H. flavipes* is uncertain because the male specimen cannot be located; Perkins' description (1899) and later key (1910) are in conflict regarding the characters that separate *H. finitimus* from the other two. The female is indistinguishable from *H. longiceps*, and it may simply be a Kaua'i population of that species.

Hylaeus gliddenae is known from a single male collected at Kīlauea in 1934. Its habitat is unknown, but the label states that it came from a nest burrow in *Myrsine*, a tree that is widespread but most common and largest in

mesic forest. Its obvious close relationship to *H. paradoxicus*, a mesic- or dry-forest species, supports this conclusion. In fact, it is conceivable that at least some of the smaller, rare females described by Perkins (1899) as *H. erythrodemas* (a name later synonymized with *H. paradoxicus*) were actually females of *H. gliddenae*. Kīlauea straddles a steep rainfall gradient, so wet, mesic, and dry habitats can be found within a few kilometers (Figure 2). It has also been protected as part of Hawai'i Volcanoes National Park since 1916. As a result, it is the most diverse locality for bees: 22 of the 28 Hawai'i Island species have been collected there, all except four coastal species and two that are confined to Kona. Eighteen of the 22 have been collected at Kīlauea recently, but several mesic- to dry-forest species, including *H. paradoxicus*, have been found exclusively or more abundantly at localities in northwestern Hawai'i such as Pu'u Wa'awa'a and Pōhakuloa. It therefore seems more likely that *H. gliddenae* will be found at these sites than at its type locality.

Hylaeus nalo is also known only from a single male, collected on O'ahu in 1914. The specific locality is not recorded on the label, and it does not show any clear affinities to other species. The most likely sister species is probably *H. rugulosus*, although there are several other possibilities. The lack of information about it obviously makes it hard to search for, which is especially frustrating in light of the difficulty in interpreting its relationships and its unique morphology. It is a large species, but its impunctate metasoma and broad scape separate it from the other groups of large species (the *pubescens* group, and *H. assimulans* and *H. ombrias*, respectively). It also possesses truncate gonocoxae, which are unique in the subgenus, and peculiar, poorly defined facial marks.

Hylaeus mauiensis, *H. melanothrix*, and *H. satelles* are all recorded from wet forests of Maui (the last has also been collected on Moloka'i and Lāna'i). The first is known from only a single male (the female was described by Perkins [1899], but the specimen could not be located); modest series of the other two exist. All three were collected from very wet areas that are difficult to access and to collect in, so it is not surprising that they have not been collected recently. Large areas of intact wet-forest habitat remain on the island, so more-intensive collecting will probably turn up these species.

Hylaeus niloticus (= *obscuratus*) is known from a few specimens collected on the coasts and lowlands of Hawai'i, Lāna'i, and Moloka'i. Little or no native habitat remains in the areas where it was collected previously (Kona coast of Hawai'i, dry lowlands of Moloka'i), and it has not been found in similar areas where other coastal *Hylaeus* species have been collected (e.g., South Point, Pōhakuloa, Mo'omomi). A few other areas of native dry habitat remain, such as at Kamiloloa in central Moloka'i, but have not been searched.

Hylaeus perspicuus is known from a few specimens collected by Perkins in mesic to wet forest at Makaweli on Kaua'i. This area is privately owned and has not been surveyed for bees recently, and the species has not turned up in similar habitat around Waimea Canyon and the Alaka'i region. Still, the wetter areas east of the canyon where it is most likely to be found have not been searched intensively, and it is also possible that it is limited to the Makaweli area.

DISCUSSION

Vegetation and Habitat

The strong dependence of all species of *Hylaeus* on native plants to the near-complete exclusion of exotics (with the sole exception of *Tournefortia* among the latter) means that to conserve them native forests and shrublands must be preserved. Conservation of the plants and bees is a reciprocal situation, given the likely status of *Hylaeus* species as primary pollinators of many important plants. Based on current distributional information, it is clear that for bees to be present, at least some level of vegetation diversity is required. This is probably due to a combination of temporal (i.e., year-round availability of floral resources) and nutritional factors. Visitation records (Daly and Magnacca 2003) and identification of pollen loads (unpubl. data) indicate that *Hylaeus* species are frequent visitors

TABLE 3

Favored and Avoided Plant Species (See Table 1 for Explanation of Habitat Types)

Scientific Name	Family	Common Name	Habitat				
			c	d	m	w	s
Favored flowers							
Chamaesyce spp.	Euphorbiaceae	ʻakoko	•	•	•	•	
Cheirodendron trigynum	Araliaceae	ʻōlapa			•	•	
Dodonaea viscosa	Sapindaceae	ʻaʻaliʻi	•	•	•		
Metrosideros polymorpha	Myrtaceae	ʻōhiʻa		•	•	•	
Myoporum sandwicense	Myoporaceae	naio	•	•	•		
Scaevola sericea	Goodeniaceae	naupaka kahakai	•				
Sida fallax	Malvaceae	ʻilima	•	•			
Sophora chrysophylla	Fabaceae	māmane		•	•		•
Styphelia tameiameiae	Epacridaceae	pūkiawe		•	•	•	•
Tournefortia argentea[a]	Boraginaceae	tree heliotrope	•				
Rare plants							
Argyroxiphium sandwicense[b]	Asteraceae	ʻāhinahina (silversword)					•
Chamaesyce olowaluana	Euphorbiaceae	ʻakoko		•	•		
Sesbania tomentosa[b]	Fabaceae	ʻohai	•	•			
Dominant dry-forest trees (rarely visited)							
Acacia koa	Fabaceae	koa		•	•	•	
Diospyros sandwicensis	Ebenaceae	lama		•	•		
Erythrina sandwicensis	Fabaceae	wiliwili		•			
Nestegis sandwicensis	Oleaceae	olopua		•	•		
Psydrax odoratum	Rubiaceae	alaheʻe	•	•	•		

[a] Nonnative species.
[b] Listed endangered.

to many of the community-dominant plants of Hawaiian ecosystems. All of the top 10 pollen types collected by *Hylaeus* species are the dominant or codominant plants in wet forest or dry or coastal shrubland (Table 3, Favored flowers). In addition, several rare species are regularly visited where they are found (Table 3, Rare plants). Although pollination rates have not been investigated, for many of these plants *Hylaeus* species are almost the only regular floral visitors and are undoubtedly important for native plant reproduction and hence ecosystem health.

Dry and mesic forests seem to be an exception to the dominant-plant rule. Aside from *Metrosideros*, most of the dominant trees characteristic of dry and mesic forest (Table 3, Dominant dry-forest trees) are not attractive to bees; many of those that potentially are attractive, such as *Reynoldsia sandwicensis* (Araliaceae, ʻohe makai), are now rare. Only *Sophora*, which is abundant in montane dry forest on Maui and Hawaiʻi but relatively rare on the other islands, and *Myoporum*, which has a similarly patchy distribution, are commonly visited dryland trees. Although it is a favored plant in all habitats, *Metrosideros* appears to be incapable of supporting bees on its own; they are rarely found where *Metrosideros* is the only native flower available. Instead, *Hylaeus* species primarily visit understory shrubs such as *Dodonaea* and *Styphelia*. As a result, composition of the flora, not merely diversity, is probably a major constraint on bee populations in this habitat. Although there are still some large, native dry and mesic areas on Kauaʻi and Hawaiʻi, much of the latter is pioneer vegetation on barren lava flows, consisting almost exclusively of scattered *Metrosideros* (Jacobi and Scott 1985). Even in many remaining forests with a native canopy, the native understory shrubs that

form a large part of the diet of *Hylaeus* species are often absent due to the presence of invasive grasses and shrubs (Cuddihy and Stone 1990, Gagné and Cuddihy 1990). On O'ahu and Maui Nui, dry and mesic forest and shrubland is restricted to small patches (Figure 2) (Mueller-Dombois 1973, Medeiros et al. 1986). At least partly as a result, the middle islands have a much higher proportion of unrecovered species than do Hawai'i and Kaua'i (Table 1).

Chamaesyce olowaluana represents a striking example of the impact that only a few individuals of a preferred host can have. It is one of the most favored host plants despite its rarity and peculiar flowers, which are minute and effectively petal-less. Nine species of bees were collected on an isolated tree in remnant mesic forest at Pu'u Wa'awa'a, but there were almost none on other flowering trees nearby. Similar areas a few hundred meters away, even at sites with greater overall diversity and density of native plants, also had very low bee numbers and diversity, consisting only of common, widespread species. Another single tree in dry forest at Pōhakuloa had similarly high diversity relative to nearby areas. This suggests that dry and mesic forests may once have supported many more bee species that are now extirpated because certain favored plants are gone. It also indicates that the remaining dry forests, especially those with high diversity and an intact native understory, should be searched intensively for bees, rather than passed over because a quick search finds none on the most common trees. Given the widespread destruction of dry forests and drastic reduction in diversity in much that remains, it is probable that some species of *Hylaeus* may have become extinct due to habitat loss before being discovered.

Coastal species face a similar situation. Although the indigenous *Scaevola sericea* is common and widespread, *Hylaeus* species are apparently not capable of surviving on it alone. Although their exact requirements are not known, coastal bees are almost exclusively found in areas dominated by a variety of native shrubs and herbs, including *Chamaesyce*, *Jacquemontia*, and *Sida*. Analysis of pollen loads (unpubl. data) shows that coastal species in particular use many different plants as food sources, not only seasonally but at any given time. In contrast, most native wet forests are capable of supporting bees, at least partially because the pollen diet of wet-forest species is overwhelmingly made up of only two species, *Metrosideros polymorpha* and *Cheirodendron trigynum* (unpubl. data). Both of these are usually present at relatively high frequency even in moderately disturbed forest. Despite its reputation for being gravely threatened worldwide, wet forest is the most intact ecosystem in Hawai'i (Figure 2) (Cuddihy and Stone 1990). Large expanses of forest are protected, to a greater or lesser degree, in montane areas of central Kaua'i; windward O'ahu, Moloka'i, Maui, and Hawai'i; and Kona and Ka'ū Districts on Hawai'i.

Nesting Biology

The nesting habits of most Hawaiian *Hylaeus* species are unknown. However, many bees are more limited by availability of nest sites than host plants (Westrich 1989), and this may be the case for Hawaiian species as well. Although most *Hylaeus* species worldwide nest in dead pithy stems, examples of species that nest in a variety of other substrates are known (Michener 2000 and references therein). Among the Hawaiian species, it appears that those inhabiting wet areas nest in stems or wood, whereas dryland species nest in the ground. *Hylaeus anomalus*, *H. dumetorum*, *H. gliddenae*, *H. pubescens*, *H. setosifrons*, and *H. unicus* are known as examples of the former, and *H. difficilis*, *H. flavipes*, *H. laetus*, *H. nivicola*, and *H. rugulosus* the latter. At least some ground-nesting species are also able to nest in crevices under rocks (Cole et al. 1992) or in rock walls. The cleptoparasitic species appear to attack only ground or crevice nesters.

Hylaeus species lack modifications for digging, such as strong mandibles and a pygidial plate that would allow them to excavate solid wood and hard-packed soil. Almost certainly in the case of wood nesters, and possibly for ground nesters as well, the nest holes are usually not initiated by the bees but are the result of burrows made by other insects, such as

Plagithmysus beetles (Cerambycidae) or *Ectemnius* wasps (Crabronidae). If this is the case, they are dependent on the abundance of other species for nest sites.

Alien Invertebrates

Competition with introduced bees is a potentially important factor that has not been investigated in Hawai'i. A large number of alien species have been introduced to Hawai'i over the past 200 yr, including some hymenopterans (such as ants and yellowjacket wasps) that have wreaked havoc on native arthropods (Perkins 1913, Zimmerman 1948, Gambino 1992, Gillespie and Reimer 1993). Fifteen species of exotic bees have been introduced into Hawai'i (Snelling 2003); 14 are adventive, nearly as many as in all of North America (J. Ascher, pers. comm.). Some introduced species (*Hylaeus leptocephala*, *Lithurgus scabrosus*, *Megachile* spp., and *Xylocopa sonorina*) occur in relatively low numbers or almost exclusively in areas dominated by introduced plants and are generally not considered a threat to native species. Others, including *Apis mellifera* (honeybee), *Ceratina arizonensis*, *C.* nr. *dentipes*, *C. smaragdula*, *Hylaeus albonitens*, and *Lasioglossum impavidum*, occur abundantly in company with native *Hylaeus* species. *Apis* species can be found in extremely high numbers in some areas. The parasites that have decimated feral honeybee populations in North America, the Asian bee mite (*Varroa jacobsoni*) and tracheal mite (*Acarapis woodi*) (Hoopingarner and Waller 1992), are not present in Hawai'i. *Apis* species readily visit a wide variety of both native and exotic plants (Arita et al. 1989) and forage throughout the day and in cloudy or even rainy weather. In some areas, it seems that by sheer numbers they could hardly fail to have an impact on *Hylaeus* species, especially with regard to the nectar supply. The pollination relationship between *Hylaeus* species and the endangered plant *Sesbania tomentosa* at Ka'ena Point on O'ahu was studied by Hopper (2002), who found that *Hylaeus* species are the primary pollinators, with *Apis* species mainly acting as nectar robbers. Still, although abundant on *Metrosideros*, *Myoporum*, *Scaevola*, and *Sophora*, honeybees are rarely found on some of the other important pollen plants for the native bees, such as *Cheirodendron*, *Dodonaea*, and *Styphelia*. Although *Hylaeus* species do not occur in native habitat where there are large numbers of honeybees, the impact of moderate populations of *Apis* species is not known. The other common species, *Ceratina* spp., *H. albonitens*, and *L. impavidum*, are more similar in size and flower visitation to native *Hylaeus* species and may have a greater impact through pollen collection. All five are almost completely unstudied in Hawai'i, and only recently has their presence and/or extent of distribution been documented (Snelling 2003).

Ants are considered the greatest threat to native arthropods (Perkins 1913), but their effect on *Hylaeus* species is not fully known. Although Cole et al. (1992) found that Argentine ants (*Linepithema humile*) on Haleakalā eliminated bees from ant-infested areas, they only compared the abundance of bee nests under rocks in ant and non-ant areas. It may be that bees in small burrows in sand or soil (the typical nesting medium for dryland *Hylaeus* species in Hawai'i) are less vulnerable than those in unexcavated nests under loose rocks. Reduction or extirpation of their *Hylaeus* pollinators by ants and/or alien bees may have been a factor in elimination of native plants from much of the coast.

CONCLUSIONS

Nearly half of the Hawaiian *Hylaeus* species face immediate threats, primarily due to habitat loss or alteration, and 10 are already possibly extinct. As a potential keystone group in all Hawaiian ecosystems, they deserve greater study of their behavior and ecology, as well as their broader influence on native habitats through pollination. The degree of reliance of both common and rare plants on pollination by *Hylaeus* species, tolerance of bees for alien bees and ants, and nesting biology are all fertile subjects for future research that would greatly enhance our understanding of the role of *Hylaeus* species in Hawaiian ecosystems and the steps necessary for their conservation.

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