Eupelmus niger (Hymenoptera: Eupelmidae), a Parasitoid of the Endangered Hawaiian Yellow-faced Bee *Hylaeus anthracinus* (Hymenoptera: Colletidae)

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Abstract. *Eupelmus* (*Eupelmus*) *niger* Ashmead, 1901 (Hymenoptera: Chalcidoidea, Eupelmidae, Eupelminae), the first-ever species of *Eupelmus* Dalman described from Hawai'i, is newly recorded from O'ahu island as a solitary, primary parasitoid of the brood of the endangered Hawaiian yellow-faced bee *Hylaeus anthracinus* (F. Smith) (Hymenoptera: Colletidae) and the non-native nimble masked bee, *Hylaeus* (*Indialaeus*) *strenuus* (Cameron). Both sexes are described, including, for the first time, males, and illustrated along with the female holotype through macrophotography. The biology of *E. niger* is discussed relative to rearing from artificial nest blocks.

Key words: yellow-faced bee, trap nest, parasitoid, endangered species

Sixty-nine species of Eupelmidae (Hymenoptera: Chalcidoidea) are recorded from Hawai'i, all from the subfamily Eupelminae, including 63 species of *Eupelmus* Dalman (Nishida 2002, Noyes 2019). Species of *Eupelmus* are currently classified in three subgenera, *E.* (*Eupelmus*), *E.* (*Episolindenia* Girault) and *E.* (*Macroneura* Walker) (Gibson 1995). The recorded *Eupelmus* fauna of Hawai'i consists of 61 species of *E.* (*Eupelmus*) plus *E.* (*Episolindenia*) *australicus* (Girault) and *E.* (*Macroneura*) *swezeyi* Crawford, of which the latter likely is a synonym of *E. semiputatus* (Girault) (Fusu 2017). The 61 species of *E.* (*Eupelmus*) recorded from Hawai'i compares to only 14 species known from North America (Gibson 2011) and 76 species for the entire Palearctic region (Gibson and Fusu 2016). The *Eupelmus* species diversity of Hawai'i is even more amazing considering that of the 43 extant world genera of Eupelmidae recognized, only six named species in four other genera are yet recorded from Hawai'i—*Anastatus koebelei* Ashmead, *A. picticornis* (Cameron), *A. tenuipes* Bolívar y Pieltain, *Brasema allynii* (French), *Lecaniobius cockerellii* Ashmead, and *Merostenus* (*Reikosiella*) *melinus* (Yoshimoto) (Noyes 2019). Some of the latter species are certainly introduced into Hawai'i, as may be some of the *Eupelmus*, but most members of *E.* (*Eupelmus*) likely are endemic. This places Hawaiian *E.* (*Eupelmus*) among only a handful of highly diverse native radiations within the Hymenoptera of the islands, along

with *Hylaeus* Fabricius (Colletidae, >60 species), *Nesodynerus* Perkins (Vespidae, >110 species), and *Sierola* Cameron (Bethylidae, likely >400 species) (Magnacca 2007, 2020a).

Ashmead (1901) described *Eupelmus niger* as the first of eight newly described species of *Eupelmus* from Hawai'i. He differentiated the unique female from those of his other described species in part by a black body color with only faint metallic lusters under some angles of light and wings that he stated were "subhyaline" except for being clear hyaline at the extreme base, though the holotype female has the fore wing disc distinctly darkened. Perkins (1910) subsequently described another 46 species of *Eupelmus* from Hawai'i, which he also keyed. Although he discussed Ashmead's species and stated that *E. niger* seemed to be very easily distinguished, he did not include it or any of Ashmead's other species in his key. The first two species keyed by Perkins, *E. setiger* Perkins and *E. subsetiger* Perkins, were differentiated in part by the wings being smoky black as opposed to uniformly hyaline or at most faintly yellow-tinged or infuscate in the other species. Timberlake (1926) subsequently included *E. setiger* along with *E. subsetiger* as a likely synonym, plus two newly described species in his new genus *Lepideupelmus*. He differentiated *Lepideupelmus* from *Eupelmus* primarily by females having squamiform setae (=spatulate setae sensu Gibson 1995, Figs. 89, 182; Gibson and Fusu 2016, Figs. 77a–d), but Gibson (1995) synonymized *Lepideupelmus* under *E.* (*Eupelmus*). Because of the extreme sexual dimorphism that characterizes Eupelminae (Gibson 1986, 1995), *Eupelmus* males look nothing like their conspecific females (Gibson 1986, 1995) and species taxonomy has been based mostly on females, with males typically being unrecognized to species unless they are associated with females through rearing. Of the 8 species described by Ashmead (1901), only 2 were based on both sexes and all 46 species described by Perkins (1910) were based only on females.

Hylaeus anthracinus (F. Smith) is one of at least 63 species of *Hylaeus* endemic to the Hawaiian archipelago that are collectively referred to as Hawaiian yellow-faced bees. Many species that were once abundant in the Hawaiian Islands now occupy just a tiny fraction of their historical ranges or are extinct (Daly and Magnacca 2003, Magnacca 2007) and *H. anthracinus* is one of seven species that received federal protection under the Endangered Species Act of 1973 (USFWS 2016). The species is restricted to a few populations on each island from O'ahu to Hawai'i, mostly near the shoreline, and are opportunistic nesters within coral rubble, rocky substrates or in stems of coastal shrub species (Magnacca and King 2013). Populations are vulnerable to extirpation from environmental change and invasive species (Magnacca 2020b), and Plentovich et al. (2021) evaluated the predatory effects of invasive ants on nesting *H. anthracinus* using artificial nest blocks (i.e., trap nests) on O'ahu. One of the present authors (P.D.K.) has subsequently investigated various aspects of the nesting behavior, parasitoids, and competitors of *H. anthracinus* on O'ahu from 2018 to the present using several nest block designs (Krushelnycky et al. 2022, unpublished data). The first of these was similar in construction to that used by Plentovich et al. (2021) and consisted of a 40 cm length of untreated lumber with 20 nest holes drilled in each side. Each hole was approximately 5.5 cm deep and of a diameter large enough to accommodate a transparent plastic tube insert of inner diameter of 3.175 mm, which enabled removal of the tube to observe nest construction and contents. In addition to rearing *H.*

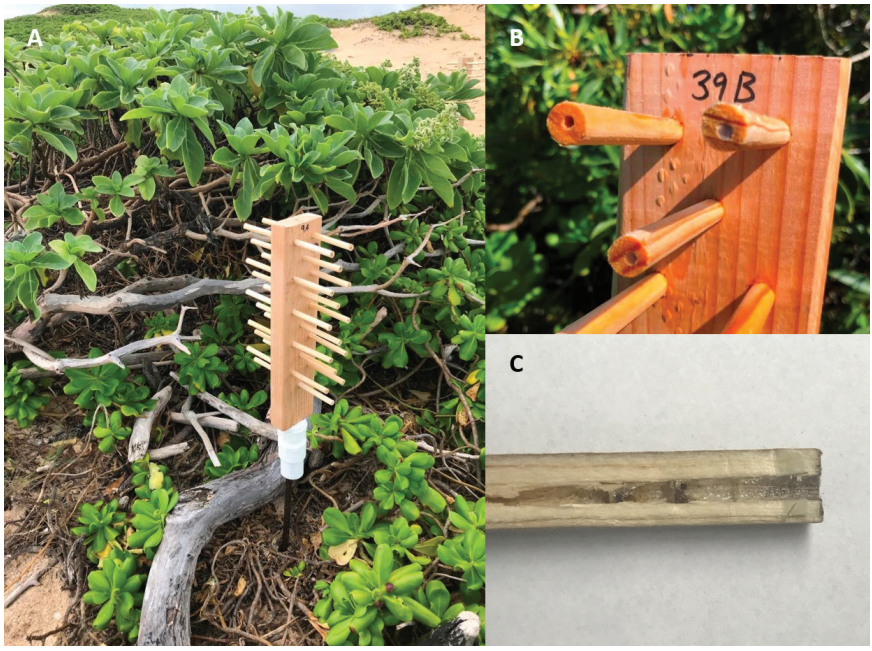

Figure 1. Design of artificial nest block that yielded *E. niger* individuals: **A**, example nest block in coastal strand habitat; **B**, close-up of dowels that serve as nesting sites (top right and lower middle dowels bear cellophane seals indicative of *Hylaeus* nests); **C**, dowel split after bee emergence, showing two previously occupied cells with fecal remains at bottom of each, plus one vestibular cell above.

anthracinus and other species of *Hylaeus* in the nest blocks, three chalcidoid parasitoid species were recovered—*Melittobia hawaiiensis* Perkins (Eulophidae) and two species of *Coelopencyrtus* Timberlake (Encyrtidae) (Krushelnycky et al. 2022). A second group of nest block designs consisted of individual wooden dowels of either 9.525 or 12.7 mm diameter that were mounted onto a 40 cm length of untreated lumber (Figs. 1A, B). Each pine dowel was drilled with a central hole of 3.175 mm diameter and lacked a plastic tube insert (Fig. 1C). These latter nests not only produced at least one of the encyrtid parasitoids reared using the first nest block design, but also both sexes of a species of *Eupelmus* (Krushelnycky et al. 2022, unpublished data).

Species of *Eupelmus* are mostly primary or secondary parasitoids of holometabolous insects that usually are concealed within protected situations such as within cocoons or gall or other plant tissue (Gibson 1995, 2011; Gibson and Fusu 2016). Consequently, twig nesting bees are potential hosts of *Eupelmus* species, though such records are very rare. Of the 433 valid world species of *Eupelmus* listed by Noyes (2019), Vickruck et al. (2010) reported *E.* (*Macroneura*) *messene* Walker, as *E.* (*M.*) *vesicularis* (Retzius), as a parasitoid of *Ceratina dupla* Say (Apidae) in Ontario, Canada. However, only a single individual was reared from 523 cells, which consumed a white-eyed bee pupa that was parasitized also by the gregarious parasitoid *Baryscapus*

americanus (Ashmead) (Eulophidae) (Vickruck et al. 2010). *Eupelmus messene* is frequently associated with hosts in stems of grasses but is a polyphagous primary or hyperparasitoid of a wide variety of holometabolous insects (Fusu 2017) and undoubtedly its parasitism of *C. dupla* was opportunistic. Two species of *E.* (*Eupelmus*), both from Hawai'i, have also been tentatively recorded as parasitizing bee brood. Perkins (1910, p. 631) cited a species "that would run down to *E. flavipes* Cam." parasitizing, among other hosts, bees of the genus *Hylaeus* (*Prosopis* Fabricius), and Swezey (1922, p.14) reported a species "coming near" to *E. euprepes* Perkins parasitizing *Hylaeus unica* (Perkins) larvae in a nest in the pith cavity of a dead *Pipturus* (Uticaceae) twig on Tantalus, O'ahu (Williams 1927, Daly and Magnacca 2003). Females of both *E. euprepes* and *E. flavipes* were described as having hyaline wings; further, the head and mesosoma of *E. euprepes* was described as being of a dull copper color, the palpi pale, the legs for the most part yellow or brownish yellow, and the ovipositor sheaths extensively yellow, whereas *E. flavipes* was described as green and the legs mostly straw-yellow. The females we reared from *Hylaeus* bees from O'ahu are almost entirely dark blue to black with metallic lusters only under some angles of light and with distinctly infuscate fore wings, and thus are more similar to what Ashmead (1901) described as *E. niger* from Maui. Comparison of the reared specimens with one other previously reared female from O'ahu and photographs of the holotype of *E. niger* indicates the specimens are conspecific. Here we report *E. niger* as a parasitoid of *Hylaeus* bees, including the endangered *H. anthracinus*, redescribe and illustrate females of the species and, for the first time, describe and illustrate males of the species, which are also recognized by their dark body color and strongly infuscate fore wings. We also provide biological data for the species based on rearing from artificial nest blocks.

Material and Methods

Material. Our concept of *E. niger* is based on photographs of the holotype female in the Natural History Museum, London, United Kingdom (NHMUK), including dorsal (Fig. 2A) and lateral (Fig. 2B) habitus, frontal (Fig. 2H) and dorsal (Fig. 3B) head, dorsal mesosoma, fore wing (Fig. 3D), mesotarsus (Fig. 3F insert), metatarsus (Fig. 3G), ovipositor stylets, and type labels, as well as a single reared female in the Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Canada (CNC) and our more recently reared females and males obtained from artificial nest blocks. The previously reared female in the CNC is one of several listed under *E. niger* in an unpublished manuscript treating the Chalcidoidea of Hawai'i by the late Carl Yoshimoto. It was produced during his tenure with the CNC and the CNC has representatives of several described Hawaiian species of *Eupelmus* treated in the manuscript. Most of the material cited in the manuscript should be in the collections of the Bernice P. Bishop Museum (BPBM), the University of Hawai'i Insect Museum (UHIM), or the Hawai'i Department of Agriculture (HDOA), Honolulu. However, we were unable to locate the specimens in any of these collections, including any of the other cited *E. niger* specimens (see further under species treatment).

Methods. *Specimen rearing.* Dowels bearing cellophane seals characteristic of *Hylaeus* nests were removed from nest blocks (Figs. 1A, B) for laboratory rearing on several occasions from September 2021 through June 2022. A total of 128 dowels were collected from three coastal locations on O'ahu: Kaiwi Scenic Shoreline

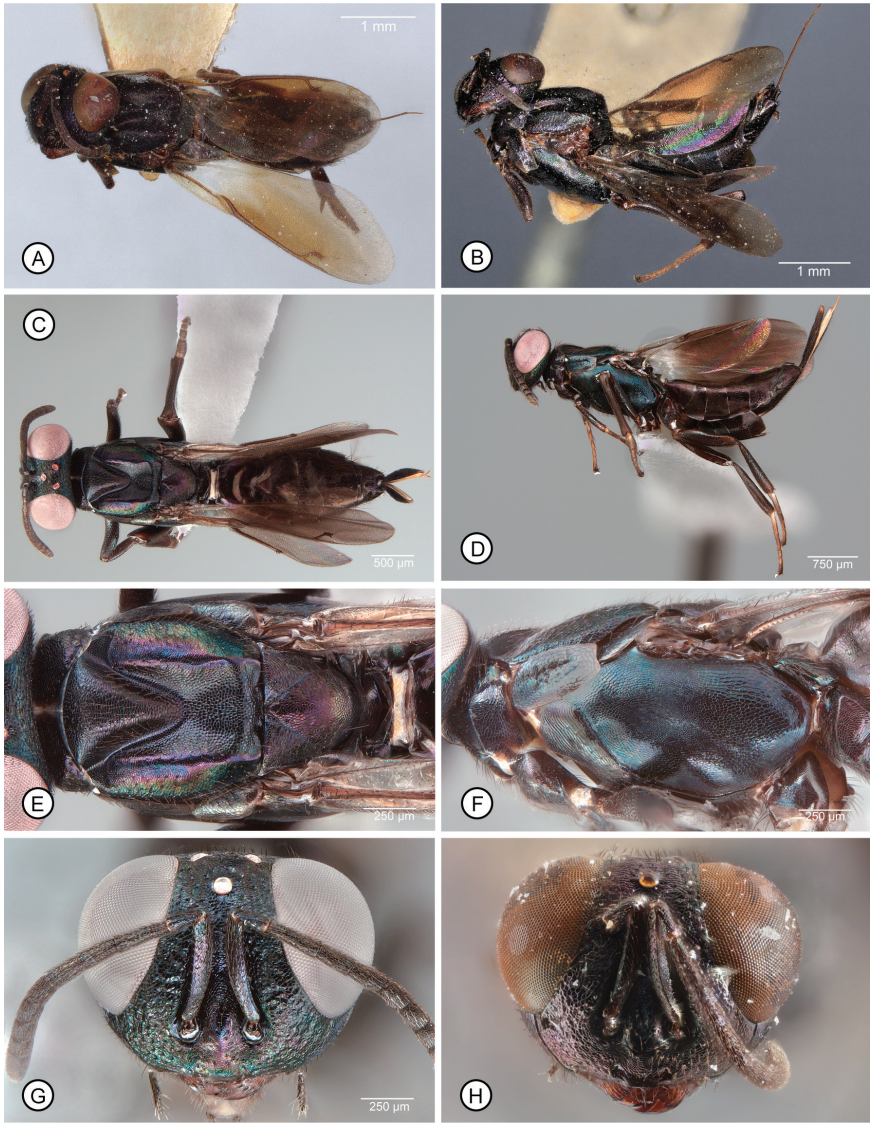

Figure 2. *Eupelmus niger* ♀. **A**, holotype, dorsal habitus; **B**, holotype, lateral habitus. **C–G**, female reared from *Hylaeus anthracinus*: **C**, dorsal habitus; **D**, lateral habitus; **E**, dorsal mesosoma; **F**, lateral mesosoma; **G**, frontal head. **H**, holotype, frontal head.

(KSS) near Makapu‘u Point, James Campbell National Wildlife Refuge (JCNWR) near Kahuku, and Marine Corps Base Hawai‘i (MCBH) near Kāne‘ohe. Dowels were either held in a 50 ml centrifuge tube with a fine mesh screened top or held exposed with a fine mesh bag tied around the end. Emergence of bees and wasps was checked several times daily, and parasitoids were transferred to a standard freezer followed by 95% ethanol for storage. After nest development was complete, 95 of the

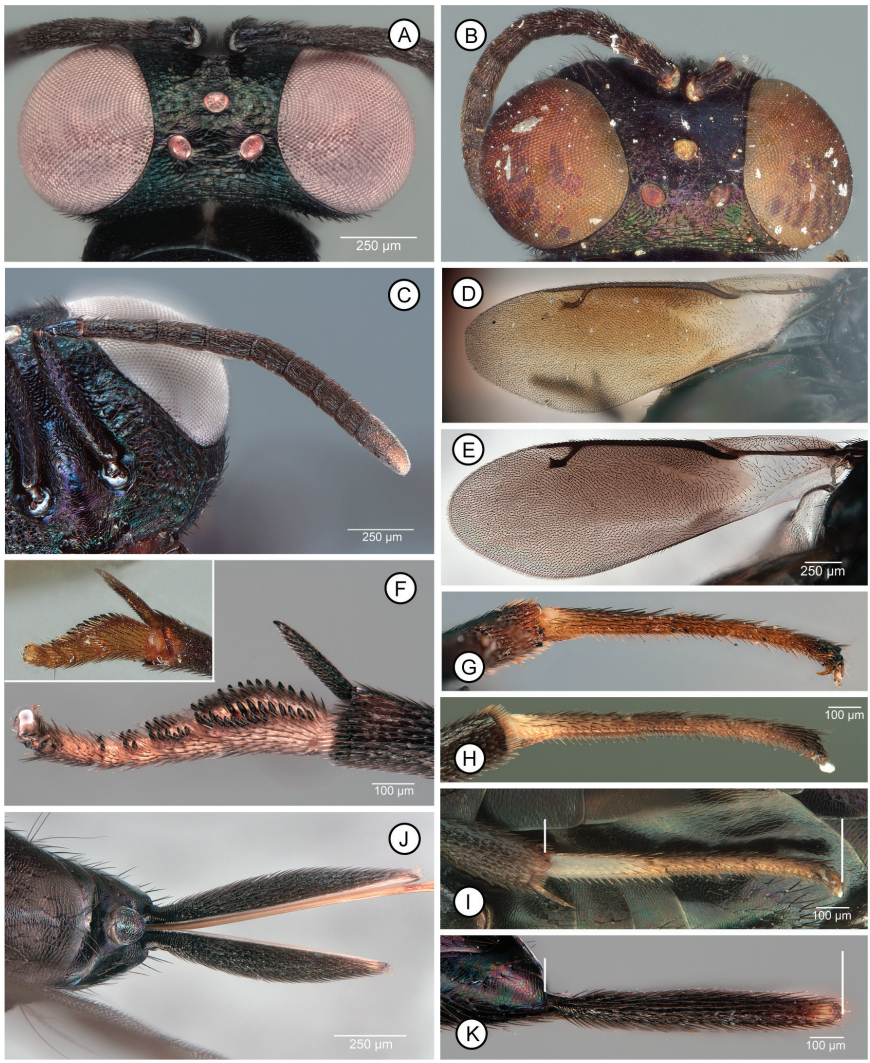

Figure 3. *Eupelmus niger* ♀. **B**, **D**, **F insert**, **G**, holotype: **B**, dorsal head; **D**, fore wing; **F insert**, apex of mesotibia and mesotarsus; **G**, apex of metatibia and metatarsis. **A**, **C**, **E**, **F**, **H–K**, female reared from *Hylaeus anthracinus*: **A**, dorsal head; **C**, head and antenna; **E**, fore wing; **F**, apex of mesotibia and mesotarsus; **H and I**, apex of metatibia and metatarsus; **J**, apex of gaster and ovipositor sheaths, dorsal; **K**, ovipositor sheaths, lateral. [Vertical lines in I and K indicate length measurements.]

dowels were carefully split lengthwise with a chisel to observe the number of brood cells constructed and the status of remaining cell contents (Fig. 1C).

Microscopy/imaging. Images of the holotype of *E. niger* were taken by Natalie Dale-Skey (curator of Chalcidoidea, NHMUK) with a Keyence VHX-7000

digital microscope (Figs. 2A, B, 3B, F insert) or a Canon 5DsR camera with a Canon 70–300 mm lens + Mitutoyo 10× ULWD lens + custom adapter (Figs. 2H, 3D, G), Canon MT-24ex flash, and Cognysis Stackshot, and the serial images stacked using Helicon Focus (these images are © The Trustees of the Natural History Museum, London, and made available under Creative Commons License 4.0, N. Dale-Skey, personal communication). All other images used to illustrate the species description were taken by G.G. at the CNC using a Leica DMC5400 20-megapixel camera attached to a Leica Z16 APO motorized macroscope and illuminated with three Leica KL2500 LCD fibre optic light sources fitted with 250-watt cold light reflector lamps. The fibre optic light sources were filtered through a polystyrene foam dome to reduce glare. The resulting image layers were combined electronically using Zerene Stacker and the final images enhanced as necessary using Adobe Photoshop. The species description was made by G.G. from specimens examined with a Nikon SMZ 1500 binocular microscope with an ocular grid having 100 divisions and were illuminated with a single Leica 100-watt halogen light source. The halogen light source was filtered through a piece of translucent Mylar tracing acetate taped to the microscope objective to reduce glare. The use of different types of light sources, among other factors such as preservation and age of a specimen, can affect the appreciation and intensity of color and because of this some images comprising the plates of illustrations may not match exactly the colors stated in the species description.

Species treatment. Descriptions of both sexes include subgeneric features and are based on critical-point dried specimens from our recent rearings; differences between these and the older, air-dried holotype and previously reared female are discussed under "variation." Terms for fore wing veins and regions follow Gibson (2004). Descriptive format, including material examined, terms for structure and sculpture, abbreviations used in the descriptions for morphological features, and citation of type and non-type label data follow Gibson and Fusu (2016). As such, in the section on material examined a forward slash (/) indicates separate labels and information given before an em-dash (—) is common to all records following the em-dash until the next given locality or specimen data. The descriptions are far more comprehensive than necessary to distinguish the sexes from those of other Hawaiian species, but we do so to provide a potential model for subsequent revisionary studies of the *Eupelmus* fauna of Hawai‘i that is necessary to resolve its true diversity and evolution.

Taxonomy

Eupelmus (*Eupelmus*) *niger* Ashmead

Eupelmus niger Ashmead, 1901: 315 (key), 316–317 (description). Published type information: one female taken in January, Lahaina, Maui [Hawai‘i].

Material examined. *Type material*. Holotype ♀ (NHMUK), photographs only examined (see methods). Type labels: Type / Lahaina, Maui, coast 1.97 / *Eupelmus niger* Ash ♀ Type / B.M. TYPE HYM. 5.979 / NHMUK010370259.

Holotype point-mounted (Figs. 2A,B); contorted (Fig. 2B); missing right antenna beyond pedicel (Fig. 2H), ovipositor sheaths (Figs. 2A,B), and apical two tarsomeres of right mesotarsus (Fig. 3F insert).

Other material. USA. **Hawai‘i**: O‘ahu, nr. Makapu Pt. [misspelling of Makapu‘u Pt], Aug 54, J.W. Beardsley, reared ex. wood *Tournefortia* (1♀ CNC). O‘ahu Is., Kahu-

ku, James Campbell Nat. Wildlife Refuge, 4m., P. Krushelnycky—21.69470°N 157.95286°W, 22.XI.2021, ex. *Hylaeus anthracinus* nest / coll# PDK1092, spec/lot# PKSP52275 (1♂ CNC); 21.69470°N 157.95286°W, 23.XI.2021, ex. *Hylaeus anthracinus* nest / coll# PDK1093, spec/lot# PKSP52276 (1♀ CNC); 21.70147°N 157.95875°W, 6.XII.2021, ex. *Hylaeus* nest / coll # PDK1094, spec/lot# PKSP52277 (1♀, 1♂ CNC); 21.69794°N 157.95644°W, 7.XII.2021, ex. *Hylaeus anthracinus* nest / coll# PDK1097, spec/lot# PKSP52267 (1♀ CNC); 21.69470°N 157.95286°W, 7.XII.2021, ex. *Hylaeus anthracinus* nest / coll# PDK1097, spec/lot# PKSP52266 (1♂ CNC); 21.69702°N 157.95567°W, 22.IX.2021, ex. *Hylaeus anthracinus* nest / coll# PDK 1088, spec/lot# PKSP51219 (1♀, 2♂ HDOA); 21.70147°N 157.95875°W, 24.IV.2022, ex. *Hylaeus* nest / coll# PDK 1155—spec/lot# PKSP52304 (1♀ BPBM), spec/lot# PKSP52305 (1♀ BPBM), spec/lot# PKSP52306 (1♂ BPBM), spec/lot# PKSP52307 (1♀ BPBM), spec/lot# PKSP52308 (1♂ BPBM); 21.70210°N 157.95966°W, 14.IV.2022, ex. bee nests, probably *Hylaeus* / coll# PDK1157—spec/lot# PKSP52326 (1♀ UHIM), spec/lot# PKSP52327 (1♀ UHIM), spec/lot# PKSP52328 (1♂ UHIM), spec/lot# PKSP52329 (1♂ UHIM), spec/lot# PKSP52330 (1♂ UHIM), spec/lot# PKSP52331 (1♀ UHIM); Kāneʻohe, Marine Corps Base Hawaiʻi, 4 m, P. Krushelnycky—21.45625°N 157.75508°W, 5.XII.2021, ex. *Hylaeus* nest / coll# PDK1096—spec/lot# PSKP52263 (1♂ CNC), spec/lot# PSKP52264 (1♀ CNC), spec/lot# PSKP52265 (1♂ CNC); 21.45625°N 157.75508°W, 6.IV.2022, ex. bee nests, probably *Hylaeus* / coll# PDK1154—spec/lot# PSKP52322 (1♀ BPBM), spec/lot# PSKP52323 (1♀ BPBM), spec/lot# PSKP52324 (1♂ BPBM), spec/lot# PSKP52325 (1♀ BPBM); 21.45392°N 157.74825°W, 13.IV.2022, ex. *Hylaeus* nest / coll# PDK1156—spec/lot# PSKP52332 (1♂ UHIM), spec/lot# PSKP52333 (1♀ UHIM).

Diagnosis. Both sexes of *E. niger* are readily differentiated from those of all other known macropterous Hawaiian *Eupelmus* by a combination of hair-like body setae and extensively, darkly infuscate fore wings (Figs. 3D, E, 5D). Most Hawaiian *Eupelmus* species have hyaline or essentially hyaline fore wings or those females with partly infuscate fore wings have white, lanceolate to spatulate setae on the body (Gibson 1995, e.g. Figs. 89, 182, Gibson and Fusu 2016, Figs. 77a–d). Both sexes are also atypically dark though with variably distinct metallic lusters under some angles of light depending on the type of light used (Figs. 2, 3A–C, 4, 5A–C, E), including the legs at least basal of the tarsi (Figs. 2D, 4B), and the ovipositor sheaths other than the extreme apex (Figs. 3J, K), whereas at least females of other Hawaiian *Eupelmus* usually are a brighter green to blue and have more extensively pale legs and/or ovipositor sheaths.

Description. FEMALE (habitus: Figs. 2A–D). Length of uncontorted individual, including ovipositor sheaths, about 6.0–7.3 mm. Head (Figs. 2G, H, 3A, B) dark, almost black, but with slight green to greenish-blue or violaceous lusters in part under some angles of light (Figs. 2G, 3A, C); setae dark, hair-like. Maxillary and labial palpi dark. Antenna dark except for paler micropilose sensory region of clava (Fig. 3C). Mesosoma (Figs. 2E, F) similarly dark with dark hair-like setae as head except as follows: frontal surface of prepectus pale (Fig. 2F); mesonotum and propodeal callar regions with slight green, blue and/or violaceous lusters under different angles of light, the scutellar-axillar complex in particular more distinctly and extensively violaceous under most angles

of light, and acropleuron with very slight blue to violaceous luster under some angles of light. Fore wing (Figs. 3D, E) with costal cell and/or base of basal cell variably distinctly brownish-infuscate, but at least mostly subhyaline to hyaline compared to more darkly, distinctly brownish-infuscate disc beyond level of base of parastigma, though disc progressively paler posterior of about level of medial fold and apically beyond venation; costal cell dorsally with row of dark setae near leading margin only over about apical one-third, but ventrally almost completely setose; basal cell entirely setose and with line of setae along mediocubital fold continuous to disc so as to differentiate bare cubital and vanal areas posterior of basal cell and oblique, rectangular speculum behind base of parastigma anterior to mediocubital setal line beyond basal cell, the disc otherwise uniformly setose except for oblique linea calva. Legs (Figs. 2C, D) similarly dark as mesosoma, including row of mesotibial apical pegs and mesotarsal pegs (Fig. 3F), except pro- and mesotarsi variably paler, brown to yellowish or white except for darker setae (Fig. 3F), and metatarsus variably extensively pale, with at least extreme base (Figs. 3G, H) and sometimes entire basitarsus (Fig. 3I) white. Gaster (Figs. 2C, D) dark with dark hair-like setae and obscure metallic lusters under some angles of light similar to head and mesosoma, the basal tergite dorsally sometimes with more distinct green luster; ovipositor sheaths entirely dark except for extreme apex (Figs. 3J, K).

Head in dorsal view (Figs. 3A, B) with interocular distance about 0.3× head width; in lateral view (Fig. 2D) lenticular with face evenly convex and parascrobal region smoothly merged with frons; vertex alutaceous-imbricate, frons above level of scrobal depression coriaceous to indistinctly coriaceous-reticulate with setiferous punctures lateral anterior ocellus, parascrobal region and lower face more distinctly reticulate with setiferous punctures except for smooth, bare clypeal apex and more coriaceous paraclypeal region apically, scrobes and scrobal depression transversely reticulate to reticulate-rugulose and bare, and interantennal prominence more finely coriaceous to coriaceous-imbricate with setiferous punctures; OOL: POL: LOL: MPOD about 0.5–0.6: 1.6–1.8: 1.4–1.5: 1.0. Antenna (Fig. 3C) with scape slightly curved, about 5.0–5.5× as long as wide and of similar width throughout; pedicel about 1.5–2.0× as long as wide; fl1 about 1.2–1.4× longer than wide and 0.55–0.66× as long as pedicel; fl2 about 2.3× as long as wide or length of fl1, and subsequent preclaval flagellomeres progressively shorter and wider, with fl3 about 1.9–2.3×, fl4 about 2.2×, fl5 about 1.5–1.6×, fl6 about 1.3–1.4×, fl7 about 1.0–1.2× and fl8 about 0.9–1.0× as long as wide; clava about 2.2–2.3× as long as wide and about 0.7–0.75× combined length of preceding three flagellomeres, with micropilose sensory region ventrally over apical two clavomeres. Mesonotum (Fig. 2E) with anteromedial lobe of mesoscutum transversely reticulate-imbricate to strigose anteriorly but increasingly more coriaceous medially to reticulate posteriorly compared to more distinctly reticulate posteriorly depressed region; lateral lobe minutely coriaceous and bare dorsolongitudinally, and coriaceous to coriaceous-reticulate with setiferous punctures laterally; scutellar-axillar complex low convex, mostly coriaceous with setiferous punctures except scutellum mediolongitudinally and posterior frenal area bare. Acropleuron (Fig. 2F) shallowly reticulate anteriorly and posteriorly of much more minutely sculptured mesal region, the reticulations posterior of mesal region larger than anteriorly. Fore wing (Figs. 3D, E) with cc: mv: pmv: stv = 4.0–4.7: 3.7–4.0: 1.2:

1.0, with stigma curved apically at abrupt angle relative to stigmal vein. Middle leg with row of 6–8 mesotibial apical pegs; mesotarsus (Fig. 3F) with symmetrical peg pattern on basitarsus and pegs clearly differentiated into two rows apically; second tarsomere with 5 or 6, third tarsomere with 2 or 3, and fourth tarsomere with 1 or 2 pegs on either side. Propodeum with medial depression broadly V-shaped and extended almost to posterior margin (Fig. 2E); callus with sparse setae not obstructing view of cuticle (Fig. 2F). Gaster (Figs. 2C, D) not atypically modified, with posterodorsal margins of Gt1–Gt4 deeply emarginate (Fig. 2C), posterior margin of Gt5 rounded and extending over medially divided Gt7 to base of syntergum (Fig. 3J); syntergum dorsally (Fig. 3J) strongly transverse to sublinear anterior of sclerotized anal plate comprising most of dorsal surface and extending to base of constriction separating exposed ovipositor sheaths from concealed second valvifers. Ovipositor sheaths in dorsal view (Fig. 3J) with lateral margins out-curved so as to be widest medially and narrowed basally and apically, in lateral view (Fig. 2K) length measured from apex of gaster about 1.0–1.1× as long as metatarsis (cf. Figs. 3I, K) and about 1.1–1.2× as long as mv.

MALE (habitus: Figs. 4A, B). Length 3.6–5.3 mm. Head (Figs. 4C, D), including maxillary and labial palpi (Fig. 4E), and body color and setation similar to female, almost black with slight green to violaceous lusters under some angles of light, except tarsi mostly pale, white to yellowish, other than darker brown apical tarsomeres (Fig. 5F) or sometimes metatarsus with only basitarsus pale and subsequent tarsomeres darker brown (Fig. 5G). Fore wing (Fig. 5D) similar in color to female, the extreme base brownish-infuscate but basally mostly hyaline to subhyaline to level about equal with apex of costal cell and with bare region of disc paler infuscate relative to surrounding setose region, the disc also paler posterior to level of medial fold and apically beyond venation; setal pattern similar to female except speculum continuous with linea calva, the bare regions not separated by setae.

Head in dorsal view (Fig. 4D) with interocular distance slightly less than 0.5× head width; vertex smoothly rounded into occiput; vertex transversely reticulate to reticulate-imbricate (Fig. 4D), frons above level of scrobal depression (Figs. 4C, D) coriaceous-reticulate, the surface of most cells slightly depressed, to variably more distinctly reticulate and with setiferous punctures lateral of anterior ocellus, parascrobal region and lower face more distinctly reticulate with setiferous punctures except for smooth, bare clypeal apex and minutely coriaceous paraclypeal region, scrobes and scrobal depression transversely reticulate-strigose and bare, and interantennal prominence finely coriaceous to almost smooth except for setiferous punctures and shiny mediolongitudinally (Figs. 4C, E, F); lower face and gena near malar sulcus with longer, but straight to only slightly curved dark setae (Fig. 4E); OOL: POL: LOL: MPOD = 0.6–0.7: 2.3–2.4: 1.4–1.6: 1.0. Antenna (Fig. 4F) with scape subrectangular, about 2.6–2.8× as long as wide; pedicel about 1.5× as long as apical width, ventrally with line of apically curved setae; fl1 strongly transverse but extensively setose with more than one row of setae, and subsequent preclaval flagellomeres with single row of mps apically and dense, short setae, with fl2 slightly longer than apical width, but fl3–fl8 all about as long as wide to slightly wider than long apically; clava about twice as long as wide and about as long as combined length of preceding two flagellomeres. Mesonotum (Fig. 5A) reticulate, the re-

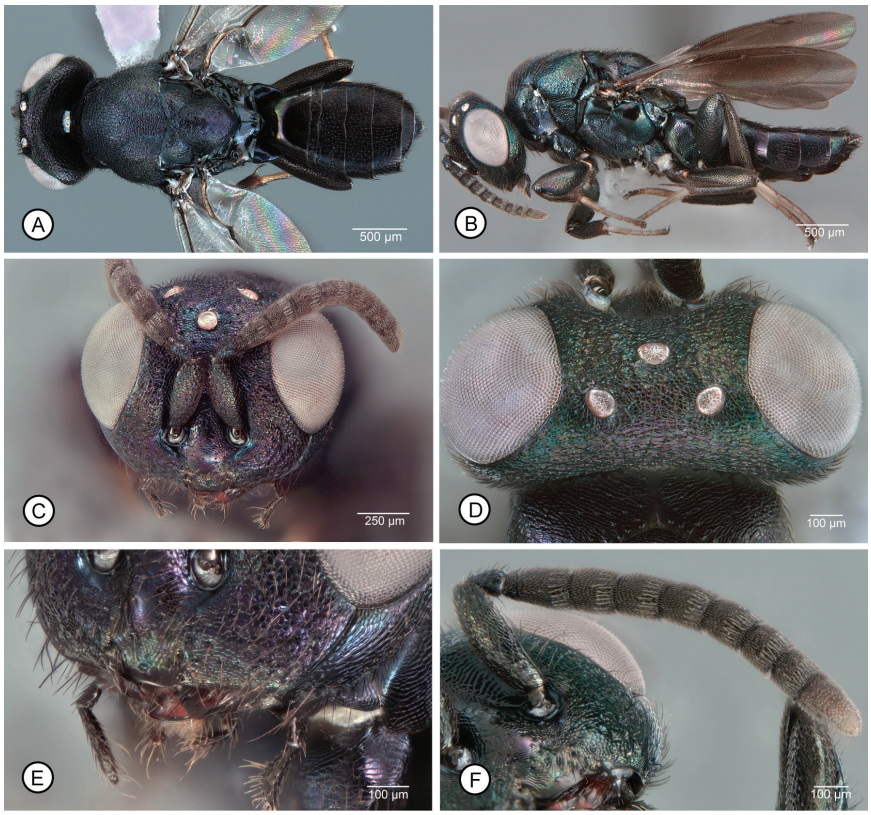

Figure 4. *Eupelmus niger* ♂ reared from *Hylaeus anthracinus*. **A**, dorsal habitus; **B**, lateral habitus; **C**, frontal head; **D**, dorsal head; **E**, lower face; **F**, antenna.

ticulations somewhat larger posteriorly on middle lobe than lateral lobe lateral of notauli; scutellar-axillar sculpture pattern and setation similar to female, the scutellum more finely sculptured and bare mediolongitudinally and with bare frenal area; prepectus and mesofemoral depression similarly reticulate (Fig. 5B); acropleuron reticulate anteriorly to coriaceous posteriorly; upper and lower mesepimeron not divided by line or pit, with upper mesepimeron almost smooth, only obscurely coriaceous relative to more coarsely coriaceous-reticulate lower mesepimeron. Metapleuron coriaceous to coriaceous-reticulate. Propodeum (Fig. 5C) with complete median carina and a few short longitudinal carinae extending anteriorly from propodeal foramen (Figs. 5C, E), and with posterolateral angle projecting into short denticle (Figs. 5C, E: arrow), but panels otherwise finely coriaceous; callar region with line of dark setae anterior to spiracle and sparsely setose lateral of spiracle. Petiole smooth, shiny, transverse. Gaster dorsally (Fig. 5E) entirely coriaceous and either entirely, uniformly setose beyond Gt2 or tergites variably broadly bare basally depending on inflation of gaster telescoping segments, but with Gt1 dorsally and Gt2 dorsomedially bare.

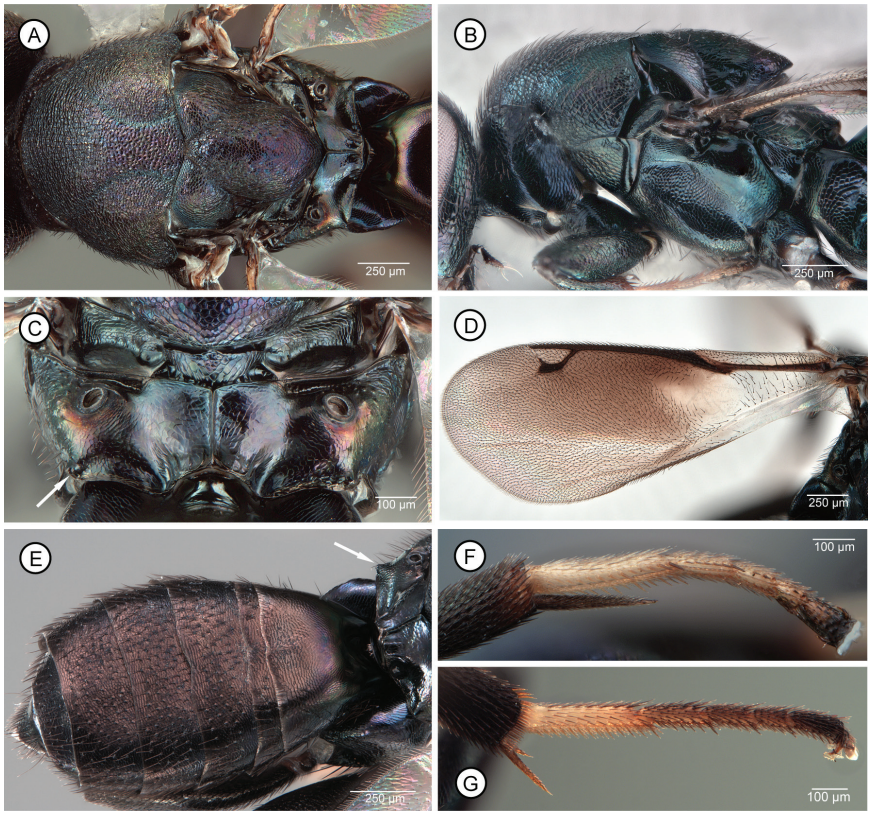

Figure 5. *Eupelmus niger* ♂ reared from *Hylaeus anthracinus*. **A**, dorsal mesosoma; **B**, lateral mesosoma; **C**, propodeum; **D**, fore wing; **E**, gaster and propodeum, dorsolateral; **F**, mesotarsus; **G**, metatarsus.

Variation. The metallic lusters evident in the plates of illustrations of both sexes, taken using the fibre optic light source, are more intense and extensive than when viewed using the halogen light source on which the descriptions are based. Further, the Makapu'u female is more dark brown than black and the fore wings somewhat paler brown, more similar to those of the holotype (Fig. 3D) than the dark brown infuscation of our reared females (Fig. 3E). Both differences may result from the holotype and Makapu'u specimen being older and, as a result, at least the Makapu'u female possibly being somewhat faded. The metatarsi of both the holotype (Fig. 3G) and the Makapu'u female are almost completely brown except for the extreme base, but extent of the pale metatarsal region varies in our reared specimens (cf. Figs. 3H, I). The Makapu'u female differs from both the holotype and our reared females in having one or two setae within the fore wing speculum so that the speculum is less conspicuous. The Makapu'u female also has Gt7 more extensively exposed and an apical portion of the second valvifers visible beyond the syntergum basal to the ovipositor sheath constriction so that the sheaths superficially appear somewhat longer, but both differences likely are an artefact resulting

from shrivelling of the gaster during air-drying. The ovipositor sheaths of the holotype are missing (Figs. 2A, B), but the original description states they were the length of the hind tarsi and black. The original description also states the wings of the holotype to be "subhyaline, clear hyaline at extreme base" (Ashmead 1910, p. 326), though the fore wing disc of the holotype is extensively brownish-infuscate (Fig. 2D).

Distribution. USA. Hawai'i: Maui, O'ahu.

Hosts. *Hylaeus* (*Nesoprosopis*) *anthracinus* (F. Smith), *Hylaeus* (*Indialaeus*) *strenuus* (Cameron).

Remarks. In the unpublished manuscript of C. Yoshimoto, six specimens (6♀ in one version, 3♀ and 3♂ in another version) are listed with similar data as the examined Makapu'u Pt. female. The manuscript does not include the specimens being reared from *Tournefortia* wood, but provides the additional information they were collected August 1954, and "apparently parasite of *Nesoprosopis* sp.". Also listed from the same site was a "pupa found in bee nest with remains of bee pupae in *Tournefortia* twig." However, we were unable to locate any of these other specimens. Another six females with different collection and host data were also listed under *E. niger* in the manuscript, including two females collected by Bridwell stated as deposited in the United States National Museum of Natural History, Washington, DC (USNM). These two specimens were located in the USNM, but photographs provided to us of the specimens revealed that one of the two is a male and neither is *E. niger*, the specimens having hyaline wings and a brighter green body color. Along with the Makapu'u Pt. female under the name *E. niger* in the CNC is a male with the same data as one specimen cited in the manuscript as a female. It is possible that the manuscript sex citation is incorrect, but the CNC male is not *E. niger*. Because of the discrepancies between the manuscript and observed specimens we do not cite the collection data of the other manuscript-listed specimens.

Biology

Eupelmus wasps are typically ectoparasitic on their hosts, producing a single adult offspring from each host larva. A total of 71 *E. niger* adults emerged from *Hylaeus* nests obtained from JCNWR near Kahuku and from MCBH near Kāne'ohe. Of these, 46% were female and 54% were male. Between one and five wasps (median = 2) emerged from parasitized nests, attacking 50 to 100% of their brood cells. *Eupelmus niger* definitively uses both *H. anthracinus* and *H. strenuus* as hosts, as adults of both species emerged from some of the parasitized nests. We suspect that *E. niger* also parasitizes the non-native *Hylaeus leptocephalus* (Morawitz), which colonized nest blocks at MCBH, but confirmation of this host was not possible because no bees emerged from the nests in question. A more detailed analysis of parasitism dynamics will be presented elsewhere, but on average 30% of the nests sampled at these two sites were parasitized by *E. niger* over the period assessed here. No *E. niger* were reared from the 12 *Hylaeus* nests obtained from KSS near Makapu'u, despite the prior collection of *E. niger* specimens from this area.

Females of *E. niger* were frequently observed resting on the dowels of the artificial nest blocks, and host searching behavior was also commonly witnessed. Females antennated the surface rapidly while traversing the dowel slowly in both directions (Fig. 6A). On several occasions, apparent oviposition was observed, which evidently occurs through the side of the dowel. After vigorous antennal tapping at a particular spot on the dowel, the female stops, having located an immature bee,

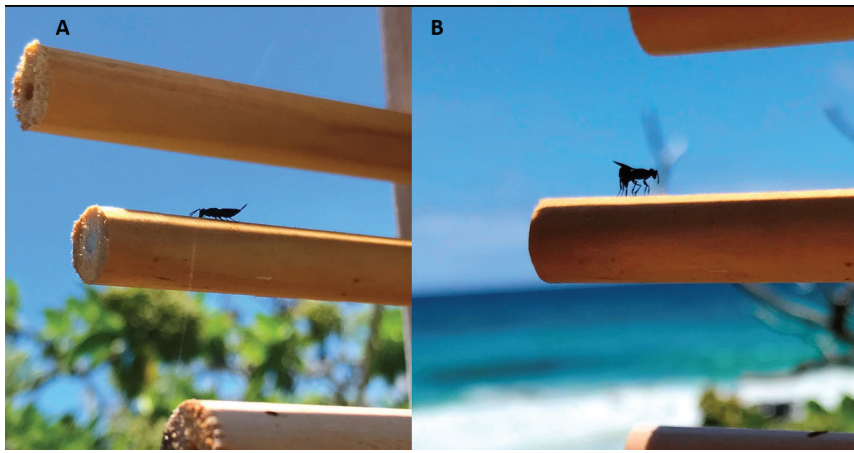

Figure 6. **A**, female *E. niger* antennating dowel while searching for *Hylaeus* hosts (note cellophane seal at end of dowel indicating the presence of a *Hylaeus* nest). **B**, female *E. niger* inserting ovipositor into same dowel.

flexes her ovipositor downward and inserts it into the wood (Fig. 6B). Adult *E. niger* wasps emerged 25 to 26 days later from the nest pictured in Figure 6. Despite their frequent presence on the nest blocks, we never observed *E. niger* females entering or exiting dowel cavities, suggesting that the observed method of oviposition is the predominant if not sole one. An ovipositor dissected from one female measured approximately 3 mm in length, indicating the maximum depth of cavities accessible to this species. The smaller 9.525 mm diameter dowels pictured in Figures 1 and 6 appear to be routinely accessible, likely because the 3.175 mm diameter drilled cavities were often not perfectly centered in the dowel. Larger diameter dowels should reduce or even eliminate *E. niger* parasitism, a hypothesis currently being tested.

Hylaeus females are frequently seen resting within the dowel cavities (Fig. 7), and nest blocks with plastic tube inserts reveal that resting often occurs above nests still under construction. We assume that this represents, in part, nest guarding behavior, preventing access to competing and/or kleptoparasitic bees, and possibly defending against eulophid and encyrtid parasitoids. Although this behavior would seem to be largely ineffective against *Eupelmus* parasitism, it may increase the detection of *Eupelmus* wasps actively searching the nesting substrate surface. On several occasions, we observed *H. strenuus* bees emerge from their resting positions within the dowel to chase away *E. niger* females.

Conclusion

Given that *E. niger* discovered and parasitized *Hylaeus* nests in our artificial blocks within several months of their initial deployment at two distant sites on O‘ahu, interactions between *E. niger* and *Hylaeus* bees are likely occurring widely within natural nesting habitats. Parasitism can have dramatic impacts on nesting activity of *H. anthracinus* in artificial nest blocks, and could contribute to spatial fluctuations in bee numbers observed within populations (Krushelnycky et al. 2022). These dynamics illustrate the necessity of testing a variety of nesting habitat designs to evade not only predatory ants and competing cavity nesting bees

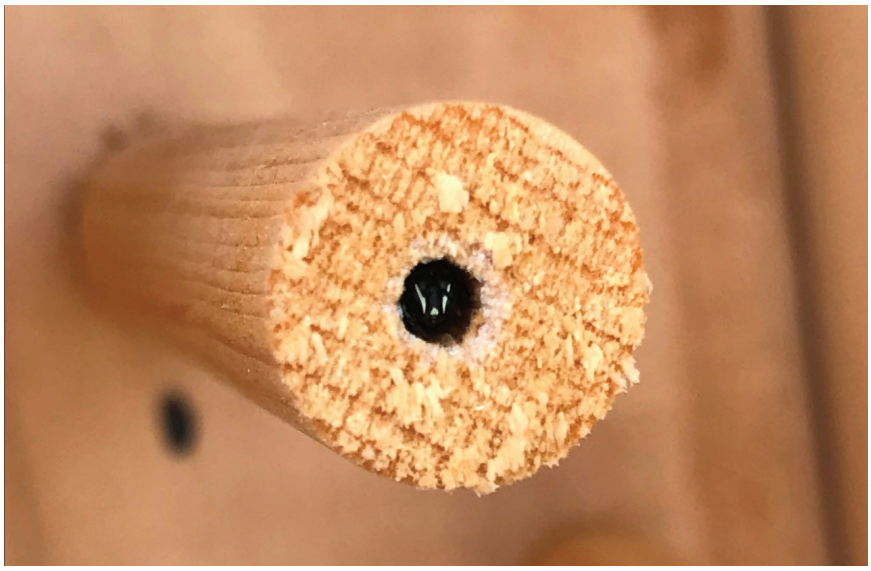

Figure 7. *Hylaeus strenuus* resting in dowel cavity, possibly guarding nest under construction.

and wasps (Graham 2018, Plentovich et al. 2021), but also different species of parasitoids. Further, they provide insight into another factor presumably contributing to the present rarity of *H. anthracinus* and potentially other endangered twig-nesting Hawaiian yellow-faced bees.

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