A journal of world insect systematics
INSECTA MUNDI

0902

Nesting behavior, ecology, and functional morphology of the trapdoor spider-hunting spider wasp *Aporus* (*Plectraporus*) *hirsutus* (Banks) (Hymenoptera: Pompilidae)

Frank E. Kurczewski
1188 Converse Drive NE
Atlanta, GA 30324
kurczewskifrank@gmail.com

Alice J. Abela
2390 Lake Marie Drive
Santa Maria, CA 93455
aliceinwl@hotmail.com

Rick C. West
6365 Willowpark Way
Sooke, BC, Canada V9Z 1L9

Date of issue: December 31, 2021

Center for Systematic Entomology, Inc., Gainesville, FL

Kurczewski FE, Abela AJ, West RC. 2021. Nesting behavior, ecology, and functional morphology of the trapdoor spider-hunting spider wasp *Aporus* (*Plectraporus*) *hirsutus* (Banks) (Hymenoptera: Pompilidae). Insecta Mundi 0902: 1–23.

Published on December 31, 2021 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
http://centerforsystematicentomology.org/

Insecta Mundi is a journal primarily devoted to insect systematics, but articles can be published on any non-marine arthropod. Topics considered for publication include systematics, taxonomy, nomenclature, checklists, faunal works, and natural history. Insecta Mundi will not consider works in the applied sciences (i.e. medical entomology, pest control research, etc.), and no longer publishes book reviews or editorials. Insecta Mundi publishes original research or discoveries in an inexpensive and timely manner, distributing them free via open access on the internet on the date of publication.

Insecta Mundi is referenced or abstracted by several sources, including the Zoological Record and CAB Abstracts. Insecta Mundi is published irregularly throughout the year, with completed manuscripts assigned an individual number. Manuscripts must be peer reviewed prior to submission, after which they are reviewed by the editorial board to ensure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

Guidelines and requirements for the preparation of manuscripts are available on the Insecta Mundi website at http://centerforsystematicentomology.org/insectamundi/

Printed copies (ISSN 0749-6737) annually deposited in libraries

Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA
The Natural History Museum, London, UK
National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia

Electronic copies (Online ISSN 1942-1354) in PDF format

Archived digitally by Portico
Florida Virtual Campus: http://purl.fcla.edu/fcla/insectamundi
University of Nebraska-Lincoln, Digital Commons: http://digitalcommons.unl.edu/insectamundi/
Goethe-Universität, Frankfurt am Main: http://nbn-resolving.de/urn/resolver.pl?urn:nbn:de:hebis:30:3-135240

0902: 1–23 **INSECTA MUNDI** 2021

Nesting behavior, ecology, and functional morphology of the trapdoor spider-hunting spider wasp *Aporus* (*Plectraporus*) *hirsutus* (Banks) (Hymenoptera: Pompilidae)

Frank E. Kurczewski
1188 Converse Drive NE
Atlanta, GA 30324
kurczewskifrank@gmail.com

Alice J. Abela
2390 Lake Marie Drive
Santa Maria, CA 93455
aliceinwl@hotmail.com

Rick C. West
6365 Willowpark Way
Sooke, BC, Canada V9Z 1L9
rickcwest@shaw.ca

Abstract. Macrophotographs in series taken by Alice Abela on sandy coastal dunes in Santa Barbara and San Luis Obispo Counties, CA in 2010–2021 supplement and enhance F. X. Williams (1928) study of the ecology and nesting behavior of the trapdoor spider-hunting spider wasp *Aporus* (*Plectraporus*) *hirsutus* (Banks) (Hymenoptera: Pompilidae: Aporini). Abela's macrophotographs and observations provide new details of adult wasp feeding, functional morphology, hunting, digging and prey transport, and host spider trapdoor, entrance, burrow structure, host capture and escape activity. Newly reported host records from this study and online photographs expand *A. hirsutus* host selection in the large wafer-lid trapdoor spider genus *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae). The *A. hirsutus* California geographic distribution map by Wasbauer and Kimsey (1985) is updated, thereby providing a broader definition of intraspecific variation in this species.

Key words. Adult feeding, functional morphology, hunting, digging, prey transport, *Aptostichus*, trapdoor, spider burrow, host capture, escape activity, geographic distribution, intraspecific variation.

ZooBank registration. urn:lsid:zoobank.org:pub:5A7CE9DD-2B2F-41B7-ADB7-932D58970505

Introduction

Aporus (*Plectraporus*) *hirsutus* (Banks) (Hymenoptera: Pompilidae: Aporini) is black, its body, antennae, legs and forewings rendered brilliant bluish, greenish or violaceous by its pubescence (Evans 1966; Wasbauer and Kimsey 1985) (Fig. 1). Females of *A. hirsutus* are 6.5–13.0 mm in body length, their size depending on the size of the host spider on which they fed as a larva (Evans 1966; F. E. Kurczewski pers. obs.). Females have the appropriate structural characteristics for preying on the wafer-lid trapdoor spider genus *Aptostichus* Simon (Araneae: Mygalomorphae: Euctenizidae) in loose sand of active and relict coastal sand dunes and deserts in the western U. S. (Williams 1928; Wasbauer and Kimsey 1985). *Aporus hirsutus* ranges from Oregon and California eastward to Idaho, Nevada and western Arizona, and southward into Sonora and Baja California, Mexico (Evans 1966; Wasbauer and Kimsey 1985) (Fig. 9; Table 1).

Aporus hirsutus is host specific on species of wafer-lid trapdoor spiders of the genus *Aptostichus*. This large genus (>40 species) is confined mainly to California and is characterized by cryptic psammophilic carapace and abdomen coloration (Bond 2012, Fig. 2). *Aptostichus* species have few readily identifiable external morphological characteristics (Bond 2012). *Aporus hirsutus* reportedly captures *A. atomarius* Simon (San Bernardino Hills

Table 1. Specimens of *Aporus* (*Plectraporus*) *hirsutus* (Banks) observed and examined in this study. Specimens without corresponding URLs or published photographs were either personally observed by the first author, or were data points obtained by the authors from the California Insect Survey.

Specimen #	Foretarsal rake	URL	Observer	Date	Latitude	Longitude
1	not reported	N/A	not reported	not reported	39.775789	−119.975119
2	not reported	N/A	not reported	not reported	39.758362	−120.255091
3	not reported	N/A	not reported	not reported	38.947564	−123.261001
4	not reported	N/A	not reported	not reported	38.299254	−122.911173
5	not reported	N/A	not reported	not reported	38.087827	−122.934049
6	not reported	N/A	not reported	not reported	37.895398	−121.896202
7	not reported	N/A	not reported	not reported	37.977479	−122.500955
8	not reported	N/A	not reported	not reported	37.738468	−122.440342
9	not reported	N/A	not reported	not reported	37.561105	−122.360439
10	not reported	N/A	not reported	not reported	37.358613	−121.731748
11	not reported	N/A	not reported	not reported	37.263488	−121.517267
12	not reported	N/A	not reported	not reported	36.989506	−121.977779
13	not reported	N/A	not reported	not reported	36.757115	−121.791402
14	not reported	N/A	not reported	not reported	36.606718	−121.845824
15	not reported	N/A	not reported	not reported	36.446631	−121.890659
16	not reported	N/A	not reported	not reported	36.480089	−121.212408
17	not reported	N/A	not reported	not reported	38.664868	−119.696519
18	not reported	N/A	not reported	not reported	38.449191	−119.700525
19	not reported	N/A	not reported	not reported	38.133398	−119.975666
20	not reported	N/A	not reported	not reported	38.221991	−119.290132
21	not reported	N/A	not reported	not reported	38.013375	−119.242396
22	not reported	N/A	not reported	not reported	37.328450	−119.492519
23	not reported	N/A	not reported	not reported	40.475021	−121.223867
24	not reported	N/A	not reported	not reported	40.407929	−120.361201
25	not reported	N/A	not reported	not reported	37.653985	−118.276155
26	not reported	N/A	not reported	not reported	37.341747	−118.166207
27	not reported	N/A	not reported	not reported	37.095808	−118.082205
28	not reported	N/A	not reported	not reported	36.630666	−117.903008
29	not reported	N/A	not reported	not reported	36.554698	−117.682984
30	not reported	N/A	not reported	not reported	36.496044	−117.474873
31	not reported	N/A	not reported	not reported	36.054359	−117.822814
32	not reported	N/A	not reported	not reported	36.049654	−117.583102
33	not reported	N/A	not reported	not reported	35.924666	−117.460113
34	not reported	N/A	not reported	not reported	35.827620	−117.649862
35	not reported	N/A	not reported	not reported	35.891443	−118.057189
36	not reported	N/A	not reported	not reported	35.673931	−118.976646
37	not reported	N/A	not reported	not reported	35.685617	−118.778404
38	not reported	N/A	not reported	not reported	35.433083	−118.979830
39	not reported	N/A	not reported	not reported	35.662668	−118.206120
40	not reported	N/A	not reported	not reported	35.458640	−118.203710
41	not reported	N/A	not reported	not reported	35.635322	−117.961062
42	not reported	N/A	not reported	not reported	35.680823	−117.792778
43	not reported	N/A	not reported	not reported	35.476706	−117.891445
44	not reported	N/A	not reported	not reported	35.450309	−117.537564
45	not reported	N/A	not reported	not reported	35.191587	−117.436651
46	not reported	N/A	not reported	not reported	35.062616	−118.106304

Specimen #	Foretarsal rake	URL	Observer	Date	Latitude	Longitude
47	not reported	N/A	not reported	not reported	35.010616	−117.908802
48	not reported	N/A	not reported	not reported	34.932550	−117.688680
49	not reported	N/A	not reported	not reported	34.845556	−117.917948
50	not reported	N/A	not reported	not reported	34.675724	−117.880057
51	not reported	N/A	not reported	not reported	34.346640	−117.856089
52	not reported	N/A	not reported	not reported	34.609592	−118.100785
53	not reported	N/A	not reported	not reported	34.593190	−118.430676
54	not reported	N/A	not reported	not reported	34.752990	−118.783555
55	not reported	N/A	not reported	not reported	34.852088	−118.980343
56	not reported	N/A	not reported	not reported	34.873056	−119.171366
57	not reported	N/A	not reported	not reported	34.653419	−118.935831
58	not reported	N/A	not reported	not reported	35.424693	−120.856523
59	not reported	N/A	not reported	not reported	35.525220	−120.629007
60	not reported	N/A	not reported	not reported	35.385951	−120.506637
61	not reported	N/A	not reported	not reported	35.200503	−120.678552
62	not reported	N/A	not reported	not reported	35.131592	−120.469437
63	not reported	N/A	not reported	not reported	35.031792	−120.617920
64	not reported	N/A	not reported	not reported	34.731350	−119.554758
65	not reported	N/A	not reported	not reported	34.654185	−119.748306
66	not reported	N/A	not reported	not reported	34.594172	−119.920280
67	not reported	N/A	not reported	not reported	34.419208	−119.929849
68	not reported	N/A	not reported	not reported	34.422805	−119.732611
69	not reported	N/A	not reported	not reported	34.494203	−119.558455
70	not reported	N/A	not reported	not reported	34.554592	−119.217071
71	not reported	N/A	not reported	not reported	34.031336	−120.453544
72	not reported	N/A	not reported	not reported	33.975797	−120.086670
73	not reported	N/A	not reported	not reported	34.018231	−119.701278
74	not reported	N/A	not reported	not reported	34.452628	−118.534504
75	not reported	N/A	not reported	not reported	34.207748	−118.400890
76	not reported	N/A	not reported	not reported	34.136509	−118.189407
77	not reported	N/A	not reported	not reported	33.991159	−118.353894
78	not reported	N/A	not reported	not reported	33.808051	−118.339061
79	not reported	N/A	not reported	not reported	33.600031	−117.783288
80	not reported	N/A	not reported	not reported	34.526428	−117.799433
81	not reported	N/A	not reported	not reported	34.197691	−117.698550
82	not reported	N/A	not reported	not reported	33.883845	−117.766003
83	not reported	N/A	not reported	not reported	34.325517	−117.577515
84	not reported	N/A	not reported	not reported	34.595021	−117.538577
85	not reported	N/A	not reported	not reported	34.480977	−117.394068
86	not reported	N/A	not reported	not reported	34.441625	−117.209761
87	not reported	N/A	not reported	not reported	34.380415	−117.019413
88	not reported	N/A	not reported	not reported	34.327112	−116.845455
89	not reported	N/A	not reported	not reported	34.849745	−116.968419
90	not reported	N/A	not reported	not reported	34.873490	−116.769014
91	not reported	N/A	not reported	not reported	35.016215	−116.339311
92	not reported	N/A	not reported	not reported	35.152429	−116.221414
93	not reported	N/A	not reported	not reported	34.915130	−115.719720
94	not reported	N/A	not reported	not reported	34.135303	−117.419544
95	not reported	N/A	not reported	not reported	34.148572	−117.007117

Specimen #	Foretarsal rake	URL	Observer	Date	Latitude	Longitude
96	not reported	N/A	not reported	not reported	34.111695	−115.625255
97	not reported	N/A	not reported	not reported	34.868340	−114.949164
98	not reported	N/A	not reported	not reported	34.206114	−114.602411
99	not reported	N/A	not reported	not reported	34.086641	−114.971195
100	not reported	N/A	not reported	not reported	34.086641	−114.971195
101	not reported	N/A	not reported	not reported	34.086641	−114.971195
102	not reported	N/A	not reported	not reported	34.181928	−115.890819
103	not reported	N/A	not reported	not reported	34.109940	−116.802668
104	not reported	N/A	not reported	not reported	34.127648	−116.235473
105	not reported	N/A	not reported	not reported	34.027937	−116.527802
106	not reported	N/A	not reported	not reported	33.574358	−114.675649
107	not reported	N/A	not reported	not reported	33.497739	−115.003840
108	not reported	N/A	not reported	not reported	33.670762	−115.456346
109	not reported	N/A	not reported	not reported	33.826140	−115.746024
110	not reported	N/A	not reported	not reported	33.766127	−115.914736
111	not reported	N/A	not reported	not reported	33.733638	−116.098126
112	not reported	N/A	not reported	not reported	33.732037	−116.282230
113	not reported	N/A	not reported	not reported	33.843973	−116.433251
114	not reported	N/A	not reported	not reported	33.889277	−116.776591
115	not reported	N/A	not reported	not reported	33.917833	−117.039198
116	not reported	N/A	not reported	not reported	33.869443	−117.283605
117	not reported	N/A	not reported	not reported	33.798936	−116.887488
118	not reported	N/A	not reported	not reported	33.704361	−116.709613
119	not reported	N/A	not reported	not reported	33.670796	−116.499226
120	not reported	N/A	not reported	not reported	33.662279	−117.092946
121	not reported	N/A	not reported	not reported	33.551942	−116.897169
122	not reported	N/A	not reported	not reported	33.494469	−116.465194
123	not reported	N/A	not reported	not reported	33.581358	−116.319511
124	not reported	N/A	not reported	not reported	33.536541	−116.086896
125	not reported	N/A	not reported	not reported	33.327760	−116.308055
126	not reported	N/A	not reported	not reported	33.293642	−116.585285
127	not reported	N/A	not reported	not reported	33.213886	−116.223070
128	not reported	N/A	not reported	not reported	33.098414	−116.325585
129	not reported	N/A	not reported	not reported	33.025015	−116.467476
130	not reported	N/A	not reported	not reported	33.181416	−117.334773
131	not reported	N/A	not reported	not reported	33.144744	−117.111788
132	not reported	N/A	not reported	not reported	33.024090	−117.273085
133	not reported	N/A	not reported	not reported	32.874942	−117.229782
134	not reported	N/A	not reported	not reported	32.737719	−117.197719
135	not reported	N/A	not reported	not reported	32.616400	−117.103203
136	not reported	N/A	not reported	not reported	32.817304	−117.033794
137	not reported	N/A	not reported	not reported	32.860874	−116.709690
138	not reported	N/A	not reported	not reported	32.862362	−116.564493
139	not reported	N/A	not reported	not reported	32.844215	−116.360269
140	not reported	N/A	not reported	not reported	32.743484	−116.203788
141	not reported	N/A	not reported	not reported	32.891015	−115.855638
142	not reported	N/A	not reported	not reported	32.732782	−115.744161
143	present, weak	https://www.inaturalist.org/observations/63142311	Trevor and Chloe Van Loon	10/18/2020	36.692557	−121.810144

Specimen #	Foretarsal rake	URL	Observer	Date	Latitude	Longitude
144	present	https://www.flickr.com/photos/treebeard/21694698334/	Marc Kummel	10/19/2015	34.504278	−119.865556
145	present	https://www.flickr.com/photos/finaticphotography/24722106069/	BJ Stacy	2/15/2016	32.545278	−117.124444
146	absent, or very weak	https://www.inaturalist.org/observations/34192071	Jame Maughn	10/10/2019	36.887370	−121.833394
147	present, weak	https://www.inaturalist.org/observations/4686198	Jay Keller (AzureJay)	11/12/2016	32.555606	−117.129136
148	undetermined	N/A	Frank Kurczewski	not reported	35.333586	−120.826845
149	undetermined	N/A	Frank Kurczewski	not reported	35.321700	−120.842000
150	undetermined	N/A	Frank Kurczewski	not reported	35.263864	−120.863235
151	undetermined	N/A	Frank Kurczewski	not reported	35.307200	−120.838400
152	present	https://bugguide.net/node/view/907159/bgimage	Erik Jacob	4/7/2014	34.421389	−119.794722
153	present, weak	https://bugguide.net/node/view/815959/bgimage	Ron Hemberger	8/1/2013	33.783056	−117.762778
154	present	https://www.inaturalist.org/observations/55114773	Martin Ruane	8/1/2020	34.112502	−119.147198
155	undetermined	https://www.inaturalist.org/observations/14429648	Allison Sheehey (natureali)	7/19/2008	35.703293	−118.306146
156	present	https://bugguide.net/node/view/31105/bgpage	Hartmut Wisch	9/1/2005	34.295224	−118.014114
157	present	https://bugguide.net/node/view/1417410/bgpage	Celise Sharpe	8/4/2017	41.727222	−122.526389
158	absent, or very weak	https://inaturalist.org/observations/4844743	BJ Stacy	11/12/2016	32.555452	−117.128988
159	present	https://inaturalist.org/observations/62365770	Susan Schalbe (naturephotosuze)	10/11/2020	34.082275	−118.560629
160	present	https://inaturalist.org/observations/32996368	Susan Schalbe (naturephotosuze)	9/19/2019	34.038221	−118.814633
161	undetermined	https://inaturalist.org/observations/1805865	Ken−ichi Ueda (kueda)	7/25/2015	35.033498	−120.631298
162	present, very strong	https://www.inaturalist.org/observations/54236872	Alice Abela	7/24/2020	35.004696	−120.607003
163	undetermined	https://www.inaturalist.org/observations/54236876	Alice Abela	7/24/2020	35.004658	−120.606633
164	present, strong	https://www.inaturalist.org/observations/54236889	Alice Abela	7/24/2020	35.013190	−120.606436
165	present, strong	https://www.inaturalist.org/observations/37292660	Alice Abela	6/12/2014	34.785556	−120.614444
166	undetermined	https://www.inaturalist.org/observations/63452613	Alice Abela	9/2/2010	34.789834	−120.612521
167	undetermined	https://www.flickr.com/photos/treebeard/50439670972/	Marc Kummel	10/8/2020	34.514198	−119.814450
168	present	https://bugguide.net/node/view/1608711/bgimage	Dirk Mezger	9/14/2014	35.281464	−120.885508
169	present, very strong	https://www.inaturalist.org/observations/2676440	Alice Abela	6/21/2015	35.031944	−120.626944
170	present, very strong	https://www.inaturalist.org/observations/36745311	Dan Fitzgerald	12/13/2019	34.964100	−120.650000
171	present	https://www.inaturalist.org/observations/62129623	Susan Schalbe (naturephotosuze)	10/8/2020	34.182087	−118.708012

Speci-men #	Foretarsal rake	URL	Observer	Date	Latitude	Longitude
172	present, very strong	https://www.inaturalist.org/observations/56888065	Daniel Johnson	8/18/2020	35.045556	−120.627870
173	present	https://www.inaturalist.org/observations/24139106	Susan Schalbe (naturephotosuze)	4/25/2019	34.116237	−118.761927
174	present, very strong	https://www.inaturalist.org/observations/2679594	Alice Abela	2/13/2016	34.785556	−120.616389
175	present, strong	https://www.inaturalist.org/observations/62535295	Trevor and Chloe Van Loon	10/10/2020	36.703556	−121.806793
176	undetermined	https://www.inaturalist.org/observations/58130071	Daniel Johnson	8/30/2020	35.026470	−120.634317
177	undetermined	https://www.inaturalist.org/observations/13566678	Joshua Willems (jswillems)	6/18/2018	35.060568	−120.621881
178	undetermined	https://www.inaturalist.org/observations/28478181	Lorri Gong	7/4/2019	35.307408	−120.867340
179	present, strong	https://www.inaturalist.org/observations/2679567	Alice Abela	3/28/2015	34.680556	−120.606944
180	undetermined	https://www.inaturalist.org/observations/53124675	Steph Grush (wildnettle)	7/13/2020	34.448498	−118.687878
181	undetermined	https://www.inaturalist.org/observations/61627460	Patricia Simpson	10/3/2020	32.857873	−116.520588
182	undetermined	https://www.inaturalist.org/observations/59504224	Bonnie Nickel	9/13/2020	32.670655	−117.243745
183	undetermined	https://www.inaturalist.org/observations/55091124	Josie Lesage	8/1/2020	34.429980	−119.914153
184	undetermined	https://www.inaturalist.org/observations/2927067	Jay Keller (AzureJay)	2/15/2016	32.545328	−117.113983
185	undetermined	https://www.instagram.com/p/CD−AzDcA5QT/	Heather Broccard−Bell	8/16/2020	33.112739	−117.176694
186	undetermined	https://www.inaturalist.org/observations/68400578	James Bailey	6/15/2019	35.717832	−121.312898
187	undetermined	https://www.inaturalist.org/observations/69803456	Adam Searcy	2/15/2021	33.480548	−119.030048
188	undetermined	https://www.inaturalist.org/observations/79881234	manidae	5/22/2021	33.741937	−118.112309
189	undetermined	https://www.inaturalist.org/observations/84664989	Cindy Roessler	6/??/2021	35.350504	−120.895224
190	undetermined	https://www.inaturalist.org/observations/91708604	Alice Abela	8/16/2021	34.780556	−120.621111
191	present, weak	https://www.inaturalist.org/observations/91603938	Alice Abela	8/13/2021	34.785278	−120.618611
192	present, very strong	https://www.inaturalist.org/observations/91374219	Alice Abela	8/13/2021	34.785278	−120.620833
193	present, very strong	https://www.inaturalist.org/observations/91374216	Alice Abela	8/13/2021	34.784167	−120.621389
194	undetermined	https://www.inaturalist.org/observations/91221393	Alice Abela	8/13/2021	34.785833	−120.617222
195	present, very strong	https://www.inaturalist.org/observations/91210733	Alice Abela	8/13/2021	34.785556	−120.616389
196	present	https://www.inaturalist.org/observations/91047001	Susan Schalbe (naturephotosuze)	8/12/2021	34.037690	−118.746496
197	present	https://www.inaturalist.org/observations/91046995	Susan Schalbe (naturephotosuze)	8/12/2021	34.037747	−118.746637

Specimen #	Foretarsal rake	URL	Observer	Date	Latitude	Longitude
198	undetermined	https://www.inaturalist.org/observations/90855095	Alice Abela	8/11/2021	34.805000	−120.603889
199	undetermined	https://www.inaturalist.org/observations/88723304	Martin Ruane	7/26/2021	34.098239	−119.117005
200	undetermined	https://www.inaturalist.org/observations/87453370	Sean Werle (axarus)	6/12/2021	35.114383	−120.632025
201	present, very strong	https://www.inaturalist.org/observations/86944488	Alice Abela	7/1/2021	34.804444	−120.605556
202	undetermined	https://www.flickr.com/photos/44150996@N06/51443807397	Alice Abela	8/30/2021	34.740833	−118.711526

trapdoor spider) (Kurczewski and Edwards 2012), *A. simus* Chamberlin (Southern coastal dune trapdoor spider) (Abela 2015b; Kurczewski et al. 2017; Willems 2018; Johnson 2020a, b) (Fig. 2), and *A.* sp., probably *stanfordianus* Smith (Stanford Hills trapdoor spider) (Williams 1928, Krombein 1979, Wasbauer and Kimsey 1985). Based on Bond's (2012) revision of the genus *Aptostichus*, *A. atomarius*, reported by Kurczewski and Edwards (2012) and *A.* sp., probably *stanfordianus*, reported by Williams (1928), were possibly misidentified. *Aptostichus atomarius* may be *A. simus* and *A.* sp., probably *stanfordianus*, is likely *A. stephencolberti* Bond and Stockman (Stephen Colbert trapdoor spider) based on their geographic distribution and specific habitat (R. C. West pers. obs.). An immobilized *A. atomarius* female was found lying on the sand surface in Santa Barbara County, CA in an area where *A. hirsutus* females were common (Abela 2013), but Abela (pers. obs.) thinks this spider could also have been the discarded prey of *A.* (*Aporus*) *luxus* (Banks) which was also present in the area.

Aptostichus stephencolberti, *A. miwok* Bond (Miwok trapdoor spider), and *A. simus* inhabit central and southern coastal California sand dunes coincident with the habitat and common occurrence of *Aporus hirsutus* and are probably typical host spiders of this wasp species. Their shallow to somewhat deep, silk-lined burrows are remarkably similar in structure to one another (Bond 2012, A. Abela pers. obs.). They are covered by flimsy, thin, silk and sand wafer-like trapdoors rendering them largely indistinguishable from the surrounding sand surface. The female spider is often restricted to living in such a burrow for most of her life. The resident spider lies beneath the trapdoor at night in anticipation of capturing unsuspecting invertebrate prey that wander too close to the entrance, but during the heat of the day the spider moves to the cooler end of the burrow, usually in the shade beneath vegetation (A. Abela pers. obs.).

Williams (1928) was the first to publish on the nesting behavior of *A. hirsutus* [as *Planiceps hirsutus* Banks] based on studies made in the San Francisco, CA sand dunes in late May and early June 1925. He observed females on the dunes searching for host spiders, running across the bare sand with their wings "quivering in the sunlight," and digging in the sand for up to half their body length. Williams (1928) noted that wasps, head downward, used their antennae and [compound] eyes during their constant searches. One wasp found the "limp, horizontal … flap" to an *Aptostichus* sp., probably *stanfordianus* Smith [det. N. Banks 1925], "delicate" silk-lined burrow "in an almost imperceptible semicircle of silk-bound sand." Instead of walking straight into the silk-lined tube, the wasp positioned herself atop the flap, turned around, grasped its edge with her swollen forelegs, and nearly somersaulted as she dove into the slit below the flap that she had pried open. She entered in this inverted position for less than her body length and immediately backed out rapidly several times in succession between standing above or next to the flap and buzzing her wings. Such activity evidently attracted the attention of the spider inside and, with it now positioned just beneath the partly open flap, the wasp ran ~4 cm behind the flap and dug rapidly and deeply into the loose sand below the spider, repeating this penetration until she induced it to abandon its burrow. Her object was to get to the rear of the spider in order to drive it from its burrow onto the sand surface. The spider ran from its burrow across the sand surface with the wasp in close pursuit. Eventually the wasp caught the spider, and, after a brief scuffle, stung it one or more times in its ventral cephalothorax thereby rendering it motionless. She positioned herself obliquely atop the spider and curved her abdomen underneath its cephalothorax while inserting her sting. After the spider acquiesced completely from the effect of the venom, the wasp grasped the comparatively large prey by a foreleg with her mandibles and dragged it slowly backwards toward its burrow. She frequently released the prey on the sand, walked to and inspected the trapdoor flap, then entered and exited several times in the usual manner, dorsal side upward. Arriving at the entrance, following a lengthy prey transport, she manipulated the spider into the burrow abdomen first, positioning its legs with her mandibles as to not impede its entry. As the spider slowly disappeared from view, the flap gradually closed behind and was eventually pulled tight from inside by the wasp's mandibles. Thirteen minutes after entering with the immobilized prey, the wasp appeared on the sand surface having exited from the same opening in the sand she dug to induce the spider to leave its burrow. She raked sand over the depression and cleaned herself. Excavation of the site by Williams (1928) revealed the paralyzed spider at the bottom of the burrow, ~6 cm deep, dorsal side upward, with the wasp's pearly white, elongate egg affixed dorsolaterally to its abdomen.

A week earlier, another *A. hirsutus* female hunting on the same dunes exhibited nearly identical behavior in dispatching its host *A.* sp., probably *stanfordianus* [det. N. Banks 1925] (Williams 1928). This female dragged her immobilized prey backwards across the sand for 1.2 m during a laborious prey transport. The wasp had burrowed into the sand headfirst, ~5 cm from the spider's entrance, to get beneath and induce the spider to leave its burrow and, 15–20 minutes later, after capture of the spider, she exited, following oviposition, from the same excavation. The immobilized spider was found in the same position as the other prey, ~6 cm deep, at the bottom of the silk-lined burrow. The largest host spider reported by Williams (1928) was 15 mm in body length. The largest female of *A. stanfordianus* in the original series described by Smith (1908) was 21 mm in body length, indicating that *A. hirsutus* might be preying on juvenile rather than adult individuals because of their smaller, more manageable size. Other large, recently stung *A.* sp., probably *stanfordianus*, females were found by Williams (1928) abandoned on the sand surface in a paralyzed state. These individuals may have been too large and heavy to be transported back to their burrows by the smaller wasps. Williams (1928) believed this species of wasp had two generations per year at this locality.

Krombein (1979) and Wasbauer and Kimsey (1985), citing Williams (1928), noted *A. hirsutus* nesting in sand dunes and using the burrows of the trapdoor spider *Aptostichus* sp., probably *stanfordianus* (likely *A. stephencolberti*). *Aporus hirsutus* and *Aptostichus simus* were both mentioned as being ecologically sensitive, dune-dependent species on Rabbit Island, Bolsa Chica Ecological Reserve, Huntington Beach, Orange County, CA, but they were not associated biologically (MITECH 1990). Kurczewski and Edwards (2012) described females of *A. hirsutus* in San Luis Obispo County, CA searching for host spiders on sand underneath dried leaves and other plant debris, flicking their wings and using their antennae but not attempting to fly. They reported *Aptostichus atomarius*, adult male [det. G. B. Edwards 2011] (possibly *A. simus*), 14.5 mm long (wasp, 11.5 mm), as prey of an *Aporus hirsutus* female. Kurczewski et al. (2017), citing Abela's macrophotographs from Santa Barbara County, CA, described an *Aptostichus simus*, juvenile [det. A. Abela 2015], 14.8 mm long (wasp, 13 mm), as host spider of *A. hirsutus*. Willems (2018) photographed an *A. hirsutus* female with a paralyzed *A. simus* at Oceano Dunes, San Luis Obispo County, CA.

Aside from Williams (1928) note on *A. hirsutus*, there is no information on the nesting behavior, ecology, or functional morphology of this trapdoor spider-hunting spider wasp species. Despite his graphic description, Williams (1928) observations were made at a time when photographic equipment to record rapid insect activity in the field was basically non-existent. Abela's 21st century cutting edge macrophotographs bring Williams (1928) and her own observations on *A. hirsutus* to the forefront of spider wasp nesting behavior study. This paper consolidates all available information on the nesting behavior, ecology and external morphology of *A. hirsutus* and presents it in an orderly sequence to clarify and illuminate the rarely seen and scarcely reported predator-prey association between *Aporus hirsutus* and its host *Aptostichus* wafer-lid trapdoor spiders.

Materials and Methods

The first step in preparing this paper for publication was a thorough literature review of the nesting behavior, ecology and external morphology of *A. hirsutus*. This involved finding, reading and interpreting Williams (1928) description of the nesting behavior and ecology of *Aporus hirsutus* [as *Planiceps hirsutus* Banks]. Krombein (1979) and Wasbauer and Kimsey (1985) referenced Williams (1928) paper in their summaries of the host and nesting behavior. Kurczewski and Edwards (2012) described hunting behavior and presented a new host record for *A. hirsutus.* Kurczewski et al. (2017) noted two new host records and described prey transport for *A. hirsutus* based on Abela's (2015a,b) macrophotographs. We searched inaturalist.org, BugGuide.net and flickr.com under Genus *Aporus* Spinola and *Aporus* (*Plectraporus*) *hirsutus* (Banks) and found photographs of hunting and excavating *A. hirsutus* females or immobilized and potentially associated individuals of *Aptostichus* (Euctenizidae) by Willems (2018), Gong (2019), Johnson (2020a, b), and Van Loon and Van Loon (2020a, b). An additional ~30 papers and reports on other species of Aporini were read, interpreted and, sometimes, documented. Important steps in formulating the "Functional Morphology" section involved reading and deciphering Evans' (1966) revision of the Mexican and Central American species of Pompilinae and Wasbauer and Kimsey's (1985) California Spider Wasps of the Subfamily Pompilinae (Hymenoptera: Pompilidae). We took their taxonomic descriptions and dichotomous keys a step further by analyzing, assessing and associating exactly how the external morphological structures of a hunting and burrowing *A. hirsutus* female might function. The final step in literature review was reading Bond's (2012) revision of the wafer-lid trapdoor spider genus *Aptostichus*, specifically in reference to actual and potential host species from central and southern California coastal sand dunes. More than 200 macrophotographs of *Aporus hirsutus* and *Aptostichus simus*, *A. miwok*, *A. atomarius*, and *A. stephencolberti* from BugGuide.net, inaturalist.org, and flickr.com, the vast majority taken by Alice Abela (2010–2021), were examined and analyzed. Abela's excellent macrophotographs and field observations combined with Williams (1928) rather detailed description of the hunting and nesting behavior of *A. hirsutus* provided the impetus for writing this paper.

Abela's macrophotographs were taken with a Canon 5D Mark III or Mark IV with a Canon EF 100mm f/2.8 Macro USM, Canon MP-E65mm f/2.8 1–5× Macro, or LAOWA 100mm F2.8 CA Dreamer Macro 2X paired with a Canon Macro Twin Lite MT-24EX or Canon Macro Twin Lite MT-26EX-RT or a Venus Kx 800 Twin Flash. All photographs were shot from a kneeling, sitting, or prone position. Her *Aporus hirsutus* and *Aptostichus* photographs and observations were made over ~50 days in 2010–2021 at 17 locations in Santa Barbara and San Luis Obispo Counties, CA. F. E. Kurczewski spent five days in 2011–2012 at four locations in San Luis Obispo County, CA observing *Aporus hirsutus* and *Aptostichus* (Kurczewski and Edwards 2012). Other photographs of *A. hirsutus*, some with host *Aptostichus*, from central coastal California in 2014–2020 were studied from inaturalist.org, BugGuide.net and flickr.com. Those by Willems (2018), Gong (2019), Johnson (2020a, b), and Van Loon and Van Loon (2020a, b) contained hunting or actual or potential host information. The California localities where *Aporus hirsutus*, *Aptostichus atomarius* and *A. simus* were photographed and studied by Abela (2010–2021) and Kurczewski and Edwards (2012), comprised [San Luis Obispo County]: Carrizo Plains Ecological Reserve [Chimineas American Ranch], Cuesta-by-the-Sea, El Moro Elfin Forest, Guadalupe-Nipomo Dunes National Wildlife Refuge, Los Osos, Montana de Oro State Park, Morro Bay, Morro Strand State Beach, Oceano Dunes State Vehicular Recreation Area, Oso Flaco Dunes Natural Area, Oso Flaco Lake Natural Area, Sweet Springs Nature Preserve; [Santa Barbara County]: Burton Mesa Ecological Reserve, More Mesa Beach, Ocean Beach Park, Santa Maria River Estuary, Vandenberg Air Force Base [Coastal Dune Scrub, Coastal Live Oak Woodlands, Coastal back dunes, Coastal foredunes, Surf Beach].

Abela excavated ~35 burrows of *Aptostichus simus* and *A. atomarius* in sand dunes with moderately steep slopes at 12 locations in Santa Barbara and San Luis Obispo Counties, CA. Using her hand as a trowel, she created a sand avalanche on the slope. As the sand slid down the slope, silk lined tubular *Aptostichus* burrows were gradually exposed. Continual digging caused more sand to slide downward, exposing more of the spider's tubular burrow which usually terminated underneath vegetation upslope. The complete silk-lined burrow was often extracted from the loose sand beneath the vegetation and, often, the spider was inside at the end.

The last step in completion of the manuscript involved Rick West configuring Abela's macrophotographs onto four plates in order of nesting behavior sequence, the eight macrophotographs representing the most important wasp behavioral activities. Lynn S. Kimsey, University of California–Davis, Davis, CA provided us with the original California geographic distribution map of *Aporus hirsutus* from her joint 1985 paper with Marius Wasbauer. Abela used California Insect Survey coordinates in creating her own *Aporus hirsutus* geographic distribution and associated maps for California (Fig. 9–11). She similarly used these GIS reference points plus geographic coordinates from inaturalist.org, BugGuide.net and flickr.com photographs in formulating Table 1. Frank E. Kurczewski wrote the manuscript based on information provided by all three authors.

Adult feeding

Aporus hirsutus females and males visit a wide variety of flowers for nectar nourishment: *Adenostoma fasciculatum* Hook and Am., *Asclepias erosa* Torr., *Baccharis pilularis* DC, *B. sarothroides* A. Gray, *Calochortus catalinae* S. Wats., *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Croton californicus* Muell. Arg., *Dalea polyadenia* F. Heller, *Ericameria bloomeri* (Gray) J. F. Macbr., *E. nauseosa* (Pall. ex Pursh) G. L. Nelson and G. I. Baird, *E. pinifolia* (Gray) H. M. Hall, *Eriogonum elongatum Benth., E. fasciculatum* Benth., *E. inflatum* Torr., *E. latifolium* Sm., *E. parvifolium* Sm. (Fig. 3), *Euphorbia albomarginata* Torr. and A. Gray, *E. serpyllifolia* Pers., *Froeniculum vulgare* Mill., *Haplopappus sonorensis* (A. Gray) S. F. Blake, *Helianthus niveus* (Benth.) Brandeg., *Heterotheca villosa* (Pursh) Shinners, *Lepidospartum squamatum* A. Gray, *Malacothrix* DC sp., *Mucronea californica* Benth., *Oenothera* L. sp., *Prosopis juliflora* (Sw.) DC, and *Tamarix gallica* L. (Williams 1928; Wasbauer and Kimsey 1985; A. Abela, Santa Maria, CA; H. Broccard-Bell, University of San Diego, San Diego, CA; S. Grush, Castaic, CA; R. Hemberger, Irvine, CA; M. Kummel, Arcata, CA; B. Nickel, San Diego, CA; C. Roessler, Midpeninsula Regional Open Space District, CA; S. Schalbe, Santa Monica, CA; C. Sharpe, Montague, CA; A. Sheehey, Kernville, CA; K. Ueda, Santa Cruz, CA; H. Wisch, Pasadena, CA; 2005–2021 pers. comm.). In addition, adults of *A. hirsutus* visit honeydew of aphids on *Chrysothamnus* Nutt., honeydew exuding from galls of *Disholcaspis eldoradensis* (Beutenmuller) on *Quercus lobata* Née, and extra-floral nectaries of *Helianthus* L. (Wasbauer and Kimsey 1985).

On 28 March 2015 on Surf Beach foredunes at Vandenberg Air Force Base an *A. hirsutus* female captured and immobilized a small immature *Aptostichus* sp., probably *simus* [det. A. Abela 2015], about half her size, and examined it with her antennae and mouthparts (Fig. 4) (Abela 2015a; Kurczewski et al. 2017). The wasp apparently imbibed hemolymph from this comparatively small spider for her own nourishment.

Functional morphology

The external morphology of *A. hirsutus* females is strongly adapted for excavating sand in search of *Aptostichus* wafer-lid trapdoor spiders in their burrows (Fig. 1). The species name "*hirsutus*" is derived from the Latin word hairy, referencing abundant, moderately long tactile hairs covering the body and legs. The antennae and forelegs are short compared to most pompilid species. The antennal orbits/sockets of most females are positioned near the bottom of the head, below the lower margin of the eyes, where they can be tucked underneath or to the side while tunneling in sand. The short forelegs are advantageous when burrowing through sand by taking up less space. The compound eyes are relatively narrow and situated to the side of the head where they receive less abrasion when moving forward underground. They are used along with the antennae when the wasp is searching on the sand surface for the presence of host spider burrow entrances. The body is streamlined and this reduces abrasion when moving through sand. The back of the head is concave to fit the convex contours of the front of the prothorax, the head and thorax thus functioning as a conjoined unit. There are no protruding sclerites that would prevent or impede the wasp's movement through sand. When tunneling downward, the head is held obliquely forward. It is quasi-triangular in frontal view and thin and flattened in sideview to facilitate ready penetration through sand. The mandibles are used to enter and excavate the sand. The pronotum is extraordinarily long, wide and flattened, being approximately as long as wide. It encloses a substantial internal musculature that moves the forelegs. The forefemur is strongly swollen and foretibia moderately enlarged for increased internal muscle size. The foretarsus has laterally a row of short, stout flattened spines or digging "rake" which, when moved backwards alternately, pushes the sand particles to the rear. The wings are folded flat on the dorsum when tunneling in sand (Fig. 5). The forewing venation is reduced to only two submarginal cells, fewer veins and cross veins, thereby providing the wasp with less flight capacity than in typical pompilids. *Aporus hirsutus* females do not fly much when searching on the sand surface for host spiders, spending most of their time on the ground. Most spider wasps have three submarginal cells, increased wing venation, are strong fliers, and sometimes pursue their host spider partly in flight.

There is intraspecific variation of *A. hirsutus* females in California, seen especially in wasps from San Diego County. Their antennal orbits/sockets are situated slightly above the lower margin of the compound eyes and the foretarsal digging spines are reduced in size (Wasbauer and Kimsey 1985) (Fig. 10). These individuals also have fewer tactile hairs on the body and legs as part of a reduction of psammophilic morphological characters (Fig. 11). Such individuals may inhabit less sandy, more compact soils and, therefore, are constrained to enter the burrows of other potential host species of *Aptostichus* or other genera of Euctenizidae through the trapdoor, but this is merely speculation.

Hunting

Aporus hirsutus females run across the sand, stop periodically to dig with their mandibles and forelegs for a few seconds to depths of ~2–3 mm, back out, then run to the next trial digging site and repeat this behavior. Wasps that constantly move from one site to another apparently do not receive appropriate information about the underground presence of potential host spiders. In certain spots, wasps dig deeper in the sand, often to half their body length (~5–6 mm), or they disappear completely in the sand spending several minutes underground. More time spent underground may be associated with the wasp sensing the presence of a potential host spider.

On 12 June 2014 on sandy coastal back dunes in Santa Barbara County, CA an *A. hirsutus* female ran across the bare sand, stopped periodically, and sampled the sand with her mandibles and other mouthparts. In certain spots, usually near vegetation, she dug into the sand with her mandibles and foretarsal digging rake, disappeared almost completely underground, then backed out quickly and repeated this behavior in other places (Fig. 5). Her attempts at finding a spider's trapdoor, entrance and burrow were unsuccessful in this area on that day. Finding the spider's entrance and burrow is not an easy task for the hunting wasp as there is no obvious visual evidence of a trapdoor on the sand surface. However, when carefully exposed, there is a flimsy thin flap covering the burrow entrance (Fig. 6).

On 24 July 2020 at the Guadalupe-Nipomo Dunes in San Luis Obispo County, CA an *A. hirsutus* female, ~13 mm long, dug repeatedly in several places at the base of an *Achillea millefolium* L. (yarrow) plant. In some spots she disappeared completely underground, the only evidence of her subterranean tunneling being the oscillating sand surface. Such a wasp may be sensing the vibrations of a spider moving through its silk-lined burrow or she may be tugging on the silk of the spider's burrow with her mandibles and forelegs at strategic points to nudge the spider toward the entrance (A. Abela pers. obs.). This female usually backed straight onto the sand surface after only seconds underground, moved a few centimeters away, and repeated this behavior. She once emerged from the sand headfirst, instead of backing out, ~13 mm from where she entered, indicating she had moved laterally underground. After 15 minutes of excavation by the wasp an *Aptostichus simus* juvenile, ~15 mm long, appeared suddenly on the sand surface, ~10 cm from where the wasp was digging, evidently responding to the wasp's underground activity. It is unknown how the spider exited its burrow. In typical *A. simus* burrows the entrance is lower down the slope and the spider's retreat/end of burrow is upslope. If the spider left through its burrow entrance, it should have exited farther down the dune rather than at the top unless there is a rear escape opening. The disturbed spider ran across the sand for 0.8 m and then dug into the sand beneath an *Ericameria ericoides* (Less.) Jeps. (Asteraceae) (California goldenbush) shrub. The wasp, unaware of the spider's escape, continued to dig unsuccessfully in the area for another several minutes.

Kurczewski and Edwards (2012) observed *A. hirsutus* females searching for *Aptostichus* at Sweet Springs Nature Preserve and El Moro Elfin Forest in Baywood-Los Osos, San Luis Obispo County, CA. The females searched on dry or damp sand as long as it was sunny. The wasps walked slowly or ran across the sand depending on time of day and sand surface temperature, flicking their wings, and holding their head and antennae downward toward or on the sand surface. No wasp attempted to fly during their brief searches. Gong (2019) observed a hunting *A. hirsutus* female at Montana de Oro State Park, San Luis Obispo County, CA running across the sand, head and antennae downward, pausing, and digging with her mandibles and forelegs. In certain spots the female dug downward in the sand for half her body length. One photograph shows the wasp on the surface, evidently in an excited state, with raised wings (Gong 2019). Such an *A. hirsutus* female may locate the spider's burrow via minute silken strands radiating from the entrance (R. C. West pers. obs.). Johnson (2020a) photographed an immobilized *Aptostichus simus* juvenile lying dorsal side upward on the sand surface at Oceano Dunes State Vehicular Area, San Luis Obispo County, CA. Over an hour later, Johnson (2020b) photographed an *A. hirsutus* female excavating in sand with her mandibles and forelegs, possibly searching for a second host spider. Five females of *A. hirsutus* were observed over two days hunting for individuals of *A. simus*, *A. atomarius* or, possibly, the recently described *Cryptocteniza kawtak* Bond and Hamilton (Euctenizidae) (Bond et al. 2020; J. Bond, University of California–Davis, Davis, CA, pers. comm. 2020; det. M. Hedin, San Diego State University, San Diego, CA, 2020) on sparsely vegetated sand at Marina State Beach, Monterey County, CA (C. J. and T. Van Loon 2020 pers. comm.). An *A. hirsutus* female and a *C. kawtak* female were photographed at that site, both on the sand surface, only ~3 m apart (Van Loon and Van Loon 2020a, b.)

Prey transport

Position of spider and location of the wasp's grasp during prey transport to the spider's burrow vary depending on the relative size of wasp and prey, distance from entrance, and number and frequency of pauses, releases and reconnaissance forays. Williams (1928) noted one immobilized spider brought back to its burrow by the wasp being grasped by a "foreleg." On 17 June 2015 an *A. hirsutus* female, ~13 mm long, with an immobilized *A. simus* juvenile [det. A. Abela 2015], 14.8 mm long, dragged the much heavier spider backwards across the sand, dorsal side upward, grasping the base or end of its left or right foreleg or femur or tibia of its 2nd left leg with her mandibles, switching her grasp between releases during transport (Abela 2015b, Kurczewski et al. 2017) (Fig. 7, 8). Willems (2018) photographed a female of *A. hirsutus* at Oceano Dunes State Vehicular Recreation Area, San Luis Obispo County, CA dragging an *Aptostichus simus* [det. A. Abela 2020], juvenile, ventral side upward, backwards on the sand grasping the base of the femur of its 3rd right leg with her mandibles. The wasp periodically released the spider on the ground, flew a short distance, then returned to the spider and continued dragging it backwards across the sand surface—probably a form of reconnaissance (J. S. Willems, California Polytechnic State University, San Luis Obispo, CA, 2020 pers. comm.). A large (~25 mm long), paralyzed *Aptostichus atomarius* female was found lying dorsal side upward on sandy back dunes at Vandenberg Air Force Base, Santa Barbara County, CA on the evening of 3 May 2013 (Abela 2013). There was no wasp in attendance, but both *A. hirsutus* and *A. luxus* females were common in the area (A. Abela 2013 pers. obs.). The spider twitched its appendages when touched. It was presumably stung earlier in the day and left abandoned on the sand surface because of its large size and difficulty in prey transport. *Aporus hirsutus* and *A. luxus* females are usually smaller and much lighter in weight than their host *Aptostichus* and prey transport to the spider's burrow is often laborious and time-consuming. Five *A. hirsutus* females collected in Santa Barbara and San Luis Obispo Counties, CA in 2011–2015 averaged only 10.8 mm (8.1–13.0) in body length, whereas two host *Aptostichus*, *simus* and *A. atomarius* or *A. simus*, from the same sites were 14.8 and 14.5 mm long (Kurczewski and Edwards 2012; Abela 2015b; Kurczewski et al. 2017).

Spider burrow

Aptostichus simus burrows are common in southern California coastal sand dune habitats such as beaches, chaparral and shrub (Bond 2012). They are often located on the moderately steep faces of sand dunes at the bases of coastal vegetation, except where *Carpobrotus edulis* (L.) N. E. Br. (ice plant) grows. The burrows have a flexible silk lining and the entrances are covered by an indistinguishable, thin flimsy trapdoor made of silk and sand (Bond 2012). Some entrances have "double-doors," the proximal portion of the burrow being Y-shaped (M. Hedin 2020 pers. comm., A. Abela pers. obs.). Burrow structure varies with slope and sand compactness. Burrows course mainly parallel beneath the sand surface on steep slopes while those in level sand descend more perpendicularly. Entrance width and burrow width and length are related to sex, size and stage of spider. Burrows of large females can be as long as 15–30 cm (M. Hedin, 2020 pers. comm., A. Abela pers. obs.,). The entrance and trapdoor are positioned lower down the slope and the spider's retreat is usually upslope beneath the base of vegetation. The resident spider rests during daytime at the end of the burrow underneath vegetation in the shade where temperatures are cooler and humidity higher rather than in the bare open sand where temperatures just below the surface are much higher and humidity much lower. One hatched wasp cocoon, possibly made by *A. hirsutus*, was found in the burrow of what was once a large *A. simus* female (A. Abela pers. obs.).

Aptostichus atomarius, when inhabiting larger sand dunes, digs burrows more or less straight into the dune face. Some *A. simus* burrows are similarly excavated directly into larger steep dunes, including one in a >3 m-high dune at the Guadalupe-Nipomo Dunes. *Aptostichus atomarius* does not have a shallow burrow retreat at the base of plants on smaller dune hummocks, as seen in *A. simus* and, probably, *A. miwok* and *A. stephencolberti* (Bond 2012; A. Abela pers. obs.). *Aporus hirsutus* females that hunt *A. atomarius* or *A. simus* on larger dunes, therefore, might attack the host spider by entering through or near the trap door and entrance. If flushed onto the surface and exposed, *A. atomarius* is reluctant to burrow into the sand, probably resulting in an easier capture by the wasp (A. Abela pers. obs.). *Aptostichus simus*, when exposed, digs hurriedly into the sand and thereby sometimes escapes capture, at least temporarily (A. Abela pers. obs.).

Discussion

Aporus hirsutus has the appropriate structural characteristics for attacking trapdoor spiders in a subterranean psammophilous environment: body and legs covered with moderately long tactile hairs; quasi-triangular, flattened, thin head with concave posterior that fits nicely into the convex contours of an elongate, heavily muscled pronotum; narrow eyes at the sides of the head; short antennae at the bottom of head below eyes; stout mandibles; short and powerful forelegs; heavily muscled forefemur and foretibia; foretarsal digging rake of short, thick spines; and, reduced wing venation (Evans 1966; Wasbauer and Kimsey 1985; Fig. 1). No other North American *Aporus* species has this set of predatory structural characteristics. *Aporus hirsutus* is so unique morphologically that it is placed in its own subgenus, *Plectraporus* Bradley (Evans 1966). *Aporus* (*Aporus*) *unicolor* Spinola preys on purse-web spiders (Atypidae) in England (Else 1975; Day 1988) and Germany (Gerth et al. 2012), cuts open the usually subterranean silken purse using its mandibles and widens the tear with its foretarsal claws in order to gain entry. This species has fewer structural modifications than *A. hirsutus* to gain access to its host spider's lair: rounded head, smaller prothorax, less swollen forefemur, and no foretarsal digging rake (Day 1988; Wahis and Durand 2012). Perhaps *A. hirsutus* once attacked different trapdoor spiders and needed its extensive arsenal of heavily muscled prothorax, forefemur and foretibia to successfully open thick and sturdy trapdoors but has since evolved to prey on psammophilous *Aptostichus* species and, in the process, acquired a hairy streamlined body and foretarsal digging rake. *Aporus* (*Aporus*) *luxus* (Banks), another common California species with less modified structural characteristics than *A. hirsutus*, has a better arsenal of predatory morphological characteristics than *A. unicolor*: slightly-triangular-shaped head, moderate-size pronotum and swollen forefemur but no hairy body and foretarsal digging rake (Evans 1966). *Aporus luxus* preys on *Aptostichus* but also other families of trapdoor spiders with much sturdier trapdoors than *Aptostichus* (Kurczewski et al. 2020).

The method of prey capture in *A. hirsutus* is not fully understood despite Williams (1928) rather detailed description and Abela's macrophotographs and observations. Williams (1928) noted wasps burrowing downward in sand to get underneath the spider in order to drive it from its burrow from the rear rather than face its powerful chelicerae head-on. Entering underground by burrowing through sand and probing or tearing open the thin burrow wall requires some time and effort if the purpose is for the wasp to chase the spider onto the sand surface. When attacking and subduing prey on the surface the wasp must relocate the burrow entrance in order to deposit the spider inside while exposing it to conspecifics, various predators and parasites. Does the wasp sometimes enter the spider's burrow by prying open the silk and sand flap or bite through it using her mandibles, as shown in captivity for another aporine, *Psorthaspis planata* (Fox) [as *Pedinaspis planatus* (Fox) (Jenks 1938)? Such an entry usually results in a "rough-and-tumble" between the smaller and lighter wasp and larger and much heavier spider. During such activity Jenks (1938) described the spider's cheliceral bites glancing "harmlessly" off the wasp's sturdy, smooth exoskeleton while the wasp's sting repeatedly penetrated the spider's undersides until it "wilted into limp paralysis." Not all such wasp attacks have a successful outcome. Jenks (1938) described one wasp that fell victim to the spider's bite, albeit in captivity under confined burrow limitations.

Ecoregion, soil type and soil texture likely influence the host spider species of *A. hirsutus* and, in turn, the manner in which the wasp searches for and gains access to the spider. The extensive geographic distribution of *A. hirsutus* from Oregon and Idaho to Baja California Sur and Sonora, Mexico (Wasbauer and Kimsey 1985), including >200 collection records from California (Table 1; Fig. 9), infers that the ecologically restricted coastal dune *Aptostichus* are probably not the only host spider species of *A. hirsutus*. In California, 36 species of *Aptostichus* inhabit a wide range of ecoregions, soil types and soil textures from the Pacific coastal sand dunes and northern Redwood forests to the Sierra Nevada Mountains and Mojave Desert (Bond 2012). Burrowing underground through sand in order to find and drive the spider from its burrow onto the surface is the common hunting method of *A. hirsutus* in coastal sand dunes (Williams 1928). The psammophilic morphological adaptations of the female wasp are integrated in this method of hunting. But, how does the wasp gain access to its potential host spider if the soil is not sandy or friable? Does compact soil constrain the wasp to enter the spider's burrow through the trapdoor regardless of how sturdy? It would certainly help answer why this spider wasp species has retained its presumably ancestral arsenal of trapdoor-opening apparatuses despite living in sand dunes and sandy deserts where entry through the trapdoor is a less desirable option. Throughout the range of *A. hirsutus* certain individuals have the antennal orbits/sockets positioned slightly above the lower margin of the compound eyes and the anterior tarsal digging spines reduced in size (Wasbauer and Kimsey 1985) (Table 1; Fig. 10). Such females from inland areas and San Diego County also have fewer tactile hairs on the body and legs in conjunction with reduced psammophilic morphological characteristics (Table 1; Fig. 11). If DNA analyses were done would *A. hirsutus* be composed of multiple species? Taxonomic studies of this species pre-date the use of DNA by several decades. Do hairless *A. hirsutus* variants inhabit non-sandy, compact soils and, therefore, enter the burrows of other potential host species of *Aptostichus* or other genera of Euctenizidae via the trapdoor instead of attempting to burrow through the impervious soil?

One possible non-*Aptostichus* host spider for *A. hirsutus* is *Cryptocteniza kawtak* (Euctenizidae). *Cryptocteniza kawtak* is comparable in size to juveniles of *Aptostichus simus*, or ~14 mm in body length. This species, *Aptostichus atomarius*, *A. simus* and *Aporus hirsutus* all cohabit the sandy coastal beaches of Monterey County, CA (Bond 2012; Bond et al. 2020; Van Loon and Van Loon 2020a, b). The unbranched burrow entrance of *C. kawtak* is covered by a thin, flimsy silk and sand trapdoor as in coastal dune inhabiting *Aptostichus* species. The burrow of *C. kawtak* is similar to that of *Aptostichus atomarius* in entering the sand quasi-vertically but it is moderately deep (>30 cm) compared to those of *A. simus*, *A. miwok*, and *A. stephencolberti* (Bond 2012; Bond et al. 2020). Would the deeper burrows eliminate *C. kawtak* as a potential host species of *A. hirsutus*?

Miranda et al. (2013) made two statements about the genus *Aporus* that need revision. In a paper on "parasitism" of the trapdoor spider genus *Neocteniza* (Araneae: Mygalomorphae: Idiopidae) by *Euplaniceps varia* Bradley (Hymenoptera: Pompilidae: Aporini) in Panama these authors stated, "Is rare to see *Aporus* dragging their prey on the ground…" This is not true. Nearly all host records and all nesting behavior information for *Aporus hirsutus* and *A. luxus* involve the wasps dragging their host spiders across the ground (Williams 1928; Kurczewski and Edwards 2012; Kurczewski et al. 2017, 2020; Willems 2018; A. Abela pers. obs.). Their second incorrect statement is, "All the evidence indicates that wasps of both genera (*Aporus*, *Euplaniceps*) paralyze the spider in its own retreat…," the key word being "paralyze." Only Jenks (1938) observation of *Psorthaspis planata*, in the tribe Aporini, subduing and ovipositing on *Bothriocyrtum californicum* supports this statement. Jenks (1938) evidence for the wasp subduing and ovipositing on the spider in its retreat is based on the spider being confined in captivity, artificially introducing the wasp into her burrow, and corking the entrance so the wasp could not escape.

Acknowledgments

We thank Steven Alm, University of Rhode Island, Kingston, RI; Sarah Crews, California Academy of Sciences, San Francisco, CA; David Plotkin, McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL; and Kevin Williams, California Department of Food and Agriculture, Sacramento, CA for reviewing the manuscript. Lynn S. Kimsey and Marius S. Wasbauer, University of California–Davis, Davis, CA, answered questions about the geographic distribution and external morphology of *Aporus hirsutus* in California. Kimsey was especially helpful in providing the original *A. hirsutus* California geographic distribution map from their joint 1985 paper on the Spider Wasps of California of the Subfamily Pompilinae. Jason E. Bond, University of California–Davis sent us information about *Cryptocteniza kawtak* from Moss Landing State Beach, Monterey County, CA. Heather Broccard-Bell, San Diego University, San Diego, CA; Steph Grush, Castaic, CA; Ron Hemberger, Irvine, CA; Marc Kummel, Arcata, CA; Bonnie Nickel, San Diego, CA; Cindy Roessler, Midpeninsula Regional Open Space District; Susan Schalbe, Santa Monica, CA; Celise Sharpe, Montague, CA; Alison Sheehey, Kernville, CA; Ken-ichi Ueda, Santa Cruz, CA; and, Hartmut Wisch, Pasadena, CA provided flower visitation records for adults of *A. hirsutus*. Marshal Hedin identified species of *Aptostichus* and sent information on the burrow structure of *A. simus*. Lori Gong, Port Reyes Station, CA; Daniel Johnson, Atascadero, CA; Susan Schalbe, Santa Monica, CA; Trevor and Chloe J. Van Loon, San Jose, CA; and Joshua S. Willems, California Polytechnic State University, San Luis Obispo, CA sent us information about wasp behavior associated with their photographs of *A. hirsutus*.

Literature Cited

Abela A. 2010. Spider Wasp (*Aporus* sp.). Available at https://www.flickr.com/photos/44150996@N06/4953526942. (Last accessed 18 July 2020).

Abela A. 2013. San Bernardino Hills Trapdoor Spider (*Aptostichus atomarius*). Available at https://www.flickr.com/photos/44150996@N06/8703323325. (Last accessed 9 October 2020).

Abela A. 2014a. *Aporus hirsutus*. Available at https://www.flickr.com/photos/44150996@N06/14662564150/in/album-72157623966061803/. (Last accessed 17 July 2020).

Abela A. 2014b. *Aporus hirsutus* – nectaring on *Croton californicus*. Available at https://www.flickr.com/photos/44150996@N06/50168818116. (Last accessed 30 July 2020).

Abela A. 2015a. *Aporus hirsutus* with *Aptostichus simus* spiderling–*Aporus hirsutus*–female. Available at https://www.bugguide.net/node/view/1050791, 1050792/bgimage. (Last accessed 17 July 2020).

Abela A. 2015b. *Aporus hirsutus* with *Aptostichus simus*–*Aporus hirsutus*–female. Available at https://bugguide.net/node/view/1104818/bgimage. (Last accessed 11 October 2021).

Abela A. 2020. *Aporus hirsutus*. Available at https://www.inaturalist.org/observations/54236876. (Last accessed 25 July 2020).

Bond JE. 2012. Phylogenetic treatment and taxonomic revision of the trapdoor spider genus *Aptostichus* Simon (Araneae, Mygalomorphae, Euctenizidae). Zookeys 252: 1–209.

Bond JE, Hamilton CA, Godwin RL, Ledford JM, Starrett J. 2020. Phylogeny, evolution, and biogeography of the North American trapdoor spider family Euctenizidae (Araneae: Mygalomorphae) and the discovery of a new 'endangered living fossil' along California's central coast. Insect Systematics and Diversity 2: 1–14.

Day MC. 1988. Spider wasps. Hymenoptera: Pompilidae. Handbooks for the identification of British insects 6: 1–60.

Else GR. 1975. *Aporous* [sic] *femoralis* (Vander Linden) (Hym. Pompilidae). In Hampshire and the Isle of Wight and a record of its prey in Britain. Entomologist's Monthly Magazine 110: 82.

Evans HE. 1966. A revision of the Mexican and Central American spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). Memoirs of the American Entomological Society 20: 1–422.

Gerth M, Mayer R, Hering L, Wolf R, Schaffer S, Bleidorn C. 2012. Zur Stechimmenfauna (Hymenopera: Aculeata) des Bienitz in Leipzig. Ampulex 5: 1–14.

Gong L. 2019. *Aporus hirsutus*. Available at https://www.inaturalist.org/observations/28478181. (Last accessed 12 July 2020).

Jenks GE. 1938. Marvels of metamorphosis. A scientific "G-man" pursues rare trapdoor spider parasites for three years with a spade and a candid camera. The National Geographic Magazine 74: 807–828.

Johnson D. 2020a. Genus *Aptostichus*. Available at https://www.inaturalist.org/observations/58093062. (Last accessed 31 August 2020).

Johnson D. 2020b. *Aporus hirsutus*. Available at https://www.inaturalist.org/observations/58130071. (Last accessed 31 August 2020).

Krombein KV. 1979. Family Pompilidae. p. 1523–1570. In: Krombein KV, Hurd PD, Jr., Smith DR, Burks BD (eds.). Catalog of Hymenoptera in America north of Mexico. Volume 2, Apocrita (Aculeata). Smithsonian Institution Press; Washington, DC. 2209 p.

Kurczewski FE, Edwards GB. 2012. Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae). Southeastern Naturalist 11 (Monograph 4): 1–71.

Kurczewski FE, Edwards GB, Pitts JP. 2017. Hosts, nesting behavior, and ecology of some North American spider wasps (Hymenoptera: Pompilidae), II. Southeastern Naturalist 16(Monograph 9): 1–82.

Kurczewski FE, West RC, Waichert C, Kissane KC, Ubick D, Pitts JP. 2020. New and unusual host records for North American and South America spider wasps (Hymenoptera: Pompilidae). Zootaxa 4891: 1–112.

Miranda RJ, Arizala S, Cambra RA. 2013. A new species of *Neocteniza* (Araneae: Idiopidae) from Coiba Island, Panama, with observations on parasitism by *Euplaniceps varia* Bradley, 1944 (Hymenoptera: Pompilidae). Revista de Aracnologia 22: 3–7.

MITECH. 1990. Unpublished data on the nearshore fish and invertebrate communities offshore Bolsa Chica Ecological Reserve.

Smith CP. 1908. A preliminary study of the Araneae Theraphosidae of California. Annals of the Entomological Society of America 1: 207–236.

Van Loon C, Van Loon T. 2020a. Genus *Aporus*. Available at https://www.inaturalist.org/observations/63142311. (Last accessed 23 October 2020).

Van Loon C, Van Loon T. 2020b. Wafer-lid Trapdoor Spiders (Family Euctenizidae). Available at https://www.inaturalist.org/observations/63142341. (Last accessed 23 October 2020).

Wahis R, Durand F. 2012. Sur les *Aporus* d'Europe et d' Afrique du nord avec descriptions des femelles d' *Aporus alanni* sp. n., *foucarti* sp. n. et *lacteipennis* (Priesner, 1955) comb. n. (Hymenoptera: Pompilidae, Pompilinae, Aporini). Arvernsis—1er semester–N° 59–60:1–32.

Wasbauer MS, Kimsey LS. 1985. California spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). Bulletin of the California Insect Survey 26: 1–130.

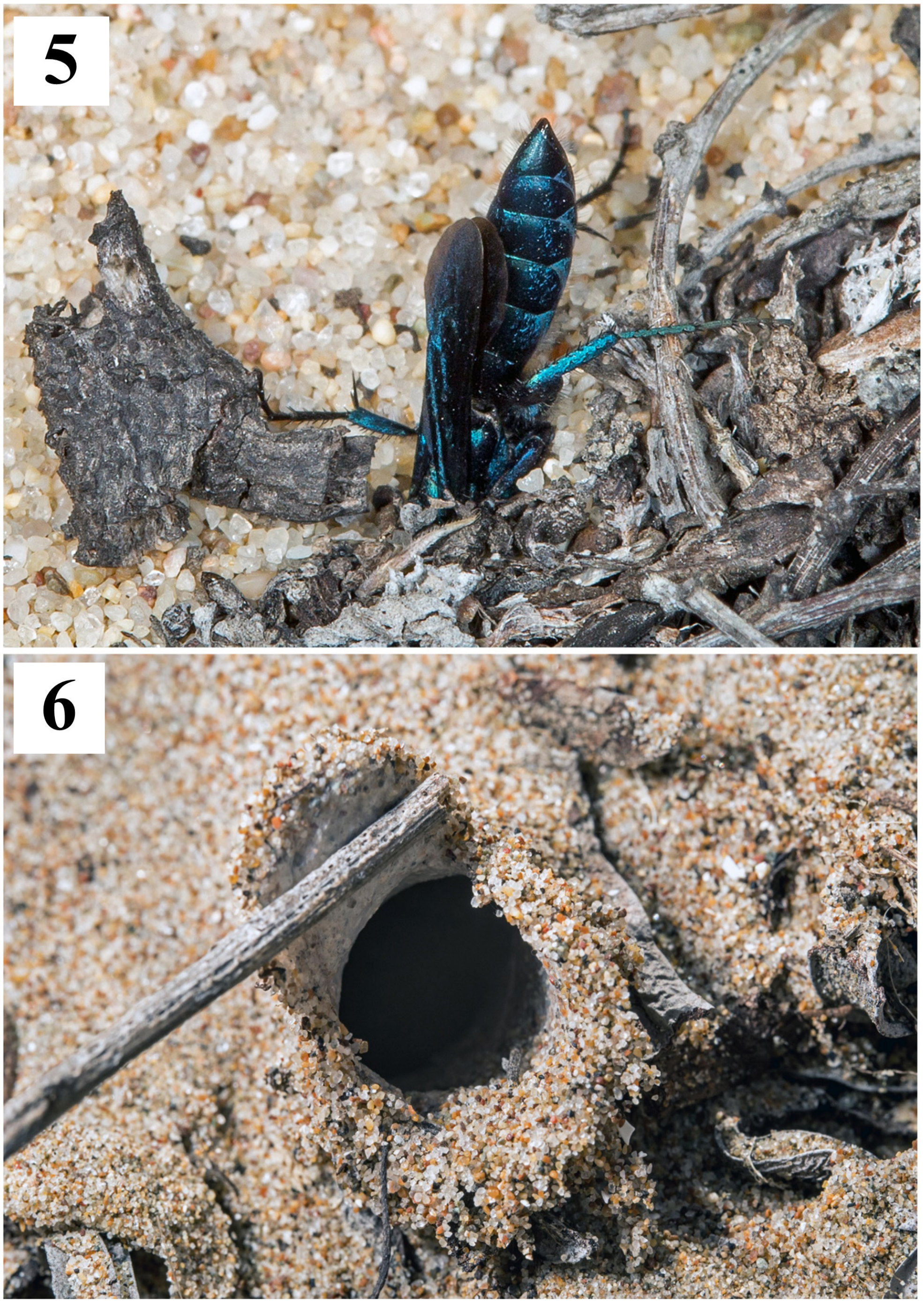
Willems JS. 2018. *Aporus hirsutus.* Available at https://www.inaturalist.org/observations/13566678. (Last accessed 12 July 2020).

Williams FX. 1928. Studies in tropical wasps—their hosts and associates (with descriptions of new species). Bulletin of the Experiment Station of the Hawaiian Sugar Planter's Association (Entomology) 19: 1–179.

Received October 11, 2021; accepted November 15, 2021.
Review editor Kevin Williams.

Figures 1–2. *Aporus hirsutus* and *Aptostichus simus*. **1)** *Aporus hirsutus* resting on sand, digging in sand, sandy coastal back dunes, Santa Barbara County, CA; 12 June 2014; A. Abela. The species name "*hirsutus*" refers to the hairiness of the body. Species identification structures include short antennae and forelegs, quasi-triangular flattened head, elongate pronotum, swollen forefemur and foretibia, thick foretarsal rake spines, and only two submarginal cells in forewing. The concave back of the head, not seen to this degree in other Nearctic *Aporus* species, fits snugly against the front of the convex pronotum, enabling the wasp to tunnel unobstructed through sand. Photograph © Alice Abela. **2)** *Aptostichus simus* female on sand, Montaña de Oro State Park, San Luis Obispo County, CA; 8 June 2014; A. Abela. Females lack obvious distinguishing external morphological features, except for sharply delineated patch of endite cuspules on abdominal venter. All *Aptostichus* species have psammophilous body coloration (Bond 2012). Photograph © Alice Abela.

Figures 3–4. *Aporus hirsutus* adult feeding. **3)** *Aporus hirsutus* female taking nectar from flowers of *Eriogonum parvifolium*, Vandenberg Air Force Base, Santa Barbara County, CA; 6 August 2014; A. Abela. Photograph © Alice Abela. **4)** *Aporus hirsutus* female with immobilized *Aptostichus simus*, immature, on sand, Surf Beach at Vandenberg Air Force Base, Santa Barbara County, CA; 28 March 2015; A. Abela. The wasp appressed her mouthparts and basal antennal segments to the paralyzed prey and, apparently, used this individual only for adult feeding. Photograph © Alice Abela.



Figures 5–6. *Aporus hirsutus* hunting behavior. **5)** *Aporus hirsutus* female digging into sand, using her mandibles and foretarsal digging rake, apparently searching for host *Aptostichus simus*, sandy coastal back dunes, Santa Barbara County, CA; 12 June 2014; A. Abela. Photograph © Alice Abela. **6)** *Aptostichus simus* trapdoor being propped open by a twig. Note the flimsy silk and sand consistency of the trapdoor and sides of entrance, Montaña de Oro State Park, San Luis Obispo, CA; 5 July 2020; A. Abela. Photograph © Alice Abela.

Figures 7–8. *Aporus hirsutus* prey transport. **7)** *Aporus hirsutus* female dragging *Aptostichus simus* juvenile backwards across sand, grasping end of its right foreleg with her mandibles. Sandy coastal back dunes, Santa Barbara County, CA; 17 June 2015; A. Abela. Photograph © Alice Abela. **8)** *Aporus hirsutus* female dragging *Aptostichus simus* juvenile backwards across sand, grasping tibia of its 2nd left leg with her mandibles. The wasp's wings are folded on her dorsum, sandy coastal back dunes, Santa Barbara County, CA; 17 June 2015; A. Abela. Photograph © Alice Abela.

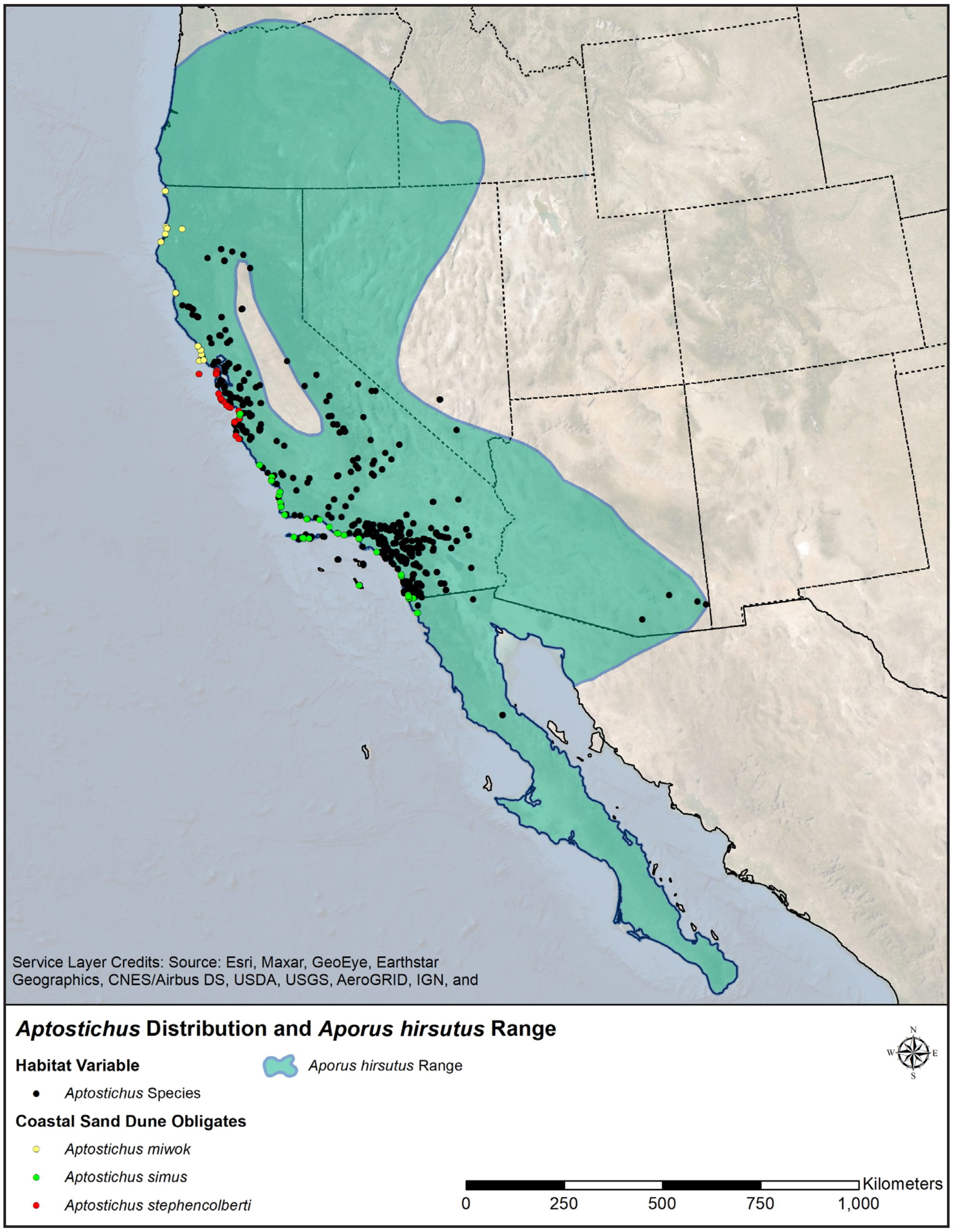


Figure 9. *Aptostichus* species California geographic distribution (from Bond 2012) and *Aporus* (*Plectraporus*) *hirsutus* (Banks) geographic range (Wasbauer and Kimsey 1985; this study).

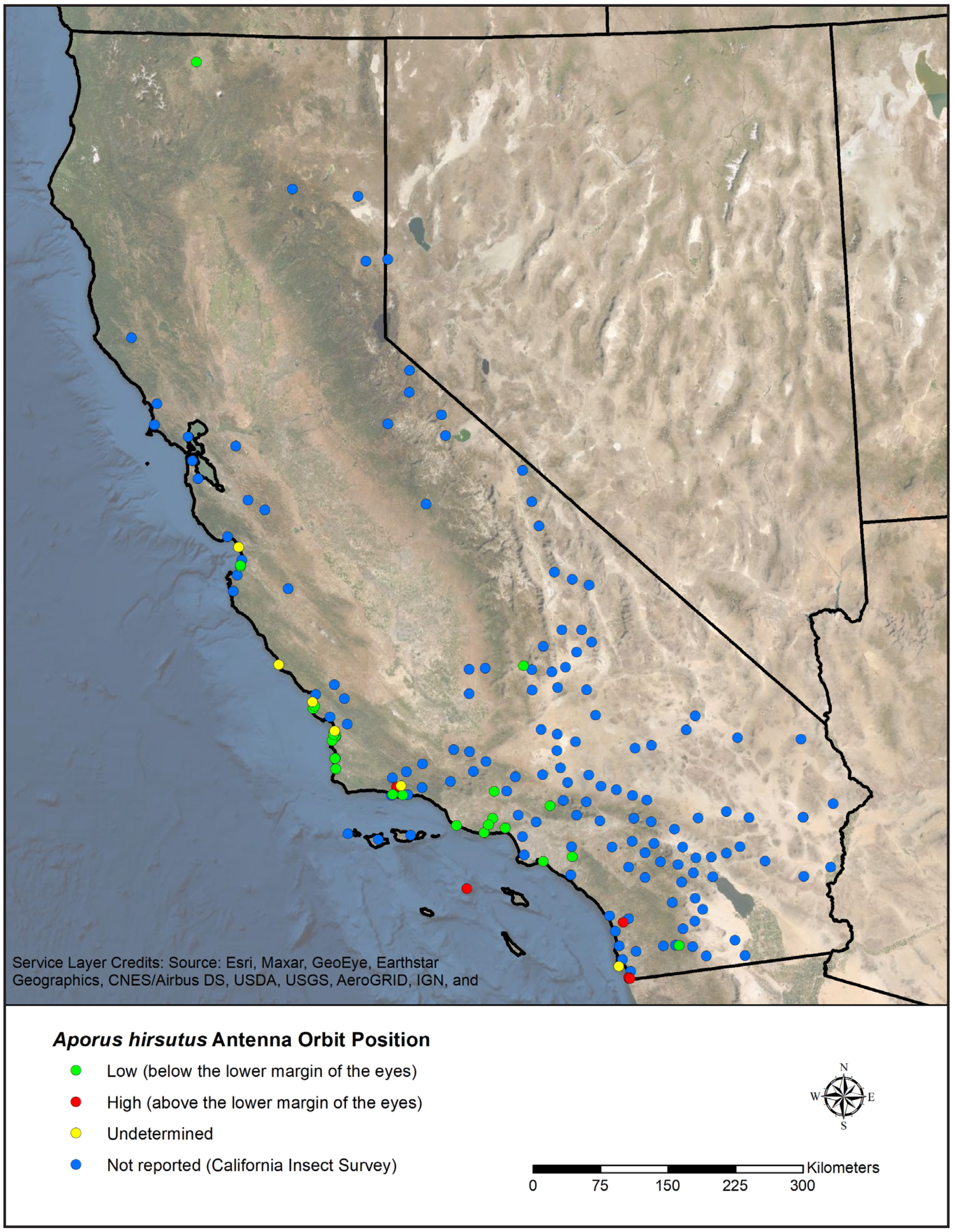


Figure 10. *Aporus* (*Plectraporus*) *hirsutus* (Banks) antenna orbit/socket position (Wasbauer and Kimsey 1985, this study).

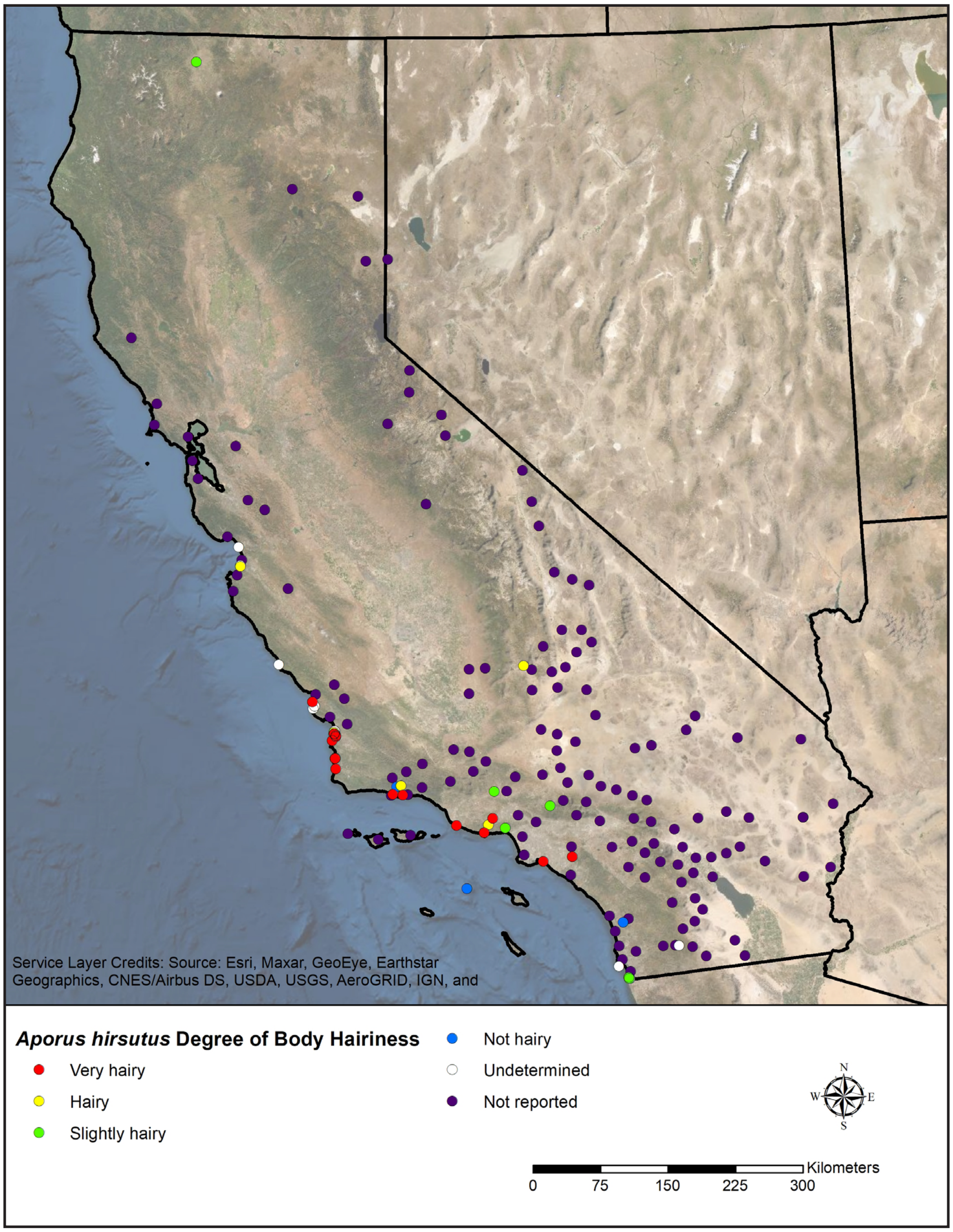


Figure 11. *Aporus* (*Plectraporus*) *hirsutus* (Banks) degree of body hairiness (Wasbauer and Kimsey 1985; this study).