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1 **Phoretic mite infestations associated with *Rhynchophorus palmarum* (Coleoptera:**
2 **Curculionidae) in southern California**

3

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10

11 **Abstract**

12

13 The South American palm weevil, *Rhynchophorus palmarum* (Coleoptera: Curculionidae),
14 established in San Diego County, California USA sometime around 2014. Attached to the motile
15 adults of this destructive palm pest, we identified three species of uropodine mites
16 (Parasitiformes: Uropodina), *Centrouropoda* n. sp., *Dinychus* n. sp. and *Fuscuropoda marginata*.
17 Two of these species, *Centrouropoda* n. sp. and *Dinychus* n. sp. are recorded for the first time in
18 the USA and were likely introduced by *R. palmarum*. Several species of mites, primarily of
19 Uropodina, have previously been recorded as phoretic on *Rhynchophorus* spp. In this study, we
20 examined 3,035 adult *R. palmarum* trapped over a 2.5-year period, July 2016 to December 2018,
21 and documented the presence of and species composition of phoretic mites and their relationship
22 with weevil morphometrics (i.e., pronotum length and width). The presence and species
23 composition of mites on weevil body parts changed over the survey period. No mites were found
24 under weevil elytra in 2016 and mite prevalence under elytra increased over 2017–2018 due to
25 an increased abundance of *Centrouropoda* n. sp per individual beetle. Mite occurrence levels
26 were significantly correlated with reduced pronotum widths of male weevils only. The
27 significance of this finding on male weevil fitness is unknown. Potential implications of phoretic
28 mites on aspects of the invasion biology of *R. palmarum* are discussed.

29

30 **Keywords:** invasive species, phoresy, South American palm weevil, species translocation

31

32 **Introduction**

33

34 Infiltration of new ecosystems by an invasive species may also result in the introduction of
35 additional species –such as endosymbionts, pathogens, parasites and predators– associated with
36 the invader (Thomas 2011). The South American palm weevil, *Rhynchophorus palmarum*,
37 established in San Diego County, California, USA sometime around 2014, likely from
38 populations that established in Tijuana, Baja California Norte, Mexico, which were first detected
39 in 2010 (Hoddle & Hoddle 2017). Adult *R. palmarum* are highly vagile and capable of flying
40 long distances in relatively short periods of time (Hoddle *et al.* 2020; Hoddle *et al.* 2021). These
41 attributes may enable *R. palmarum* and associated symbionts, such as phoretic mites, to disperse
42 naturally into new areas from infested regions.

43 *Rhynchophorus palmarum* is a notorious palm pest in its native range, which includes
44 parts of Mexico, Central and South America, and the Caribbean (EPPO 2021). Larvae feed
45 inside the palm crown, killing the apical growing region (Giblin-Davis 2001; Milosavljević *et al.*
46 2019). It is estimated that more than 10,000 ornamental *Phoenix canariensis* have been killed by
47 *R. palmarum* in San Diego Co. (APC 2020). The risk posed to palms by *R. palmarum* is
48 increased by its ability to vector a plant pathogenic nematode, *Bursaphelenchus cocophilus*
49 (Cobb) (Aphelenchida: Parasitaphelenchidae), the causative agent of a lethal palm malady, red
50 ring disease. This nematode has not yet been detected in California, but in its native range it is a
51 significant mortality agent in commercial oil palm and coconut plantations (Giblin-Davis 2001;
52 Milosavljević *et al.* 2019).

53 Phoresy is a phenomenon by which an organism is actively carried to favorable habitats
54 either on or in a host and for a limited period of time (OConnor 1982; Kaliszewski *et al.* 1995).
55 Phoretic mite species that are adapted to their host insects are often specialists on the same
56 resources used by their insect transporters (OConnor 1982; Wilson & Knollenberg 1987).
57 Association with phoretic mites, primarily species belonging to the Uropodina (Acari:
58 Mesostigmata), have been documented for several *Rhynchophorus* spp. in their native ranges
59 including *R. phoenicis* (Fabricius) in Cameroon (Kontschan *et al.* 2012), *R. vulneratus* (Panzer)
60 in Indonesia (Hoddle & Hoddle 2015), *R. ferrugineus* (Olivier) in the Philippines (Hoddle &

61 Hoddle 2011) and Malaysia (Dilipkumar *et al.* 2015), *R. cruentatus* (Fabricius) in Florida
62 (Wattanapongsiri 1966, Giblin-Davis 2001), and *R. palmarum* in Central and South America
63 (Husband & Flechtmann 1972; Husband & OConnor 1999; Rodriguez-Morell *et al.* 2012).
64 Additionally, phoretic mites have been recorded infesting invasive populations of *R. ferrugineus*
65 in the Mediterranean basin (Gomaa 2006; Longo & Ragusa Di Chiara 2006; Atakan *et al.* 2009;
66 Porcelli *et al.* 2009; El-Sharabasy 2010; Mazza *et al.* 2011), the Canary Islands, Spain (Abolafia
67 & Ruiz-Cuenca 2020), the Middle East (Al-Deeb *et al.* 2011; Farahani *et al.* 2016), and Aruba
68 and Curaçao Islands in the Caribbean (Amy Roda, USDA-APHIS pers. comm. 2021).

69 Phoretic mites may stimulate the onset of weevil flight and consequently colonization
70 behavior which would favor the spread of mites and weevils (Porcelli *et al.* 2009). In contrast,
71 secondary consequences of phoresy could result in deleterious effects on hosts. Heavy (i.e.,
72 hundreds of mites) mite loads on adult weevils may reduce the efficiency of foraging activities
73 such as flying and increase susceptibility to predation and other stress-related causes that result in
74 premature mortality (Bajerlein & Bloszyk 2004; Porcelli *et al.* 2009; Al-Deeb *et al.* 2011; Mazza
75 *et al.* 2014). A possible parasitic interaction with hosts has been also suggested (Elzinga & Broce
76 1988; Houck & Cohen 1995; Holte *et al.* 2001; Cardoza *et al.* 2008; Al-Deeb *et al.* 2011;) and
77 the life span of adult *R. ferrugineus* is reportedly reduced when weevils are infested with high
78 numbers of phoretic mites (Mazza *et al.* 2011).

79 The life cycle and behavior of one phoretic mite species, *Centrouropoda almerodai*
80 Hiramatsu & Hirschmann 1992 (Uropodina), found in association with *R. ferrugineus*, have been
81 documented in some detail (Longo & Ragusa Di Chiara 2006; Porcelli *et al.* 2009). Female *C.*
82 *almerodai* lay eggs on rotting palm fibers. Larvae that emerge from eggs and protonymphs feed
83 on rotting ligneous palm material. Deutonymphs search for mature *R. ferrugineus* larvae,
84 especially the last larval, or pre-pupal stage. Deutonymphs remain on pre-pupal weevil larvae as
85 they build pupal cocoons from palm fibers within which they pupate. Prior to weevil emergence
86 from the cocoon, deutonymphs cluster on different body parts of the teneral adult. Once attached
87 to adult weevils, deutonymphs develop an anal pedicel which immobilizes and fixes mites onto
88 hosts. This process occurs most commonly on the underside of the elytra. Stalks remain under
89 elytra even after deutonymphs abandon hosts (Porcelli *et al.* 2009).

90 *Centrouropoda almerodai* has been reported in association with *R. ferrugineus* and from
91 *R. palmarum* collected in Central America (Porcelli *et al.* 2009; Rodriguez-Morell *et al.* 2012).
92 However, Kontschán *et al.* (2014) state that *C. almerodai* is not present in Central America and
93 phoretic *Centrouropoda* mites associated with *R. palmarum* represent an undescribed species.
94 Another species of phoretic mite associated with *R. ferrugineus* is the mycetophagous,
95 *Fuscuropoda marginata* (Koch) 1839 (Uropodina: Urodinychidae) (often listed as *Uroobovella*
96 *marginata*) (Bowman 2021). In contrast to *C. almerodai*, *F. marginata* preferentially attaches to
97 exposed surfaces of the sternum, pygidium, head, and legs. In the context of uropodine-
98 *Rhynchophorus* associations, attachment site has been hypothesized as a good indicator of mite
99 species (Porcelli *et al.* 2009). *Fuscuropoda* spp. have not previously been recorded in association
100 with *R. palmarum*.

101 In 2016, a trapping program monitoring *R. palmarum* phenology in Bonita, San Diego
102 County was initiated. As part of this effort, captured adult weevils were counted and sexed.
103 During this handling and record keeping process it was noticed that numerous weevils were
104 infested with phoretic mites which indicated the possible introduction of new mite species into
105 California. Due to the presence of heavy mite loads on captured adult weevils, we hypothesized
106 that the presence of heavy mite loads imposes detrimental fitness consequences on weevils. To
107 test this hypothesis, the presence or absence and position of phoretic mites on individual
108 captured weevils was recorded. Infestation levels were compared to an indicator of host size by
109 measuring weevil thorax size (i.e., width and length). The prediction to be tested was that higher
110 numbers of mites are correlated with smaller weevils as measured by thorax size. We also
111 investigated the species diversity of phoretic mites associated with collected weevils and
112 reported here on the chronological sequence of their appearance on *R. palmarum* in California.

113

114 **Material and Methods**

115 *Sampling and locations*

116 From July 2016 to December 2018, *R. palmarum* populations were monitored monthly at
117 the Sweetwater Recreational Reserve, Bonita, San Diego County in California, USA (N 32° 40'
118 57''; W 117° 00' 09''). This riparian area has more than 800 wilding *P. canariensis* many of
119 which are infested with *R. palmarum*. Adult weevils were captured using traps made from white

120 7.5-liter paint buckets with lids (ULINE S-9941W, Pleasant Prairie, Wisconsin, USA). Buckets
121 had four evenly spaced 5-cm circular holes cut into the sides of the upper half of the bucket to
122 allow weevil entry (Milosavljević *et al.* 2020). Each bucket trap was wrapped with burlap fabric
123 (ULINE S-14512, Pleasant Prairie, Wisconsin, USA) to enable adult weevils attracted to traps to
124 climb the sides of the bucket to reach entry holes. Buckets were loaded with fermenting bait and
125 commercially available aggregation pheromone to attract weevils. The fermenting bait was
126 composed of dates, baker's yeast, and water held within containers (470 ml plastic containers
127 Uline Inc., Pleasant Prairie, WI) fitted with perforated lids (~ten 0.3 mm diameter holes) to
128 permit release of attractive fermentation volatiles. The commercial aggregation pheromone
129 dispenser (ISCALure IT192, 700mg at 98% purity of [4S,2E-6]-methyl-2-hepten-4-ol, ISCA
130 Technologies, Riverside CA, USA) was suspended within the bucket from the lid. To increase
131 the combined attractiveness of the pheromone and bait, a synergist, ethyl-acetate (20 ml,
132 Grainger Industrial Supply, Jackson, MS, USA), contained within a 25 ml plastic vial (Thermo
133 Fisher Scientific, Waltham, MA, USA) with a single perforation hole (~ 1–2 mm in diameter) in
134 the screw cap, was hung inside the bucket from the lid. The bucket contained antifreeze (i.e., 1.5
135 L of 50% propylene glycol solution) to drown and preserve captured weevils. Bucket traps were
136 suspended 1.5 m above the ground on tree branches. A total of 10 traps were hung in the reserve.
137 Traps were cleared and lures and baits replaced monthly (i.e., approximately every 30 days).

138

139 *Rhynchophorus palmarum* populations and pronotum size, mite presence on body parts and
140 species identification

141 Captured weevils were counted, sexed, preserved in 95% ethanol in labeled containers,
142 and stored in a freezer at ~ -5° C until examined. For this study, 3,035 weevils were sexed (sex
143 ratio was calculated as the number of females divided by the total number of male and female
144 weevils per trap) and pronotum width and length was measured in mm with a digital caliper
145 (Digital Caliper-Fractional & Decimal Display, Neiko Tools USA) and recorded.

146 The presence or absence of mites in four areas of the body: head and pronotum,
147 abdomen, legs, and the underside of the elytra (Figures 1–2) were recorded. Weevils with
148 missing body parts (e.g., heads) were excluded from the study. A subsample of mites attached to
149 the four body areas examined were removed and preserved in 95% ethanol in labeled vials for

150 species-level identification. The discovery of deutonymphs of three species of Uropodina led to a
151 secondary investigation of attachment site preference by each species and possible sequence of
152 species appearances in California. To this end, a limited sample consisting of three weevils each,
153 collected in Fall of 2016, 2017 and 2018, was examined for presence and, if present, attachment
154 site by different mite species. A subsample of 50–150 mites / year for both external and
155 subelytral sites (if available) were cleared and slide mounted (see Walter & Krantz 2009 for
156 mounting details) and identified to genus or species using available taxonomic keys (Karg 1989;
157 Krantz & Ainscough 1990; Hirschmann 1993).

158 *Statistical Analyses*

159 Generalized linear models were used to compare sex ratios of *R. palmarum* captures
160 between months and years. Quasibinomial error variance was used in model fittings as over-
161 dispersion in the sex ratio data was detected (Crawley 2007). A generalized linear model was
162 used to analyze the presence/absence of mites by sex and month. To analyze whether *R.*
163 *palmarum* pronotum size (i.e., width and length) was affected by sex and/or mite presence on
164 sampled weevils repeated measures generalized mixed-effects models were used to analyze data
165 for two complete years, 2017 and 2018 (2016 was excluded from this analysis as only six months
166 of data were available for this year). The factors for the repeated measures generalized mixed-
167 effects model were sex, mite presence/absence, their interactions, and month as a random factor.
168 The sample size was large (n=2,957 of the 3,035 weevils were used for analyses [see below]) and
169 data were normally distributed. The level of significance for all the analyses was set at < 0.05.
170 Analytical packages “*stats*”, “*glm*” and “*nlm*” in R (3.6.2. version) (R Core Team 2021) were
171 used for analyses.

172

173 **Results**

174 *Rhynchophorus palmarum* populations

175 Bucket traps deployed at the Sweetwater Reserve captured a total number of 3,035 *R.*
176 *palmarum* from July 2016 to December 2018. A total of 2,957 weevils were undamaged (i.e., not
177 missing heads or legs) and used for data collection. The maximum total number of weevils
178 captured in all 10 traps in a single month was 245 in April of 2018. Female sex ratio averaged
179 0.623 ± 0.188 (Figure 2). There were no significant differences in female sex ratio between

180 months across years (GLM: Month, $F_{1,116}=0.497$, $P=0.931$; Year, $F_{1,130}=0.794$, $P=0.375$) (Figure
181 2).

182 *Mite presence on body parts*

183 The infestation levels of mites under the elytra increased over the three years of this
184 survey. Of the 2,957 adult *R. palmarum* examined for mite presence and from which pronotum
185 measurements were taken, 91.5 % of captured adults were infested with phoretic mites on some
186 part of the body, with 68% of weevils harboring mites under the elytra. Half of the weevils were
187 infested with mites in summer of 2016 (n=136 weevils) and only one weevil had mites under the
188 elytra during this period (Figure 3). From January 2017 until the end of the survey in December
189 2018, more than 85% of captured weevils were infested with mites in any given period (i.e.,
190 season). Specifically, 99% of weevils captured over winter (January–March) and spring (April–
191 June) of 2018 were infested with mites (Figure 3). In comparison with 2016, weevils captured in
192 summer (July–September) and fall (October–December) of 2017 exhibited 95% and 94% levels
193 of infestation, respectively. The maximum prevalence of mites under elytra reached 79% of
194 captured weevils and was observed in winter 2018 (Figure 3). The percentage of weevils infested
195 with mites differed significantly ($F_{1,256}=5.72$, $P=0.017$) between the sexes and averaged $86.6\% \pm$
196 1.9 and $92.5\% \pm 1.5$ for females and males, respectively.

197 *Rhynchophorus palmarum* pronotum size

198 For weevils captured over 2017 and 2018, weevil sex and the presence of mites were
199 correlated with reduced pronotum width in males only. A similar relationship was not observed
200 for female weevils (Table 1 and Figure 4). The pronotum width of males infested with mites
201 averaged 10.74 ± 0.02 (mm \pm SE) and was significantly smaller than the average pronotum width
202 (11.08 ± 0.1) for males with no mites on any body part. However, the average size difference is
203 small being only a 3% difference in width (Table 1). Greater differences in the average pronotum
204 width between males and females were found in May 2018 [10.776 ± 0.779 and 10.294 ± 0.116
205 for females (n=77) and males (n=67) respectively] and in June 2018 [10.356 ± 0.108 and $9.913 \pm$
206 0.124 for females (n=88) and males (n=53) respectively]. Pronotum length was not affected by
207 sex, mite presence, and/or their interaction (Table 1 and Figure 5).

208 *Mite species identification*

209 Mites infesting *R. palmarum* were identified as *Centrouropoda* n. sp., *Fuscuropoda*
210 *marginata*, and *Dinychus* n. sp. (Figure 6–11). Kontschan *et al.* (2014) noted that the
211 *Centrouropoda* deutonymphs from *R. palmarum* in Panama identified as *C. almerodai* by
212 Rodriguez-Morell *et al.* (2012) differed from typical *C. almerodai* by the lack of a fourth pair of
213 setae on the ventrianal shield and by the presence of a pair of long ventrals caudal (JV5?) setae.
214 Specimens collected in this study share these characters (Figure 7), suggesting that the
215 *Centrouropoda* specimens associated with *R. palmarum* throughout the Americas represents a
216 new species. The identification of *Dinychus* n. sp. is tentative, as this species may represent a
217 new genus (Figure 10, 11). Voucher specimens are deposited in the Ohio State University
218 Acarology Collection, with respective accession numbers OSAL 0153163-5, OSAL 0153166-7,
219 and OSAL 0153737-41.

220 *Centrouropoda* n. sp. was commonly found under the elytra but was also found on the
221 venter and legs of weevils. Its occurrence on the legs and venter seemed to happen most
222 commonly as the numbers and subsequent densities of *Centrouropoda* n. sp. increased,
223 suggesting mites may “spill-over” from preferred attachment sites to occupy less preferred
224 attachment sites on adult weevils. As noted previously for *R. ferrugineus* (Porcelli *et al.* 2009),
225 *F. marginata* attaches to a variety of external locations on weevils (i.e., head, coxal region,
226 ventral abdomen, around the anus, femora and tibiae). *Fuscuropoda marginata* does not attach to
227 sites under the elytra. Among the “external” attachment sites there was no clear site preference
228 by either *Centrouropoda* n. sp. or *F. marginata*. Nearly all recovered specimens of *Dinychus* n.
229 sp. (n=43) were located under the elytra, with only a few (n=3) individuals found among
230 removed specimens of the other, externally attached, mite species. Deutonymphs of
231 *Centrouropoda* n. sp. and *F. marginata* attach to weevil hosts via stalks secreted by anal glands.
232 Our observations on *Dinychus* n. sp. suggest that this species does not generate stalks for host
233 attachment.

234 *Invasion sequence and species interactions*

235 Based on the limited sampling of weevils inspected for mites in Fall of 2016, 2017, and
236 2018, *F. marginata* was present and common in 2016, but *Centrouropoda* n. sp. and *Dinychus* n.
237 sp. were not recovered until 2017. When recovered, these latter two species were initially found
238 predominantly under the elytra. In 2018, *Centrouropoda* n. sp. was dominant not only under the

239 elytra, but also externally (Table 2). These observations are consistent with the observation that
240 the 2016 collections seldom included subelytral mites. Observed numbers of subelytral mites
241 were large (>200 / elytron), occupying nearly all the space under elytra. External mites can be
242 equally numerous and were often attached in clusters on body parts (Figures 1, 2). Members of
243 *Centrouropoda* n. sp. and *F. marginata* were found in mixed species clusters, often with
244 intertwined anal stalks.

245

246 **Discussion**

247 This study documents the association between *R. palmarum* and phoretic mites in southern
248 California for the first time. Three species of phoretic mite were detected from weevil trapping
249 surveys conducted over a 2.5-year period: *Centrouropoda* n. sp., *Fuscuropoda marginata*, and
250 *Dinychus* n. sp. (this species may actually represent a new genus). The percentage of *R.*
251 *palmarum* infested with mites ranged from 51% (in 2016) to 99% (in 2018). Previous studies
252 examining relationships between *R. palmarum* and phoretic mites did not specify the percentage
253 of weevils infested. However, Mazza *et al.* (2011) found similar infestation levels of phoretic
254 mites on *R. ferrugineus* in Italy.

255 The composition of the phoretic mite fauna of California collected on *R. palmarum* is
256 comparable to that of *R. ferrugineus* in the Mediterranean region where *C. almerodai* and *F.*
257 *marginata* typically infest weevils (Porcelli *et al.* 2009; Farahani *et al.* 2016). The detection of
258 *Centrouropoda* n. sp. and *Dinychus* n. sp. in this study may be the first official record of these
259 species in the U.S. Notably, phoretic mites have been observed infesting *R. cruentatus* in Florida
260 (R. Giblin-Davis, Univ. Florida, pers. comm. June 2021). This palm weevil is native to the
261 southeast U.S. but the identities of associated phoretic mites have not been determined/published
262 and warrant investigation. With respect to the association of *Dinychus* n. sp. with a
263 *Rhynchophorus* sp., this is an unusual finding given that other members of this genus are rarely
264 recorded in association with beetles (Wisniewski & Hirschmann 1993).

265 Each phoretic mite species observed in this study appears to have site attachment
266 preferences on *R. palmarum*. However, *Centrouropoda* n. sp. appear to “spill over” to attach to
267 external sites if its preferred subelytral sites are occupied. If this hypothesis is correct it suggests
268 that this mite may exhibit flexibility in attachment site selection. Data presented here also

269 suggest that the three species of phoretic mites associated with *R. palmarum* in California
270 invaded sequentially, specifically *Centrouropoda* n. sp. arrived later than *F. marginata*. The
271 situation for *Dinychus* n. sp. is less clear as the abundance of this species is substantially lower
272 than the other two species and its relative rarity, especially at invasion onset, may have made
273 detection difficult. Interestingly, our data suggests that the increase in numbers of *Centrouropoda*
274 n. sp. on weevils may have led to the competitive exclusion of *F. marginata* in 2018 (Table 2).
275 The putative mechanism for such preferred attachment site changes (from subelytral to external
276 sites) and the subsequent exclusion mechanism of mites from preferred weevil body parts is
277 unclear for two reasons. First, mites rarely occupied all available external sites, and second, the
278 observation of mixed species clusters suggests some inter-species tolerance. Collectively, these
279 observations are tentative given the relatively small sample sizes examined. Consequently, these
280 hypotheses of attachment site preferences and exclusion mechanisms between species of phoretic
281 mites infesting *R. palmarum* are tentative given the relatively small sample size examined and
282 would greatly benefit from additional investigation.

283 Finally, it is important to note that Uropodina are not the only mites, or even the only
284 mesostigmatid mites, associated with *Rhynchophorus* spp. Phoretic mites of the family
285 Diplogyniidae (Mesostigmata: Trigynaspida) were found attached to *R. palmarum* adults in
286 Brazil (Negrisoli Junior *et al.*, 2011). Halliday (2019) suggested that these mites may be
287 *Crenamargo binuseta* Hicks (Diplogyniidae) which has been previously found on *R. palmarum*
288 in Nicaragua (Hicks 1958) and Brazil (Flechtmann 1981). Collections from California have not
289 yet generated any confirmed cases of Diplogyniidae on *R. palmarum*, but these mites, when
290 present, typically occur in small numbers and may be overlooked. It is possible that diplogyniid
291 mites may have invaded California with *R. palmarum*, and if so, they may be detected with
292 additional sampling efforts.

293 The infestation severity of mites on male *R. palmarum* was slightly higher than those
294 observed for female weevils. This finding may indicate a minor preference of phoretic mites for
295 male weevils. This finding is tentatively supported by previous studies which found male biased
296 associations of phoretic mites on some species of beetles (Grossman & Smith 2008). In this
297 study, the presence of mites on *R. palmarum* males was associated with a significant, but
298 relatively small, 3% reduction in pronotum widths (but not lengths) in male weevils only. This

299 finding may suggest that the presence of phoretic mites, assuming that they are associated with
300 pre-pupal and pupal weevils prior to infesting their respective adult hosts, could impose a fitness
301 cost in terms of resulting male size as measured by pronotum width. The exact nature of that
302 possible fitness cost on male weevils is unknown.

303 In the Mesostigmata, the phoretic stage is usually either the last immature instar (the
304 deutonymph) of both sexes, or the adult female (Athias-Binche 1993; Walter & Proctor 1998).
305 The other stages (i.e., eggs, protonymphs) of phoretic mites are usually free-living forms. In this
306 study, the free-living forms share the same ecological niche, rotting plant material in the interior
307 of palm trees, with *R. palmarum* larvae. Uropodid mites are generally considered mycophagous
308 (OConnor 1984). However, some species of the Uropodidea have been described as predators or
309 parasitic haemolymph feeders (Walter & Proctor 1998). Weevil fitness could be adversely
310 affected by phoretic mites if those mites feed on immature hosts to obtain protein (Longo &
311 Ragusa Di Chiara 2006; Mazza *et al.* 2011). Consequently, mites may not only exploit weevils
312 for dispersal, but they could also engage in a parasitic relationship by using hosts as a protein
313 source as suggested by Mazza *et al.* (2011). For example, Holte *et al.* (2001) reported that the
314 phoretic (heteromorphic) deutonymphs of *Hemisarcoptes cooremani* (Astigmata:
315 Hemisarcoptidae) extract materials from adult coccinellid hosts, suggesting a parasitic
316 relationship between mites and beetle hosts. A similar process may explain why adult *R.*
317 *ferrugineus* infested with phoretic mites exhibit reduced longevity (by ~33%) when compared to
318 uninfested weevils (Mazza *et al.* 2011).

319 Substantial loads of phoretic mites on adult weevils may impede flight capabilities
320 (Atakan *et al.* 2009). However, mites might not impede completely flight capacity as mite-
321 infested weevils are readily captured in traps (Mazza *et al.* 2011). Similarly, in this study, 91.5 %
322 of weevils that flew to bucket traps and were captured hosted mites on some part of the body.
323 However, the distances flown to reach traps are unknown and substantial mite loads on weevils
324 might have a strong negative effect on long-distance flight capacities. Interestingly, phoretic
325 mites may stimulate weevils to abandon palms of declining quality to search for healthy palms to
326 infest, which promotes the spread of both mites and weevils (Porcelli *et al.* 2009). Flight mill
327 studies are ideally suited to test these hypotheses regarding the effects of infestations of varying

328 densities of single or mixed species loads of phoretic mites on the flight capabilities of male and
329 female *R. palmarum* (Hoddle *et al.* 2020; 2021).

330 Mazza *et al.* (2011) suggested that the chronological spread of invasive palm weevils into
331 new areas may be reconstructed by tracking the spread of accompanying species that have
332 dependent interspecific relationships with the host or vector. When surveys of *R. palmarum* in
333 southern California commenced in 2016, phoretic mites were found primarily on the pronotum,
334 legs, and abdomen and the only identified species was *F. marginata* (Figure 6 and 7). Over the
335 course of this 2.5-year study, increasing densities of mites were found on the underside of elytra
336 while mite infestation levels on other body parts remained relatively consistent. Mite species
337 composition changed with subsequent detections of *Centrouropoda* n. sp. (one and three weevils
338 with mites under elytra in September/October 2016 and February 2017, respectively) (Figure 3).
339 This observation of sequential additions of phoretic mite species associated with *R. palmarum*
340 over time, if confirmed, could be used to determine the relative age of weevil local infestations as
341 this pest spreads into new areas of California. The strength of the relationship and its utility for
342 reconstructing invasion timelines could be investigated by examining mite infestation loads on
343 weevils captured at the leading edges of the invasion and comparing mite loads (i.e., proportions
344 of weevils infested with phoretic mites, and mite species compositions and densities) to
345 populations with known residency times in infested areas.

346 Additionally, the identification of the phoretic mite fauna associated with specific
347 *Rhynchophorus* species could be studied to determine the competitive interactions amongst
348 different mite species. For example, the phoretic mite fauna on *R. cruentatus* (native to Florida)
349 has not been studied and needs documentation. It is possible that at some future time *R.*
350 *palmarum*, *R. ferrugineus* (established in the Caribbean), and *R. cruentatus* could become
351 sympatric in southeast USA. Baseline data on the phoretic mite fauna for *R. cruentatus* while in
352 allopatry would be essential for determining mite interactions after congeneric weevil species
353 become sympatric. Similarly, *R. palmarum* (native) and *R. ferrugineus* (invasive and introduced
354 from Egypt) co-exist in Aruba and Curaçao islands, in the Caribbean (A. Roda, USDA-APHIS,
355 pers. comm. June 2021). The phoretic mite fauna associated with these two weevil species has
356 not been studied in the Caribbean but might exhibit mixed species compositions comprised of
357 mite species from the Caribbean, the Middle East, and/or possibly from the original native range

358 of *R. ferrugineus* in tropical Asia. This possibility could be determined by characterizing the
359 phoretic mite fauna for each weevil species in allopatry and then comparing mite species
360 compositions to weevil populations that occur in sympatry.

361 In conclusion, work presented here suggests that two species, *Centrouropoda* n. sp. and
362 *Dinychus* n. sp., of phoretic mites have sequentially invaded California with *R. Palmarum*.
363 *Fuscuropoda marginata* is considered cosmopolitan and was likely already present in California
364 and may not have invaded in association with *R. palmarum*. Data presented here documented
365 that mite densities and potentially species compositions changed over the course of this ~2.5-
366 year study. Phoretic mites may extract a fitness cost on adult male *R. palmarum* as infested
367 males, on average, tend to exhibit reduced (~3%) pronotum widths when compared to uninfested
368 males. However, the fitness effects of possible size reduction in males are unclear. Manipulative
369 experiments that assess the effects of varying phoretic mite loads associated with prepupal
370 larvae, pupae, and adults have on adult male and female size (e.g., flight mill studies to quantify
371 dispersal capabilities), or on longevity could be undertaken to better understand the potential
372 fitness costs of phoretic mites on *R. palmarum*.

373

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375

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384

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534 *vergleichende Milbenkunde, Nürnberg, 40, 1-220.*

535 **Table 1.** Results of repeated measures generalized mixed-effects model examining the effects of
 536 sex and mite occurrence (presence vs absence) on pronotum width and length of *Rhynchophorus*
 537 *palmarum* captured in bucket traps at the Sweetwater Recreational Reserve, San Diego,
 538 California in 2017 and 2018.

	df	pronotum width		pronotum length	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Sex (S)	2752	18.562	< 0.001	3.389	0.066
mite presence (MP)		5.015	0.025	0.040	0.842
S x MP		2.132	0.144	3.807	0.051

539

540 **Table 2.** Relative abundance of uropodine deutonymphs on *Rhynchophorus palmarum* by
 541 attachment site, based on subsamples of mites identified and taken from weevils collected during
 542 Fall of 2016, 2017 and 2018. Format: total number of mites on the subsampled weevils
 543 (percentage of total for *Centrouropoda* n. sp. and plus *F. marginata*)
 544

Site	External			Sub-elytral		
	<i>Centrouropoda</i>	<i>Fuscuropoda</i>	<i>Dinychus</i>	<i>Centrouropoda</i>	<i>Fuscuropoda</i>	<i>Dinychus</i>
Year	n. sp.	<i>marginata</i>	n. sp.	n. sp.	<i>marginata</i>	n. sp.
2016	0	73 (100%)	0	0	0	0
2017	15 (25%)	45 (75%)	0	74	0	39
2018	123 (94%)	8 (6%)	3	55	0	4

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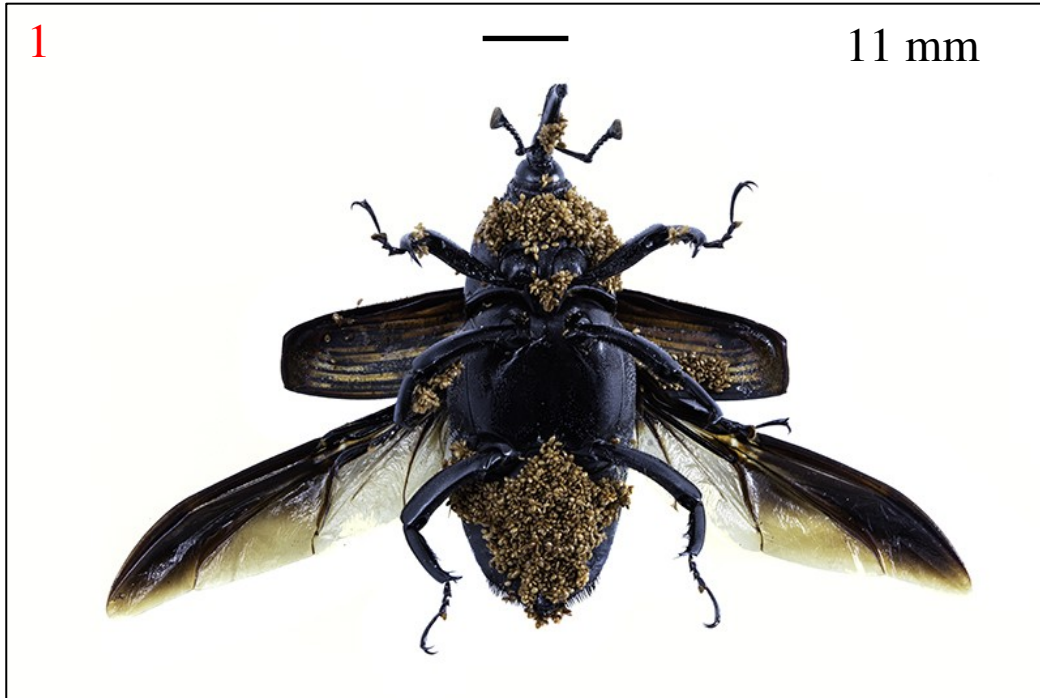
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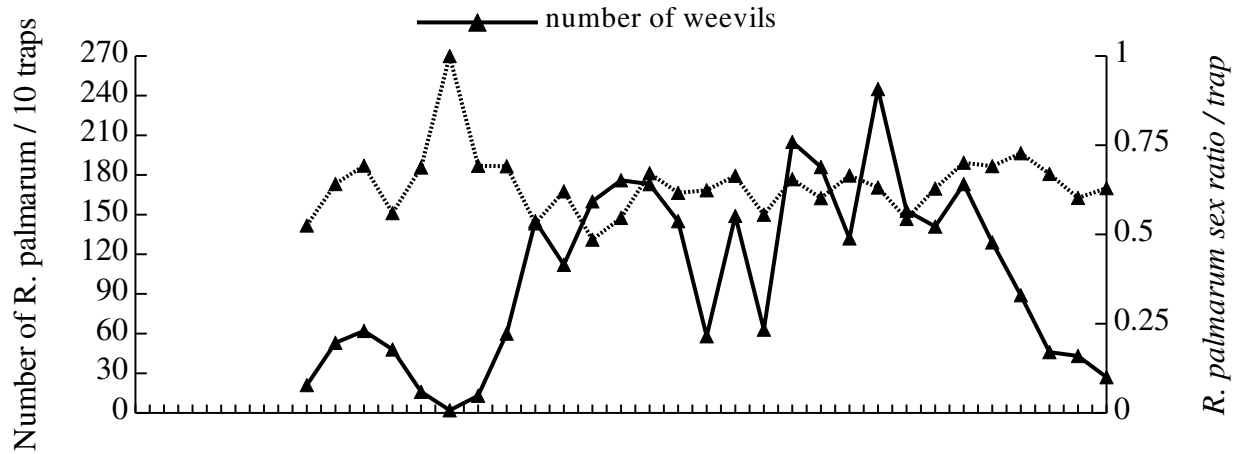


571

572 **Figures 1–2.** *Rhynchophorus palmarum* male infested with phoretic uropodine mites on (1)

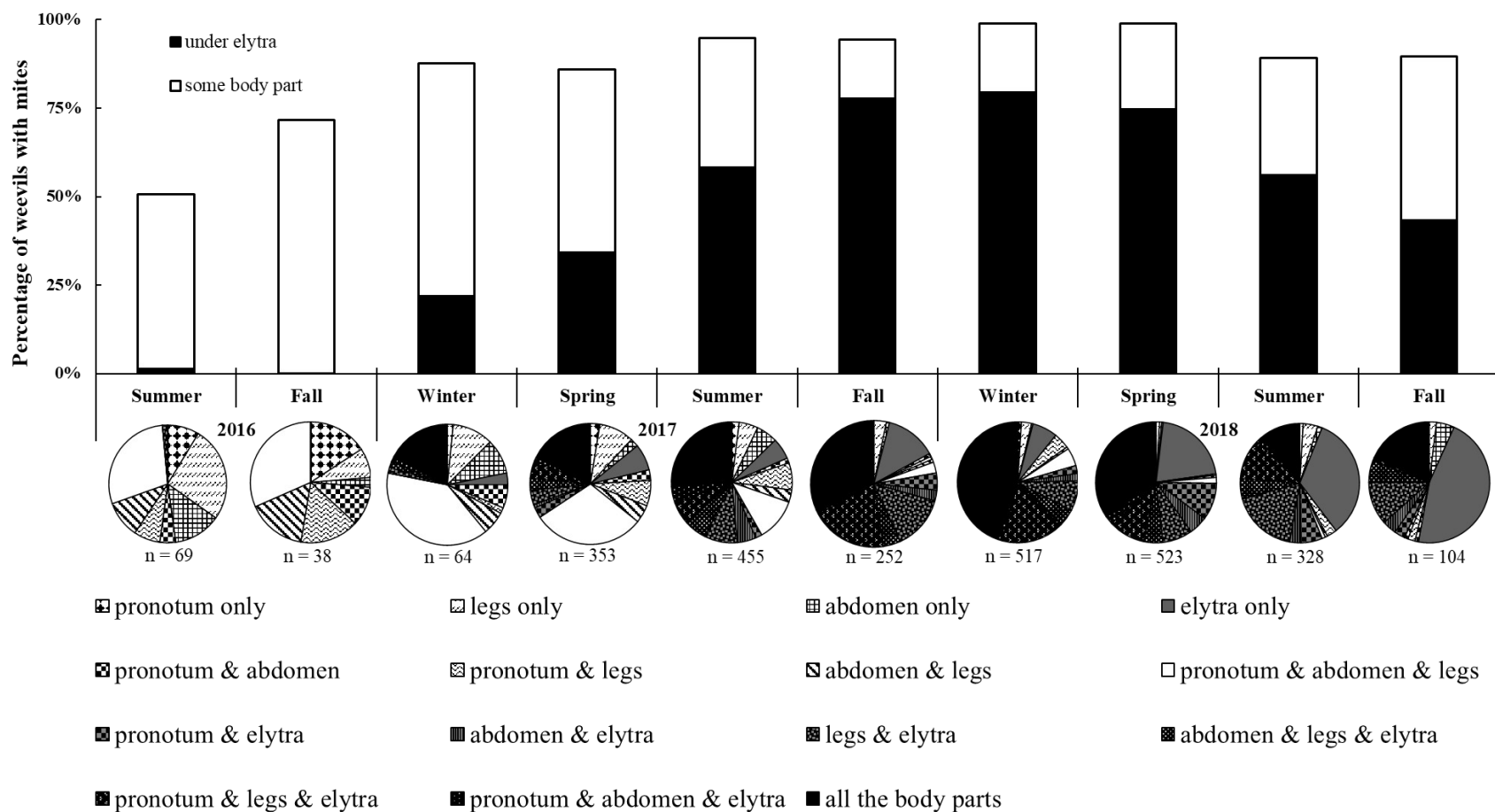
573 ventral side including underneath wing elytra and (2) lateral view of head, pronotum, and

574 foreleg.



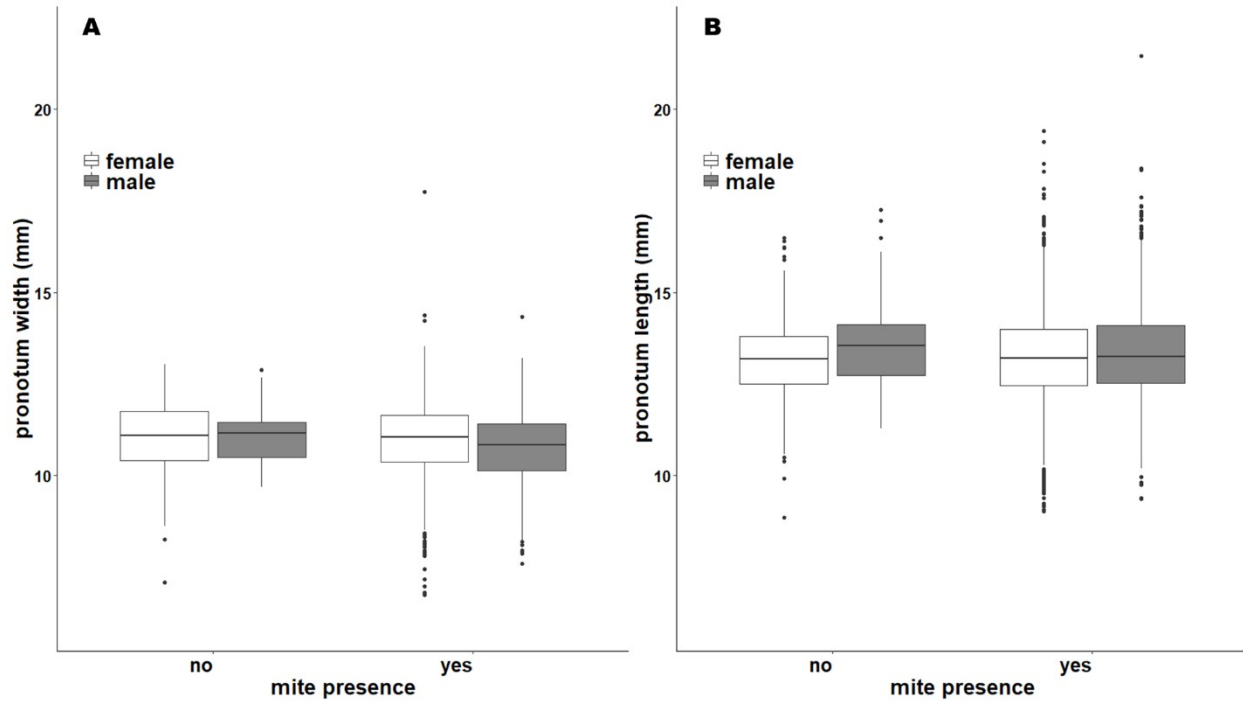
575

576 **Figure 3.** *Rhynchophorus palmarum* population dynamics and proportion of captured females
 577 (sex ratio) in the Sweetwater Recreational Reserve, Bonita, San Diego County, California, USA
 578 from July 2016 to December 2018. The total number of weevils was calculated as the sum of 10
 579 traps per month and the average sex ratio was calculated (females/total number of male and
 580 female weevils captured) for each trap with weevils.



581

582 **Figure 4.** Percentage of *Rhynchophorus palmarum* infested with mites, and proportion of mites on each body part. Bars show the
 583 percentage of weevils with mites detected on some part of the body (excluding elytra) and black areas correspond to the percentage of
 584 weevils with (one or more) mites under elytra (other body parts not excluded). Pie charts represent the percentage of weevils infested
 585 with mites on different parts of the body (“n” indicates the number of weevils with mites within each season by year).



586

587 **Figures 5.** *Rhynchophorus palmarum* A) pronotum width and B) pronotum length (mm \pm SE)
 588 for females and males that were infested and not infested with phoretic mites in 2017 and 2018
 589 (uninfested females n=121 and uninfested males n=50, infested females n=1595 and infested
 590 males n=1001).



591
 592 **Figures 6–11.** Phoretic mites (uropodine deutonymphs) found on *Rhynchophorus palmarum*
 593 collected in Fall of 2016, 2017, and 2018 in Sweetwater Recreational Reserve, Bonita, San
 594 Diego County in California, USA. Dorsal (6, 8, 10) and ventral (7, 9, 11) views of
 595 *Centrouropoda* n. sp. (6, 7), *Fuscuropoda marginata* (8, 9), and *Dinychus* n. sp. (10, 11) (this
 596 species may represent a new genus). Scale bars are 100 μ m.