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Phoretic mite assemblage of the pinyon pine beetle, *Ips confusus* (Curculionidae: Scolytinae), in Arizona

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Original research

ABSTRACT

Mites are among the most common associates of bark beetles and they can influence the ecology and microbial composition within bark beetle-colonized trees. The pinyon pine engraver, *Ips confusus* is a common beetle in pinyon trees in the southwestern United States, but the mite composition associated with this beetle has been little studied. In this study, we quantify the abundance, diversity, and attachment locations of phoretic mites on *Ips confusus* that emerge from naturally infested trees. In total, we observed 342 beetles for mites, 95% of which had at least one mite. We collected a total of 5842 mites, representing seven families and seven species: *Cercoleipus coelonotus* (Cercomegistidae) *Dendrolaelaps quadrisetosimilis* (Digamasellidae), *Ereynetes propescutulis* (Ereynetidae), *Iponemus confusus confusus* (Tarsonemidae), *Mexecheles* cf. *virginiensis* (Cheyletidae), *Proctolaelaps subcorticalis* (Melicharidae), and *Trichouropoda californica* (Trematuridae). We calculated the average number of mites per beetle to be 18, with a maximum of 147 mites on a single beetle. The vast majority of mites (98% of total abundance) was represented by three species (*I. c. confusus*, *D. quadrisetosimilis*, and *T. californica*). Attachment locations on the beetle varied across mite species, with mite species exhibiting a preference for specific locations. Mite abundances on emerging host beetles varied over time, with some species occurring mostly on early-emerging beetles, while others occurred on later emerging beetles.

Keywords Acari; bark beetle; phoresy; piñon pine; *Pinus edulis*; *Iponemus*; *Dendrolaelaps*; *Trichouropoda*

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Introduction

The pinyon pine beetle, *Ips confusus* (LeConte) (Coleoptera: Curculionidae) commonly known as the pinyon Ips or pinyon pine engraver is a pest of pinyon pine (*Pinus edulis* and *P. monophylla*) as well as other pine species (Furniss and Carolin 1977, USDA 2003). The beetle lives in northern Mexico and the western United States (U.S.) from southern California west to Texas and north into Wyoming (Wood and Bright 1982). Beetles of this species target the phloem and cambium layers of the tree which is where they mate, feed, lay eggs and complete their larval development (Wood 1982, Eager 1999). The tunneling behavior of beetles and resulting reduction in phloem reduces resources for the tree, and ultimately may lead to tree death (Raffa *et al.* 2008, 2015). In most of its range, the pinyon pine engraver has 3–4 generations per year, and during winter months adult beetles congregate under the bark and feed at the base of pinyon trees (Chansler 1964, Cognato 2015).

Pinyon forests of the southwest U.S. have suffered greatly from pinyon pine engraver outbreaks (Wilson & Tkacz 1992, Floyd *et al.* 2009, Santos and Whitham 2010, Kleinman *et al.*

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2012, Wion *et al.* 2022). High stand density, drought stress and mistletoe infections increase susceptibility to pinyon pine engraver by causing trees to have reduced defenses (Wilson and Tkacz 1992, Negron and Wilson 2003). Although the pinyon pine engraver have caused significant tree mortality over large areas of the southwestern U.S., little is known about their phoretic mite composition (Lindquist and Bedard 1961, Lindquist 1969, Boss 1970).

A phoretic relationship is one in which one organism uses another primarily for transport, with typically no other direct interactions (Evans and Proctor 1999, Seeman and Walter 2022). The pinyon pine engraver, similar to many other bark beetles, is associated with a broad assemblage of mites (Kinn and Witcosky 1978, Moser *et al.* 2010, Hofstetter *et al.* 2013, 2015). As beetles enter the bark and phloem of a tree, mites detach from beetles (Pfammatter *et al.* 2016b) and colonize the beetle galleries and surrounding tissues (Klepzig and Hofstetter 2011, Hofstetter *et al.* 2015). The life history and feeding ecology of bark beetle-associated mites vary across mite species and even life stages and includes fungivores; detritivores; omnivores; predators of mites, nematodes or insects; parasites and parasitoids (Lindquist 1970, Walter and Proctor 1999, Seeman and Walter 2022). The symbiotic relationships between mites and their hosts can vary from beneficial to detrimental; however, our knowledge of the exact nature of these relationships is largely incomplete (Hofstetter *et al.* 2015). Many mites have short generation times and can have multiple generations during the time it takes for bark beetles to complete development. When the next generation of beetles emerges from the host tree, they carry with them a new generation of mites, dispersing to new trees (Hofstetter *et al.* 2015).

Bark beetle mites have been surveyed worldwide (e.g., Takov *et al.* 2009, Hodgkin *et al.* 2010, Čejka and Holuša 2014, Khaustov *et al.* 2018, Milosavljević *et al.* 2022); however, despite the ubiquity of these mites our understanding of the mites associated with the pinyon pine engraver is limited (e.g. Boss 1970). Herein, we describe the mite species composition and attachment location of phoretic mites associated with the pinyon pine engraver emerging from naturally infested pinyon trees in northern Arizona. Additionally, we characterize the phoretic mite species patterns over the entire emergence window of bark beetle brood from these trees.

Material and methods

We located two pinyon pine (*Pinus edulis*) trees naturally infested with the pinyon pine engraver (*Ips confusus*) southeast of Flagstaff Arizona (35.0815, -111.4153; elevation 2080m, October 2020). Prior to beetle emergence, we cut trees into 0.5m logs (20–25cm diameter) and placed them into rearing containers in the laboratory. We stored logs at 25°C and 50% relative humidity. Beetles started emerging 12 days after the trees were cut. We collected emerging beetles daily, placed them into individual gel capsules (Capsoline Co., size 1) and stored them at -5°C to immobilize the mites on the beetle. We examined a subset (37.7%, 342 of 850 total beetles that emerged) of pinyon pine engraver beetles over the entire emergence period for phoretic mites using a stereoscope (Meiji SMD-5TR), and we quantified any mites that fell off the beetle and into the gel capsule. We recorded and quantified mite attachment location on the beetle (head, ventral pronotum and legs, dorsal thorax, ventral abdomen, on elytra and elytra declivity, under elytra, in gel capsule (Figure 1)) of all mites. We mounted mites on glass slides with a drop of lactophenol (MilliporeSigma™ Fisher Scientific) and placed them on heat (35°C) for 24 hours. We mounted voucher specimens in polyvinyl alcohol medium (6371A, BioQuip Products, Rancho Dominguez, California, USA) and cured them on a slide warmer at 40°C for 3–4 days. We stored slide-mounted voucher specimens in the personal collection of W. Knee, and information and images are on the online database Symbiota. Other insects that emerged from the infested trees include *Aulonium* sp. (Coleoptera: Colydiidae), *Hypophoeus* sp. (Coleoptera: Tenebrionidae), *Pityophthorus* sp. (Coleoptera: Curculionidae), and *Temnochila chlorodia* (Coleoptera: Trogoxetidae). The phoretic mites of these other insects are not presented in this study.

We performed chi-square tests to determine whether mites exhibited a significant preference for specific attachment locations on host beetles (R Statistical test: `chisq.test(table(locations,`

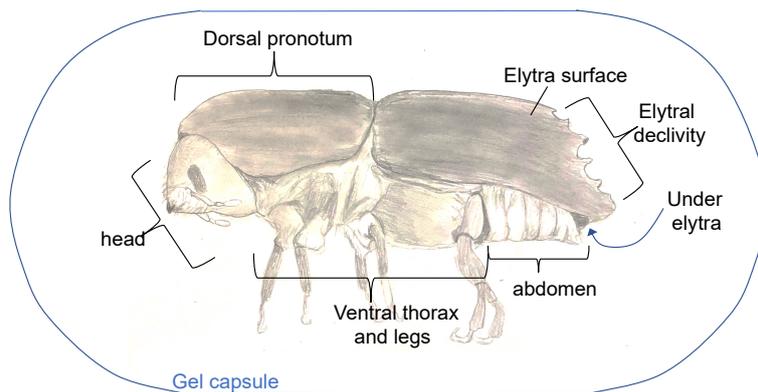


Figure 1 Attachment locations of phoretic mites on the pinyon pine engraver *Ips confusus* and gel capsule. Drawing by E.M.H.

mites))). We performed tests for correlations among mite species found on the beetles (R Statistical test: `chisq.test(mite1, mite2...)`). We performed ANOVA tests on phoretic mite abundances (total and by mite species) across time periods to determine significant difference in abundance across beetle emergence (R Statistical test: `model <- lm(abundance ~ time; anova(model))`). We excluded *Proctolaelaps subcorticalis* from statistical tests due to low abundance and incidence. We performed all tests using R Statistical Software v.2.15.3 (<http://www.R-Project.org>).

Results

A total of 5,842 mites from 342 beetles were collected, representing seven species and seven families (Figure 2): *Cercoleipus coelonotus* Kinn (Cercomegistidae), *Dendrolaelaps quadrisetosimilis* Hirschmann (Digamasellidae), *Ereynetes propescutulis* Hunter & Rosario (Ereynetidae), *Iponemus confusus confusus* Lindquist (Tarsonemidae), *Mexeches* cf. *virginiensis* (Baker) (Cheyletidae), *Proctolaelaps subcorticalis* Lindquist (Melicharidae), and *Trichouropoda californica* Wisniewski & Hirschmann (Trematuridae). Mites were found on 95% of beetles and average abundance was 18 (± 16 std dev) mites per beetle (Figure 3). The highest abundance on a single beetle was 147 mites, with 131 of these mites being *I. c. confusus*. Three mite species (*I. c. confusus*, *D. quadrisetosimilis*, and *T. californica*) made up 98.4% of all phoretic mites. Histograms of these three mite species show that they varied slightly from each other in their abundances on beetles (Figures 4a-c).

Most mite species exhibited a significant preference for specific attachment locations (Figure 1) on beetles (Table 1) (p -values < 0.01 for each mite species). In general, 47.5% of all mites were located on the elytral declivity, 22.9% were under the elytra, and 11.8% were on the ventral thorax (coxa area). A sizeable portion of mites (16.6%) were found in the gel capsule (Table 1). Excluding mites collected in the gel capsule, 92% of all *D. quadrisetosimilis* were found under the elytra, 92% of *I. c. confusus* were on the elytra declivity, while 39% and 55% of *T. californica* were collected on the ventral thorax and elytra declivity, respectively. *Ereynetes propescutulis* were more dispersed than other mite species, being collected in multiple locations on the beetle (30% on elytra declivity, 12.5% under the elytra and 12.5% on the dorsal thorax) and gel capsule (37.5%). Three species (*C. coelonotus*, *M. virginiensis*, *P. subcorticalis*) were found predominantly in the gel capsules rather than on the host beetles.

Mite abundances on emerging beetles varied over time (Figure 5, $F_{10,320}=9.68$, $p<0.01$) as well as across mite species (Figure 6). Combined across all mite species, abundance per beetle

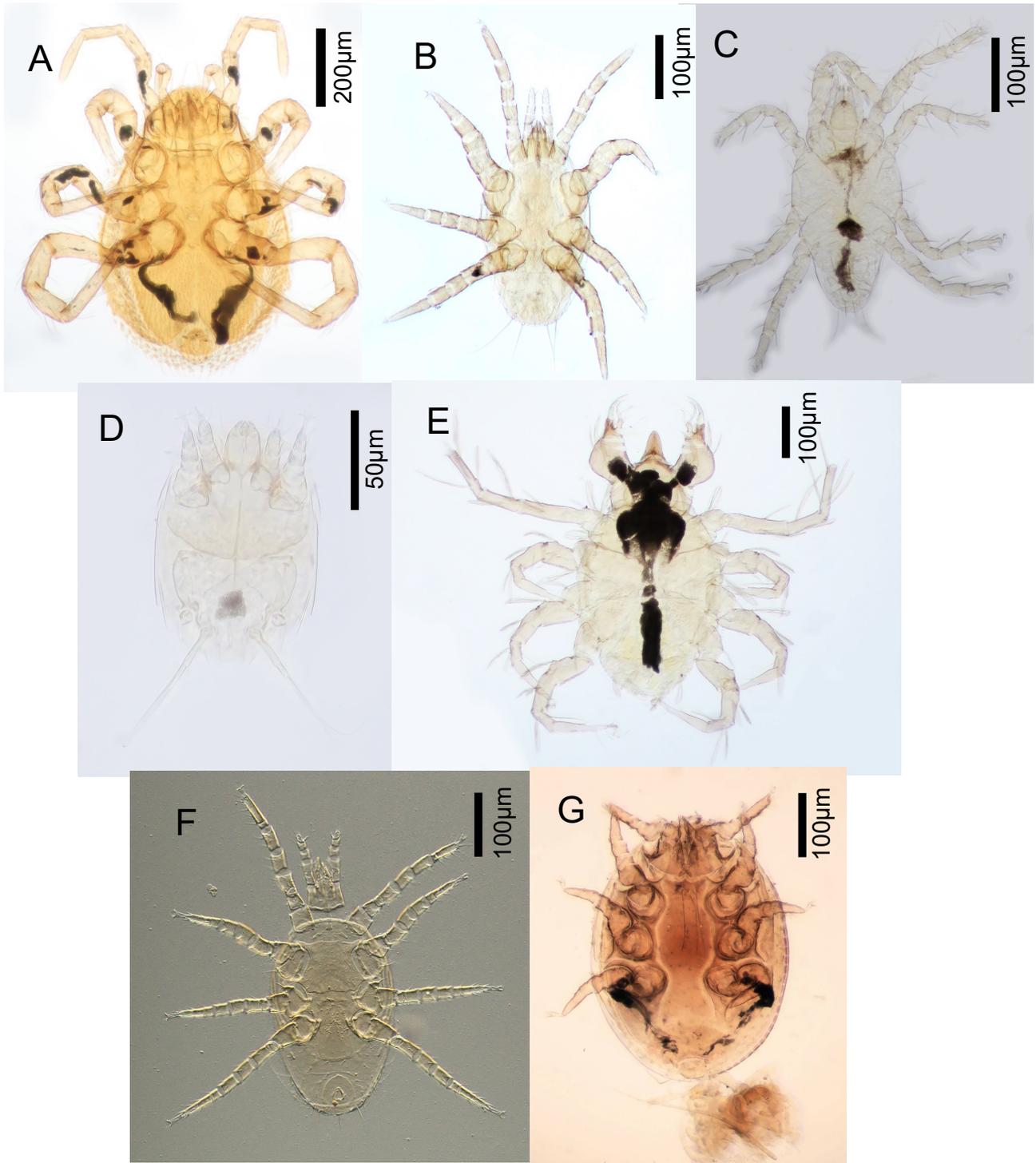


Figure 2 Phoretic mites of *Ips confusus*. A – *Cercoleipus coelonotus*, B – *Dendrolaelaps quadrisetosimilis*, C – *Ereynetes propescutulis*, D – *Iponemus confusus confusus*, E – *Mexecheles* cf. *virginensis*, F – *Protolaelaps subcorticalis*, G – *Trichouropoda californica*.

was low at the start and end of the beetle emergence interval, but consistently high otherwise (Figure 5). Some species (e.g., *I. confusus*, *D. quadrisetosimilis*, and *E. propescutulis*) were most abundant early during beetle emergence, while other species (e.g., *T. californica*, *P. subcorticalis*, and *M. cf. virginensis*) were most abundant later during emergence (Figure 6).

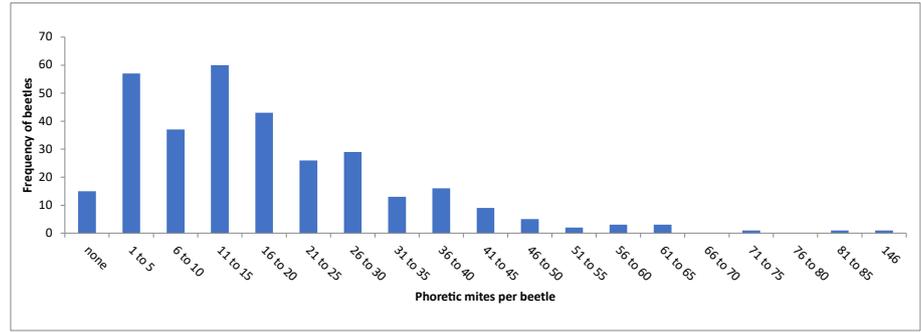


Figure 3 Histogram of all mites (x-axis: number of mites on beetles, placed into number groups) and number of pinyon pine engravers (y-axis: number of beetles with phoretic mites based on groups in x-axis).

Cercoleipus coelonotus abundances were constant across the emergence period (Figure 6).

Some mite species were weakly correlated with other mite species (Table 2). The presence of *M. cf. virginiensis* was negatively correlated with all other mite species, except *T. californica*. *Iponemus c. confusus* was weakly positively correlated with *D. quadrisetosimilis*, and *C. coelonotus* was weakly positively corrected with *E. propescutulis* and *T. californica*.

Table 1 Abundance, prevalence, and attachment location of phoretic mites associated with adult pinyon pine beetles, *Ips confusus*.

Mite species	Mite total abundance	Mite prevalence (%)	Attachment location (%)						
			head	Dorsal pronotum	Ventral thoxas	Ventral abdomen	Elytral surface	Under elytra	Gel capsule
<i>Cercoleipus coelonotus</i>	21	6.9	0	4.8	0	0	19	0	76.2
<i>Dendrolaelaps quadrisetosimilis</i>	1963	86.6	0.2	1.4	0.7	0.1	3.2	61.8	32.6
<i>Ereynetes propescutulis</i>	42	6.2	0	5	12.5	2.5	30	12.5	37.5
<i>Iponemus confusus</i>	2210	64.5	0	4.4	0.1	0	85.8	2.8	6.9
<i>Mexecheles cf. virginiensis</i>	6	2.8	0	0	0	0	0	0	100
<i>Proctolaelaps subcorticalis</i>	11	1.6	0	27.3	0	0	9.1	9.1	54.5
<i>Trichouropoda californica</i>	1573	52.6	0	35.8	0.3	2.4	50.8	2.5	8.1
Total	5842	95	0.1	11.8	0.4	0.7	47.5	22.9	16.6

Table 2 Pearson’s correlation coefficients of mite species abundances on the pinyon pine beetle *Ips confusus*. The mite, *Proctolaelaps subcorticalis*, is removed from the analyses because of low abundances.

Phoretic mite species	<i>C. coelonotus</i>	<i>D. quadrisetosimilis</i>	<i>E. propescutulis</i>	<i>I. c. confusus</i>	<i>M. cf. virginiensis</i>	<i>T. californica</i>
<i>Cercoleipus coelonotus</i>	1					
<i>Dendrolaelaps quadrisetosimilis</i>	0.019	1				
<i>Ereynetes propescutulis</i>	0.172	-0.002	1			
<i>Iponemus confusus</i>	-0.031	0.252	0.113	1		
<i>Mexecheles cf. virginiensis</i>	-0.035	-0.145	-0.022	-0.079	1	
<i>Trichouropoda californica</i>	0.156	0.029	-0.06	-0.169	0.025	1

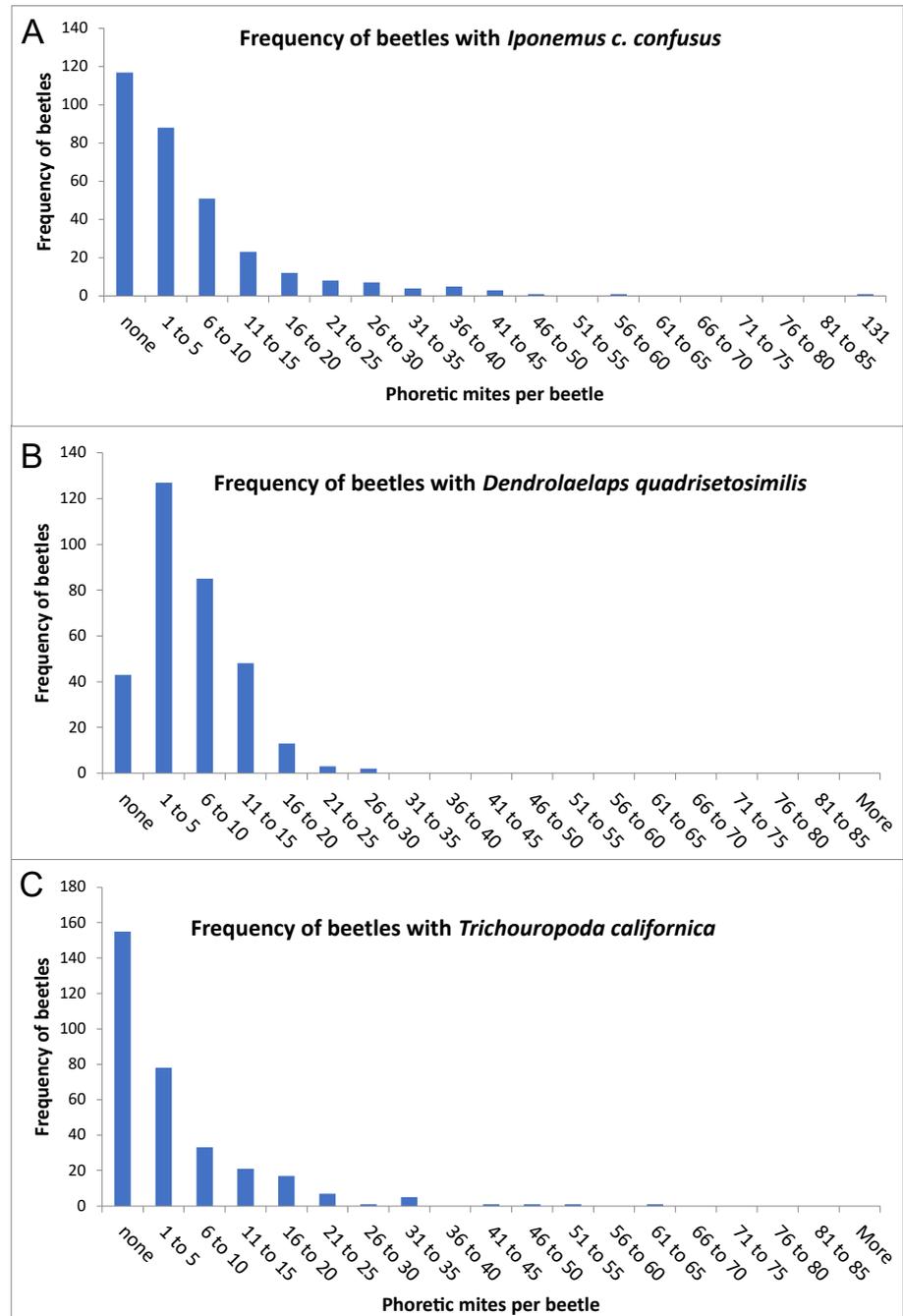


Figure 4 Histograms of the three most abundant phoretic mites (x-axis: numbers of phoretic mites on a beetle) and number of pinyon pine engraver beetles (y-axis: number of beetles with those numbers of mites). A – *Iponemus confusus confusus* mite abundance on beetles; B – *Dendrolaelaps quadrisetosimilis* mite abundance on beetles, and C – *Trichouropoda californica* mite abundance on beetles.

Discussion

The number of phoretic species found on the pinyon pine engraver, *Ips confusus*, in this study is typical for the number of beetles observed compared to other bark beetle species (Moser *et al.* 2005, Pernek *et al.* 2008, Milosavljević *et al.* 2022). However the abundance of phoretic mites per beetle and percent beetles with mites was higher than most studies (Moser 1976, Pernek *et al.* 2008, Cilbircioğlu *et al.* 2021). This is not unexpected as we collected beetles emerging

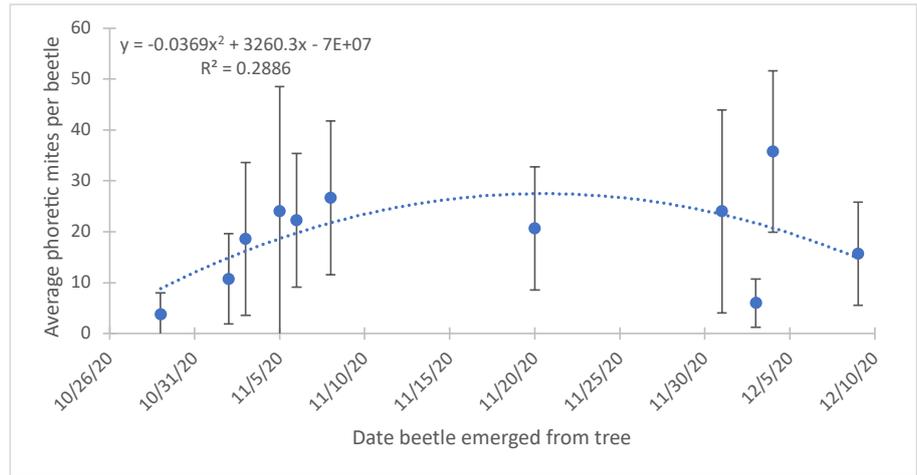


Figure 5 Mean phoretic mite abundance (all mite species combined) per pinyon pine engraver beetle over time (ANOVA, $p < 0.01$). Date (x-axis) represents the day the beetle emerged from the infested tree. Bars represent standard deviations.

directly from logs as opposed to flight traps. This implies that a high proportion of mites fall off beetles during flight or that the lab conditions promoted high mite abundances. Although we only collected beetles from two trees, previous studies looking at phoretic mite-bark beetle systems have shown that intensive sampling of a single tree will reveal most or all of the common mite species, although uncommon associates may be missed (Moser and Roton 1971, Moser and Bogenschütz 1984, Moser *et al.* 1997).

The most frequently encountered genera in this study (*Iponemus*, *Dendroctonus*, *Trichouropoda*) are also some of the most common genera associated with other *Ips* species in North America (Hofstetter *et al.* 2013; Knee *et al.* 2013, Pfammatter *et al.* 2013); however, some of the other frequently collected species and genera such as *Histiostoma* or *Elattoma* on *Ips* species (Pfammatter *et al.* 2013, 2016a) were not encountered. Five of the seven mite species collected in this study are predators and of the other two species, one is a parasitoid (*Iponemus* primarily feeding on bark beetle eggs, Lindquist 1969) and the other is a generalist omnivore (*Trichouropoda*, Pfammatter *et al.* 2013). Thus, the only mite species found in this

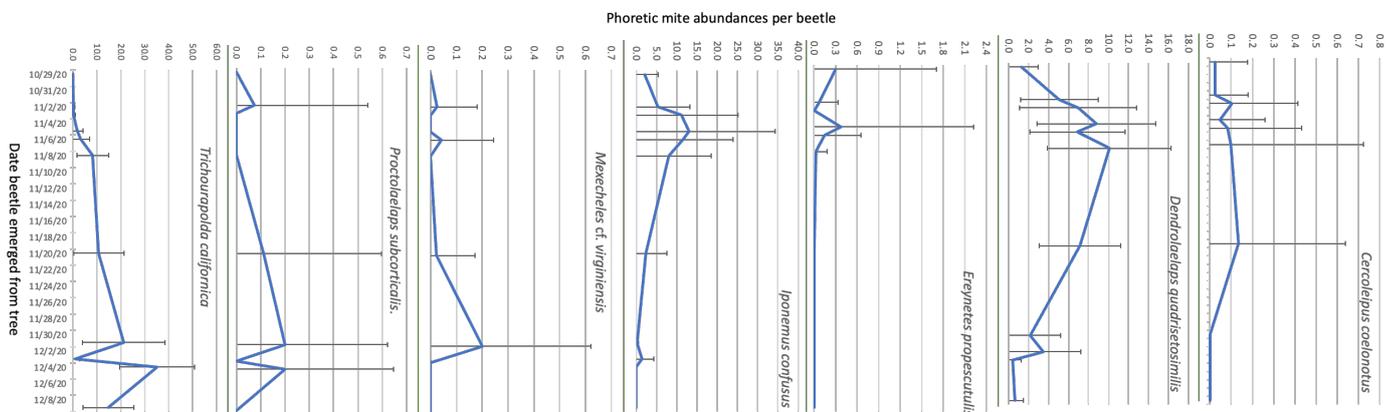


Figure 6 Phoretic mite intensities over time for each mite species found on the pinyon pine engraver, *Ips confusus*.

study that feeds on microbes, such as fungi and bacteria, is *Trichouropoda californica*. The hot, dry habitat of pinyon pine forests might not be conducive to high levels of fungi and decay under beetle-infested bark needed to support mycophagous mites, unlike other pine forest habitats. This explains the lack of common bark beetle-mite genera such as *Histiogaster*, *Histiostoma*, and *Tarsonemus* that rely on fungi for food. The heavy predatory mite composition found on the pinyon pine engraver differs from most bark beetle-mite systems, where feeding guilds are evenly represented across mite species (Pfammatter *et al.* 2016a; Hofstetter *et al.* 2015).

Distribution of phoretic mite species on the pinyon pine engraver was nonrandom (Table 1), with species showing a preference for specific attachment locations on the host beetle. *Iponemus c. confusus* was primarily located on the elytra declivity, presumably to avoid being rubbed off during beetle tunneling. *Iponemus c. confusus* and *T. californica* were rarely found in the gel capsule, meaning they did not easily dislodge from the host beetle after collection. Uropodines, like *T. californica*, attach to their host by gluing onto their host with an anal pedicel, (Wayne *et al.* 2013) which likely explains their relatively low occurrence in the gel capsule. *Trichouropoda californica* was primarily found on the elytra and the dorsal pronotum, which are two areas of high surface area with relatively few moving parts. *Dendrolaelaps quadrisetosimilis* was found underneath elytra, which may provide protection from predators and mechanical removal during beetle tunneling and flight. *Dendrolaelaps* and *Proctolaelaps* lack specialized structures for phoretic dispersal, which may be why many *Proctolaelaps* were found in the gel capsule and *Dendrolaelaps* under the elytra (Knee *et al.* 2012, Milosavljević *et al.* 2022). *Ereynetes propescutulis* were found on various locations on the beetle and in the gel capsule, which may be due to a lack of specialized adaptations for phoresy in this species (Khaustov *et al.* 2018). *Ereynetes propescutulis* is also the fastest and most mobile mite found in this study (Fernández *et al.* 2013). *Cercoleipus coelonotus* was one of the larger species found, which is a likely cause of it being primarily found off the beetle (Kinn 1970), with 76% of them in the gel capsule. Only six *Mexechesles virginiensis* were found, all in the gel capsules. This species is a mobile predator and is fairly large, so it is to be expected that it would easily fall off and therefore be found in the gel capsule. This species, as well as other species with low frequency, may not be well adapted for phoresy, and their densities may be higher in beetle galleries than suggested by their phoretic abundance.

Mite species varied in their emergence (i.e., presence on emerging beetles) over time. Two of the three most abundant mite species (*I. c. confusus* and *D. quadrisetosimilis*) typically occurred on early emerging beetles, the exception being *T. californica* which become more common on emerging beetles over time (Figure 6). Almost all of the *E. propescutulis* mites exited early in beetle emergence. Some of the larger mites (e.g., *Mexechesles cf. virginiensis* and *T. californica*) tended to occur on beetles emerging late. When combining all mite species, the phoretic mite abundance per beetle was consistently high except for the beginning and end of beetle emergence (Figure 5), suggesting that early emerging beetles have few phoretic mites and may result in higher fecundity if they reach new host trees. The low phoretic mite rates at the end of beetle emergence could suggest that most mites have found phoretic hosts and that few mites remain in the galleries.

Five mite species (*C. coelonotus*, *D. quadrisetosimilis*, *E. propescutulis*, *M. cf. virginiensis*, and *P. subcorticalis*) out of the seven found in this study are predatory, which depending on the type of predation can be either beneficial or harmful to the pinyon pine engraver. Additionally, the mite *Iponemus c. confusus* is a beetle egg and 1st-instar larval parasitoid that is harmful to beetles (Pfammatter and Raffa 2015), although we do not know what this mite feeds on once beetles have reached later larval stages. *Proctolaelaps subcorticalis*, *Dendrolaelaps quadrisetosimilis*, and *Mexechesles cf. virginiensis*, which predate beetle eggs and larvae feed on other organisms such as nematodes that could be parasitic on beetles (Moser 2005, Hofstetter *et al.* 2015). Such interactions could result in a positive effect on pinyon pine engraver fitness (Wegensteiner *et al.* 2015). Additionally, Kinn (1983) suggests that *Proctolaelaps* may primarily be a nematode feeder, further benefiting beetles. In any case, several studies have found that predation by mites can cause beetle egg mortality of up to 90% (Moser *et al.* 1978).

High phoretic loads can also negatively affect beetle flight by interfering with and adding drag during beetle flight (Kinn & Witcosky, 1978). Interestingly, only one mite species (*T. californica*) associated with the pinyon pine engraver feeds upon fungi which is indicative of the low levels of fungi associated with this beetle in pinyon. The dry and hot temperatures may limit growth and diversity of fungi within beetle-infested pinyon trees.

In conclusion, this survey is the first to quantify the abundance, diversity and phoretic locations of phoretic mites on the pinyon pine engraver. Emerging beetles had high phoretic mite loads and densities, likely resulting from their collection directly from tree material, rather than from flight traps. Only two trees were sampled and thus we suggest further sampling both temporally across seasons and geographically across the pinyon pine distribution. Further studies are also needed regarding microbial composition and fungal association with the pinyon pine engraver in pinyon pine.

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