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CAUGHT BETWEEN A ROCK AND A HARD MINERAL ENCRUSTATION: LONG-LIVED AQUATIC INSECTS ACCUMULATE CALCIUM CARBONATE DEPOSITS IN A MONTANE DESERT STREAM

Eric K. Moody¹, Jessica R. Corman^{1,2}, and Michael T. Bogan³

ABSTRACT.—Aquatic ecosystems overlying regions of limestone bedrock can feature active deposition of calcium carbonate in the form of travertine or tufa. Although most travertine deposits form a cement-like layer on stream substrates, mineral deposits can also form on benthic invertebrates. However, little is known about which taxa may be prone to calcium carbonate encrustation and which life history traits may make taxa more susceptible to becoming encrusted. Here we report the presence of calcium carbonate deposits on live insects collected from a montane stream in the Madrean Sky Islands (Huachuca Mountains) of Arizona between 2011 and 2013. Life history differences are examined between taxa with and without travertine deposits. Thirteen genera of aquatic insects were found with calcium carbonate deposits on the exoskeleton as well as 22 other genera, also encountered in the study stream, that have not previously been found with such deposits. Taxa with calcium carbonate encrustation had significantly longer-lived aquatic stages than those without encrustation. Furthermore, encrustation presence did not differ among aerial dispersal modes. These results suggest that the extent of calcium carbonate deposition on aquatic insects is primarily related to the length of time they are in the stream. Since mineral encrustation may reduce predation pressure and mobility, changes in patterns of travertine formation in these systems may have profound effects on ecological interactions.

RESUMEN.—Los ecosistemas dulceacuícolas ubicados en regiones de roca caliza pueden contener depósitos de carbonato de calcio en forma de travertino o tufa. Aunque muchos depósitos de travertino se encuentran como una capa o manto de cemento sobre el fondo del arroyo, los depósitos también pueden formarse sobre los invertebrados bentónicos. Sin embargo, poco se sabe acerca de las especies que son propensas a los depósitos de travertino, o acerca de las características de estas especies que influyen en tal proceso. En este manuscrito reportamos la presencia de depósitos de travertino en insectos vivos y recolectados en un arroyo montañoso en el Archipiélago Madreño de Arizona durante 2011–2013 y examinamos las diferencias en las historias de vida entre taxones con o sin depósitos de travertino. Encontramos trece géneros de insectos acuáticos con travertino sobre el exoesqueleto y vintidos géneros sin travertino. Los taxones con travertino tienen una fase acuática significativamente más larga que los taxones sin travertino. Además, la presencia de travertino no difirió entre especies con distintas maneras de dispersión aérea. Estos resultados sugieren que las diferencias en los depósitos de travertino en insectos acuáticos ocurren principalmente a causa de la duración del período de vida acuática del insecto. Aunque los depósitos de travertino pueden reducir la presión por depredación y movilidad, cambios en los patrones de formación de travertino en estos sistemas pueden afectar profundamente las interacciones ecológicas.

Calcium carbonate minerals such as travertine are common in aquatic ecosystems worldwide (Pentecost 2005). Travertine, as defined by Pentecost (2005), is a chemically precipitated limestone formed in aquatic systems principally when the water is supersaturated with calcium carbonate. In western North America, travertine precipitation is common in areas with limestone bedrock, including Arizona (Marks et al. 2006, Limburg et al. 2013), California (Rundio 2009), Nevada (Hay et al. 1986), New Mexico (Goff and Shevenell 1987), and throughout Mexico (Minckley 1968, Whitacre 1989, Beltrán-Magos et al. 2013). Travertine systems often differ from nearby water bodies

that lack travertine because of their unique physical and biogeochemical environment (Otsuki and Wetzel 1972, Kock et al. 2006, Marks et al. 2006, Corman et al. 2015). One way travertine deposition can impact stream ecosystems is by forming a coating on organic matter, such as leaves and wood, potentially altering rates of decomposition and downstream transport (Casas and Gessner 1999, Compson et al. 2009, Harrop et al. 2009). Although various studies report that the formation of such deposits on detrital organic matter is widespread in travertine streams, the prevalence of deposits on living organisms, especially insects, remains underreported in the literature.

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Calcium carbonate (CaCO_3) deposition on aquatic organisms is influenced by autotrophic growth. Photosynthesis drives CaCO_3 deposition in some systems, and many primary producers in travertine streams and springs form calcified growths (Beltrán-Magos et al. 2013, Brusa and Cerabolini 2009, Pentecost 1996). CaCO_3 deposition can also occur on and be promoted by the activities of some macro-invertebrates. Brown (1972), referring to riffle beetles, described “the stony encrustation which covers the beetles in waters of high mineral content.” Calcareous deposits have also been reported on amphipods, fly larvae, stoneflies, and aquatic mites (Krüper 1930, Minckley 1963, Durrenfeldt 1978, Ruff and Maier 2000). Additionally, certain hydropsychid caddisflies are known to influence deposition of travertine through their construction of silken nets, which collect organic material and provide surface area for travertine deposition (Drysedale 1999, Paprocki et al. 2003). However, these observations are limited in geographical extent (e.g., streams in Kentucky, [Minckley 1963], Germany [Durrenfeldt 1978, Ruff and Maier 2000], Australia [Drysedale 1999], and Venezuela [Paprocki et al. 2003]). Further, the full taxonomic extent of CaCO_3 encrustation on live insects remains under-reported, and the factors influencing the prevalence of such deposits are largely unknown.

From what is known about CaCO_3 deposition on live insects, a few conclusions can be made about what affects this process. Travertine deposits are common on sedentary detrital and organic substances (Casas and Gessner 1999, Paprocki et al. 2003), so it is likely that long-lived species, particularly those with sedentary periods, may be most prone to encrustation. However, some fly larvae have been found with CaCO_3 encrustation on certain body parts, particularly dorsal regions with setae that may serve as sites for encrustation (Durrenfeldt 1978, Ruff and Maier 2000). Thus the presence of certain structures and/or certain regions of the body may lead to interspecific differences in the presence of encrustation. These encrustation differences may also be due to varying life histories. Long-lived larval instars and infrequent aerial dispersal are 2 nonmutually exclusive life history characteristics that may result in some insects being more subject to encrustation than others. Because molting would likely serve as a method

to cleanse the exoskeleton of any encrusted deposits, insects with long-lived immature instars and/or aquatic adult stages, such as some caddisflies and true bugs (Gray 1981, Lytle 2002), may be particularly susceptible. In contrast, groups such as mayflies, which are characterized by rapid development and large numbers of short-lived larval instars, may not maintain the same exoskeleton for sufficient time to allow CaCO_3 encrustation to develop in any significant quantity (Fink 1980). Still, groups with long-lived life stages may not become encrusted if they spend time in the terrestrial environment or frequently move between calcifying and noncalcifying aquatic habitats. Many long-lived aquatic beetles frequently disperse aerially (Bogan and Boersma 2012) and thus may not accumulate high levels of encrustation. These insects may also face higher selective pressure to prevent CaCO_3 encrustation, as it could impair flight; whereas flightless adults and larval stages may not incur fitness costs from having an encrusted exoskeleton. Indeed, CaCO_3 encrustation has even been suggested to provide potential fitness benefits in some cases (e.g., Ruff and Maier 2000). If CaCO_3 deposition is a process selectively impacting some species more than others, changes in the rate or presence of travertine deposition in a stream could have dramatic effects on competitive interactions between species.

In this paper, we report CaCO_3 deposits on a variety of live insects from a travertine-depositing montane stream in southeastern Arizona. Life histories of species found with and without CaCO_3 deposits are compared to examine which organismal traits are related to the deposition of travertine on the exoskeleton. We predict that species with rapid growth and short aquatic stages will be less prone to CaCO_3 deposition than species with long-lived aquatic stages, particularly those that do not disperse aerially. Finally, we discuss potential ecological consequences of these findings for travertine stream food webs.

METHODS

Aquatic insect samples were taken from perennial reaches of Garden Canyon in the Huachuca Mountains of southeastern Arizona, where travertine is actively depositing. These mountains are primarily composed of limestone



Fig. 1. Insects encrusted with CaCO_3 in Garden Canyon, Huachuca Mountains, Arizona. Clockwise from top left: *Abedus herberti* (Belostomatidae), *Euparyphus* sp. (Stratiomyidae), *Oplonaeschna armata* (Aeshnidae), and *Ranatra quadridentata* (Nepidae). All photos by Eric Moody.

bedrock. As a result, perennial reaches of streams in the range are generally characterized by active travertine deposition (Bogan and Lytle 2011, Bogan et al. 2013a, Corman et al. 2015). We sampled aquatic insects 4 times in riffles and pools of Garden Canyon between 2009 and 2011 (methods outlined in Bogan et al. 2013a). Samples were preserved in 95% ethanol, which also preserved any CaCO_3 deposits present on insect exoskeletons. We identified insects to the lowest practical taxonomic level and noted whether any travertine encrustation was present on the exoskeleton. We assumed that all intact insects were alive at the time of collection. Designations of CaCO_3 encrustation on live insects were also supported by field observations of live organisms in the stream (Fig. 1).

We searched the peer-reviewed literature for life history information on species that did and did not exhibit CaCO_3 encrustation. In some cases, data were available for our study species; but in other cases, data for closely related species were used as the best available estimates (see Schriever et al. 2015). We chose to compare 2 traits: the lifespan of aquatic stages and aerial dispersal mode. These traits combined determine how long an individual organism is exposed to travertine-depositing

water, so we felt that they were the most relevant traits for our study. We defined aquatic lifespan as the amount of time the insect lives in the stream. For many taxa, aquatic lifespan includes a number of larval instars; but for beetles and true bugs, it also includes adults. For aerial dispersal ability, we used the 5 aerial dispersal modes identified by Bogan and Boersma (2012): (1) *widespread common* (flies far and frequently), (2) *widespread hap-hazard* (flies far but with lower frequency), (3) *range-restricted* (flies frequently over short distances), (4) *cue-limited* (only flies after rain-fall events), and (5) *infrequent* (flight events are rare). We also included an additional category of *none* for insects with only immature aquatic stages or insects that are flightless as adults.

To test whether the lifespan of aquatic stages differed between taxa with and without CaCO_3 encrustation, we used a two-tailed *t* test. We analyzed differences among taxa at the genus level, with the exception of Chironomidae which we combined into one taxon because we found no variation in CaCO_3 encrustation among genera. We used a natural logarithmic transformation on lifespan data because they were right-skewed. We used Q-Q plots and *F* tests to assess normality and

TABLE 1. Common taxa with and without CaCO₃ deposits in Garden Canyon, Huachuca Mountains, Arizona. Mayflies, caddisflies, and true flies are represented only as immatures; beetles are represented only as adults; and true bugs are represented as both immatures and adults. Bold letters after each taxon indicate aerial dispersal capability of aquatic life stages: CL = cue-limited, IN = infrequent, NO = none, WH = widespread haphazard.

With CaCO ₃	Without CaCO ₃
<i>Abedus herberti</i> (Belostomatidae) NO	<i>Acentrella</i> sp. (Baetidae) NO
<i>Argia</i> spp. (Coenagrionidae) NO	<i>Berosus</i> spp. (Hydrophilidae) CL
<i>Caloparyphus</i> sp. (Stratiomyidae) NO	<i>Boreonectes aequinoctialis</i> (Dytiscidae) WH
<i>Cordulegaster diadema</i> (Cordulegastridae) NO	<i>Buenoa</i> spp. (Notonectidae) IN
<i>Curicta pronotata</i> (Nepidae) IN	<i>Ecdyonurus</i> sp. (Heptageniidae) NO
<i>Euparyphus</i> sp. (Stratiomyidae) NO	<i>Erpetogomphus</i> sp. (Gomphidae) NO
<i>Helichus</i> spp. (Dryopidae) CL	<i>Eukiefferiella</i> sp. (Chironomidae) NO
<i>Helicopsyche</i> sp. (Helicopsychidae) NO	<i>Fallceon</i> sp. (Baetidae) NO
<i>Lethocerus medius</i> (Belostomatidae) IN	<i>Graptocorixa</i> spp. (Corixidae) CL
<i>Oplonaeschna armata</i> (Aeshnidae) NO	<i>Laccophilus</i> spp. (Dytiscidae) IN
<i>Phylloicus mexicanus</i> (Calamoceratidae) NO	<i>Notonecta</i> spp. (Notonectidae) IN
<i>Postelichus</i> spp. (Dryopidae) CL	<i>Parametriocnemus</i> sp. (Chironomidae) NO
<i>Ranatra quadridentata</i> (Nepidae) IN	<i>Polycentropus</i> sp. (Polycentropidae) NO
	<i>Rhantus</i> spp. (Dytiscidae) CL
	<i>Rheotanytarsus</i> sp. (Chironomidae) NO
	<i>Simulium</i> spp. (Simuliidae) NO
	<i>Tanytarsus</i> sp. (Chironomidae) NO
	<i>Thermonectus</i> spp. (Dytiscidae) CL
	<i>Thienemanniella</i> sp. (Chironomidae) NO
	<i>Tipula</i> sp. (Tipulidae) NO
	<i>Tropisternus</i> spp. (Hydrophilidae) WH
	<i>Wormaldia</i> sp. (Philopotamidae) NO

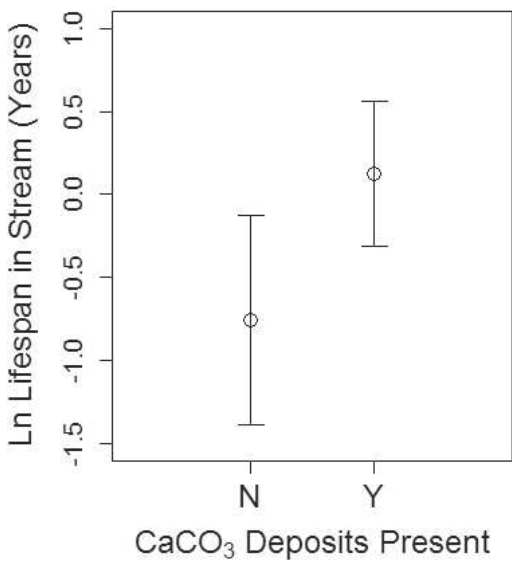


Fig. 2. Mean (± 2 SE) lifespan in stream of aquatic insect genera with and without CaCO₃ deposits present from streams in the Huachuca Mountains of southeastern Arizona. Lifespan data are ln-transformed to improve normality in statistical analysis. Mean lifespan in stream is significantly higher for genera with CaCO₃ present (untransformed \bar{x} = 1.13 years) than for those without (untransformed \bar{x} = 0.47 years) (2-tailed t test: t = -3.24, ν = 28, P = 0.003).

homoscedasticity, respectively. To test whether aerial dispersal mode differed between taxa with and without CaCO₃ encrustation, we used a χ^2 contingency table test because both variables were categorical. All analyses were performed using the statistical software R version 3.2.2 (R Development Core Team 2014).

RESULTS

In total, we found 15 species in 13 genera of aquatic insects that exhibited at least some degree of CaCO₃ encrustation in Garden Canyon; we also found over 30 other common species in 22 genera without any CaCO₃ deposits (Table 1). Among the taxa we encountered with CaCO₃ deposits, 7 represent families with no prior reports of mineral encrustation: Aeshnidae (Odonata), Belostomatidae (Hemiptera), Calamoceratidae (Trichoptera), Coenagrionidae (Odonata), Cordulegastridae (Odonata), Helicopsychidae (Trichoptera), and Nepidae (Hemiptera). Taxa with CaCO₃ deposits had significantly longer aquatic lifespans than those without CaCO₃ deposits (2-tailed t test: t = -3.24, ν = 28, P = 0.003; Fig. 2). In contrast, CaCO₃ encrustation on insects did not differ among aerial dispersal modes (χ^2 = 1.69,

TABLE 2. Mean lifespan in stream (in years) of aquatic invertebrate taxa of each aerial dispersal mode (following Bogan and Boersma 2012) with and without CaCO₃ deposits present. We observed no taxa with widespread haphazard dispersal with CaCO₃ deposits.

Aerial dispersal mode	Mean lifespan with CaCO ₃	Mean lifespan without CaCO ₃
Widespread haphazard	N/A	0.33
Cue-limited	0.75	0.39
Infrequent	1.00	0.57
None	1.28	0.48

$\nu = 2, P = 0.43$). However, for each aerial dispersal mode, the mean aquatic lifespan of taxa with CaCO₃ deposits was higher than that for taxa without CaCO₃ (Table 2).

DISCUSSION

Our study confirmed that CaCO₃ encrustation is relatively widespread among insects living in the perennial, travertine-depositing reaches of our study stream. Additionally, we found a number of taxa with CaCO₃ deposits that had not previously been reported to have such deposits. In particular, we found this phenomenon to be common among aquatic stages of Hemiptera and Odonata, but we found no prior references to CaCO₃ deposits occurring on either. Although some true bugs such as backswimmers (Notonectidae) and water boatmen (Corixidae) disperse aerially, a number of species present in the study stream, such as *Abedus herberti* (Belostomatidae) and *Curicta pronotata* (Nepidae), are either flightless or fly infrequently (Smith 1974, Lytle et al. 2008, Bogan and Boersma 2012). Further, both true bugs and odonates have final larval instars with relatively long durations. *Abedus herberti* spend nearly one month in their last instar (Smith 1974), whereas *Oplonaeschna armata* (Aeshnidae) can spend up to 6 months in their last immature instar (Johnson 1968). These long-lived final instars can certainly accumulate substantial CaCO₃ deposits during their aquatic stages, since notable amounts of calcium carbonate precipitated on leaf litter in Garden Canyon after just one month (Corman et al. 2015). In contrast, mayflies may molt every 4–12 d during development (Humpesch 1981, Benton and Pritchard 1988), which may not be enough time for encrustation to form. We also found CaCO₃ deposits on a number of smaller nonpredatory taxa,

including soldier flies (Stratiomyidae), long-toed beetles (Dryopidae), and some case-building caddisflies (Calamoceratidae and Helicopsychidae), which are all relatively long-lived (>6 months) species with few immature instars (as in all holometabolous insects). This finding supports the idea that taxa with longer aquatic lifespans are more likely to have CaCO₃ encrustation. Ruff and Maier (2000) demonstrated that CaCO₃ encrustation on benthic invertebrates can actually deter predation, but it is unclear if any of the taxa found in our study stream benefit from encrustation.

Although CaCO₃ encrustation may provide benefits in some cases, it could also be a nuisance to other species. In several cases, we noted individuals, particularly of *A. herberti*, with CaCO₃ encrusting nearly all of the eyes (Fig. 1). *Abedus* are visual predators that feed upon both live and dead invertebrate prey (Velasco and Millan 1998); thus this encrustation likely would affect feeding success. Since *Abedus* is the top predator in headwater streams in our study region (Boersma et al. 2014), this phenomenon could have consequences for the trophic dynamics in this system and deserves further study. Additionally, CaCO₃ encrustation increases insect weight and could interfere with the unfolding of wing membranes, which would both impair flight ability. Species characterized as “widespread haphazard dispersers,” which regularly disperse over long distances aerially (Bogan and Boersma 2012), were never found with CaCO₃ deposits (Table 2). However, this result could simply reflect the fact that taxa that frequently disperse aerially spend less time in the water, or may spend less time in a particular stream with active travertine deposition, rather than reflecting any active removal or prevention of encrustation by the insects. The same is true of insects with many short-lived larval instars that molt before substantial encrustation forms. Further, we found no difference in the prevalence of CaCO₃ encrustation among aerial dispersal modes. Although very actively dispersing taxa may be less likely to have CaCO₃ deposition, it appears that aquatic lifespan or individual instar lifespan may be more important in determining whether a species will be subject to encrustation.

Many of the long-lived taxa that were prone to CaCO₃ encrustation in our study have aquatic adult stages or belong to orders with relatively

low numbers of larval instars. Long-lived species that go through many larval instars may be less likely to accumulate CaCO_3 encrustation due to their higher molting frequency. Of the aquatic insects, mayflies tend to have particularly high numbers of larval instars (Fink 1980), but only one long-lived mayfly was represented in our stream: *Ecdyonurus criddlei*. Although the life history of *E. criddlei* has not been studied, congeneric species pass through at least 18 larval instars (Rawlinson 1939). This high molting frequency might explain why we never found *Ecdyonurus* with CaCO_3 deposits. However, several hemipterans in our study that were never found with encrustations (e.g., *Notonecta* and *Graptocorixa*) have relatively long-lived immature stages (4–10 months) that pass through only 5 instars (Hungerford 1933, 1948). Unfortunately, genus- and species-specific data on the number of instars are lacking for many of the taxa present in our study stream, which prevented us from making comparisons between encrustation and the numbers and duration of larval instars. Additionally, these species are commonly found in noncalcifying habitats such as cattle tanks and intermittent reaches (Bogan et al. 2013b) where they would not be subject to encrustation.

The study of travertine depositional impacts on insect communities is timely because travertine deposition rates are dependent on stream discharge (Chen et al. 2004, Pentecost and Coletta 2007, Brusa and Cerabolini 2009). Drought is causing flow reduction and complete drying in other travertine streams in Arizona (Bogan and Lytle 2011), thus ending active deposition of travertine in those systems. The loss of perennial flow causes drastic changes in local aquatic invertebrate communities (Bogan and Lytle 2011), but it remains unknown whether altered travertine deposition rates play any role in these community changes. Species occupying desert streams are adapted to a variable hydrology, including droughts and floods (Gray 1981, Lytle et al. 2008). Some species are long-lived and have evolved flood-escape behaviors, whereas others have rapid growth and leave the stream before drought or floods arrive. As lifespan in our study stream significantly differed between species with and without encrustation (Fig. 2), these varying strategies to survive environmental variability likely

shape and are shaped by the effects of travertine deposition. For example, travertine streams may favor long-lived primary consumers if CaCO_3 deposits afford them protection from predation, whereas no such selection pressure may occur in nontravertine streams. Indeed, we found a higher abundance of certain taxa which are subject to encrustation (e.g., soldier flies and long-toed beetles) in Garden Canyon than in the adjacent perennial Ramsey Canyon, which does not have active travertine deposition (Corman et al. 2015). However, the causes and effects of these apparent travertine-induced changes in community composition remain speculative.

Calcium carbonate deposition is a relatively widespread phenomenon in aquatic ecosystems (Pentecost 2005). Although its effects on biogeochemical and sedimentary processes have been the subject of several studies (e.g., Otsuki and Wetzel 1972, Kock et al. 2006, Marks et al. 2006), its effects on aquatic animals are understudied. Given the wide array of taxa we discovered with CaCO_3 encrustation in Garden Canyon, this phenomenon is likely more widespread than has been reported in the published literature. The effects of travertine deposition on higher trophic levels and food-web dynamics would be promising topics for future research.

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