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Population Dynamics of the Northern Tamarisk Beetle (*Diorhabda carinulata*) in the Colorado River Basin

By Levi R. Jamison and Charles van Riper III

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Introduction

Throughout the Southwestern United States, riparian systems contain narrow belts of vegetation along streams and rivers. Although riparian vegetation contributes to only a small percentage of the total land cover (<10 percent), it is important for maintaining high species diversity and population densities of birds (Anderson and Ohmart, 1977; Krueper and others, 2003; Brand and others, 2010). Anthropogenic changes to Western riverine systems have enhanced their susceptibility to invasion by introduced plant species (Baker, 1986, Mack and others, 2000), in particular, beginning in the late 1800s, the invasion of ornamental plants from the genus *Tamarix*, called "saltcedar" (*Tamarix* spp.) or "tamarisk" (Robinson, 1965; Knopf and others, 1988; Earnst and others, 2005; Stromberg and others, 2007).

Tamarisk had been credited with many negative ecologic and economic effects (Cleverly and others, 1997; Shafroth and others, 2005) because the plant can establish itself in dry, salty conditions and spread at rates of >20 kilometers per year (km/yr). In many areas, tamarisk is now a dominant plant on the banks of rivers, streams, springs, and ponds throughout the Southwest (Busch and Smith, 1995; Glenn and Nagler, 2005; Hultine and others, 2010). Tamarisk is considered to have negative impacts on riparian ecosystem structure and processes, including disruption of water use (Shafroth and others, 2005), displacement of native vegetation (Stromberg and others, 2007; Glenn and Nagler, 2005), increased fire frequencies (Busch and Smith, 1993), decreased biodiversity (Harms and Hiebert, 2006), and reduced habitat quality for wildlife (Rice and others, 1980; Bailey and others, 2001; van Riper and others, 2008). Current financial losses due to tamarisk invasion along riparian areas in the United States, adjusted for inflation, are estimated at $169–362 million (Zevaleta, 2000) and certainly millions of dollars more are spent annually for eradication and restoration projects.

Owing to these great financial losses, the biological control of invasive plant species is commonly a priority for land management in the restoration of Southwestern riparian ecosystems. Although tamarisk control has become targeted as an important aspect of local, State, and Federal programs, attempts to eradicate this introduced plant have been met with varying success. Traditional control strategies, such as mechanical removal, fire, and herbicide treatments, can be costly, unsuccessful, or have negative impacts on the establishment of native plant and soil communities.

In 1996, the U.S. Department of Agriculture Animal and Plant Health Inspection Service approved the release of the central Asian saltcedar leaf beetle (or tamarisk beetle), *Diorhabda elongata* Brulle (De Loach and others, 2000; Dudley, 2005), as a biocontrol for tamarisk. On the

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Colorado Plateau, the biological control of tamarisk by the tamarisk beetle, first implemented in 2001, has resulted in expanding beetle populations in Nevada, Utah, Colorado, and Wyoming (Bloodworth and others, 2016), leading to widespread tamarisk defoliation (Dennison and others, 2009; Meng and others, 2012) and concerns from land managers regarding the consequences of the environmental impact. Repeated herbivory and defoliation can result in as much as 40 percent tamarisk mortality within 5 years (Dudley and others, 2001; Hultine and others, 2010) in many areas. Defoliation can also negatively impact avian communities in the short term by decreasing insect abundance and nesting success, owing to increased solar radiation or loss of camouflage (Paxton and others, 2011; Peterson and others, 2015). Biologic control agents may also have other unexpected effects, especially on native bird species (Simberloff and Stiling, 1996). Therefore, careful monitoring of ecosystem restoration activities and of the interactions between biologic control agents and native wildlife communities is essential, so that the appropriateness of any control method and its overall success can be objectively evaluated (Blossey, 1999).

This report consists of two chapters detailing two recent studies that examine the spread of the introduced tamarisk beetle (*Diorhabda carinulata*) over parts of the Southwestern United States. The first chapter, entitled "The Influence of *Tamarix ramosissima* Defoliation on Population Movements of the Northern Tamarisk Beetle (*Diorhabda carinulata*) on the Colorado Plateau," documents plant phenology and beetle abundance and movement along the Dolores and San Juan Rivers, two major tributaries of the Colorado River. This study demonstrates that *D. carinulata* population-movement patterns can be highly influenced by the availability of beetle food resources and that local beetle "boom and bust" events are common. Beetles have defoliated 35 to 65 kilometers (km) of river-corridor tamarisk habitat each year, with a pattern of temporary abandonment followed by recolonization of that habitat in the subsequent year. Larvae occurred primarily in areas of partial defoliation, whereas adults occurred throughout the river corridor, but mostly on the leading edge of defoliated reaches. Understanding this type of beetle behavior and population movement will be useful in the management of areas where *D. carinulata* has been established, as well as areas that it has not yet colonized. This information will also assist land managers to better understand how defoliation and the presence of *D. carinulata* influence tamarisk-dominated habitats within Colorado Plateau riparian ecosystems.

The second chapter, entitled "Utilizing Temperature, Day Length, and *Diorhabda carinulata* Geographic Distribution for Predictions of *Tamarix* spp. Defoliation," carries forward a similar theme of predicting tamarisk beetle abundance and movement. This study demonstrates that the extent and timing of tamarisk defoliation are predictable on the basis of (1) abiotic cues for *D. carinulata* activity, (2) spatial distributions and abundances of *D. carinulata* across a site, and (3) movement of *D. carinulata* as a result of available tamarisk foliage. The study also demonstrates that when spring temperatures averaged >15 °C, *D. carinulata* soon began reproducing, increasing the rate of defoliation at a site. The defoliation pattern also led to variations in *D. carinulata* voltinism rates.

Critical day length is important for inducing diapause in *D. carinulata*, and this diapause is now 33–47 minutes shorter than that of the populations first released in North America in 2001, suggesting adaptation by the tamarisk beetle in response to abiotic cues. A significant positive correlation exists between the spatial distributions of *D. carinulata* populations in the fall and those of the first generation of larvae in the following spring, suggesting that the extent of tamarisk defoliation as a result of abundant larval populations is predictable. The abundance of *D. carinulata* decreased significantly at sites of 50 percent defoliation relative to sites of 100

percent defoliation, indicating that *D. carinulata* will abandon certain areas once defoliation levels become high. At one site, beetle populations spread 19.3±5.6 km along a river corridor, and the overall range of this population over several years increased by 62.8±5.6 km along a linear riparian corridor.

The results of these two studies will enable conservationists to better understand the variable timing of tamarisk defoliation events across a landscape and provide a template to forecast tamarisk defoliation levels and rates in areas that have yet to be colonized by *D. carinulata*.

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Chapter 1. The Influence of *Tamarix ramosissima* Defoliation on Population Movements of the Northern Tamarisk Beetle (*Diorhabda carinulata*) on the Colorado Plateau

Abstract

The northern tamarisk beetle (*Diorhabda carinulata*) was introduced into the Colorado River basin on the Colorado Plateau in 2004 in an effort to control invasive/exotic tamarisk (*Tamarix ramosissima*) plants. Since the initial release, rapid beetle colonization and subsequent defoliation of tamarisk have occurred along the Colorado River corridor. We collected plant phenology and beetle abundance data from the Dolores and San Juan Rivers, two major tributaries of the Colorado River, to document tamarisk defoliation and beetle movement patterns. We observed that *D. carinulata* population movement patterns are strongly influenced by the availability of food resources and local beetle "boom and bust" events appear to be common. Beetles defoliated from 35 to 65 kilometers (km) of river-corridor tamarisk habitat each year. After intensive tamarisk defoliation of large riparian reaches, beetles displayed a pattern of temporary abandonment with recolonization of that same habitat in the subsequent year. Larvae appeared primarily in areas of partial defoliation, whereas adults appeared throughout the river corridor but most commonly on the leading edge of defoliated reaches. Understanding this type of beetle behavior and movement patterns will be useful in the management of both areas where *D. carinulata* has already been established and areas that it has not yet colonized. It will also assist land managers to better understand how defoliation and the presence of *D. carinulata* affect tamarisk-dominated habitats within Colorado Plateau riparian ecosystems.

Introduction

The northern tamarisk beetle (*Diorhabda carinulata*) was first formally introduced into the Western United States in 2001 (DeLoach and others, 2003) as a biological control agent for the invasive/exotic plant tamarisk (*Tamarix ramosissima*, or saltcedar). Since its introduction into the Colorado River basin in 2004, *D. carinulata* has rapidly expanded across the Colorado Plateau (Meng and others, 2012). Interest in *D. carinulata* has increased since these initial releases, owing to the beetle's rapid expansion and its ability to quickly defoliate large reaches of tamarisk habitat (Hultine and others, 2010a; Dudley and Bean, 2012; Snyder and others, 2012). With tamarisk now becoming a dominant part of many riparian ecosystems (Friedman and others, 2005), scientists and managers have questioned what influence *D. carinulata* would have on the plant component of these important ecosystems (van Riper and others, 2008; Hultine and others, 2010b; Dudley and Bean, 2012).

A foliage feeder within the family Chrysomelidae, *D. carinulata* feeds on the leaves of tamarisk, commonly leading to complete plant defoliation (Lewis and others, 2003; Hudgeons and others, 2007a, b; Snyder and others, 2012). Larvae appear to be responsible for most of the defoliation. During the adult beetle stage, aggregation events occur based on attraction to the males' aggregation pheromone (Cossé and others, 2005), resulting in extensive beetle concentrations in focused areas, similar to that for other Chrysomelid beetles (Bartelt and others, 2008). This aggregative characteristic can lead to the later establishment of dense larval populations in those areas. When larval development is synchronous, intensive episodic

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defoliation events result (Hultine and others, 2010a; Nagler and others, 2014). After larvae pupate, they emerge as winged adults. Individuals fly in search of food and are attracted to conspecific aggregations (Cossé and others, 2005; Bean and others, 2007a). Although tamarisk can commonly resprout new leaves within a few weeks after initial defoliation (Hultine and others, 2010a; Snyder and others, 2012), whole-plant mortality likely occurs after multiple years of repeated defoliation events (DeLoach and others, 2003; Dudley and Bean, 2012).

As day length begins to shorten in the fall, adult *D. carinulata* begin diapause and crawl into the leaf litter to overwinter (Bean and others, 2007a, b; Bean and others, 2012). Eventually, tamarisk also go dormant, and leaves senesce before the winter season (especially in northern colder climates), leaving both the host plant and *D. carinulata* dormant for a period of time. As days begin to lengthen and temperatures rise in the spring, tamarisk resprouts to form new canopies (minus any accrued branch mortality from past defoliation). As tamarisk develops green canopies, *D. carinulata* emerges as adults and searches for trees upon which to feed and reproduce (Lewis and others, 2003). Knowledge of the timing of *D. carinulata* activity and defoliation is useful when considering the extrinsic effects of defoliation (for example, cover for wildlife, avian nesting and foraging, and tamarisk evapotranspiration rates).

This chapter discusses the patterns of tamarisk defoliation and large-scale defoliation events that lead to temporary abandonment of an area by *D. carinulata*, when adult beetles emigrate in search of food resources. We demonstrate that tamarisk defoliation intensity and pattern greatly influence the future extent, timing, and abundance of *D. carinulata* and of subsequent beetle colonization and defoliation events.

Methods

Study Sites

We collected tamarisk phenologic and beetle-abundance data in 2008–10 along the Dolores and San Juan Rivers, two major tributaries of the Colorado River (fig. 1). This study complements our general 2006–13 landscape-distribution surveys of *D. carinulata* across the Colorado Plateau. The Dolores River in southwestern Colorado flows generally westward from the Rocky Mountains and then northwestward, where it joins the Colorado River north of Moab, Utah. Vegetation along the Dolores River consists of a fairly dense mix of tamarisk, willow (*Salix exigua*), scattered cottonwood (*Populus fremontii*), and boxelder (*Acer negundo*) riparian forests. The river within our study area flows through deep-walled (~100–300 meter [m]) sedimentary rock canyons, with higher mountains and mesas above. The San Juan River in southern Utah flows through a more constricted and deep (~300 m) sedimentary rock canyon, with sparser riparian vegetation cover consisting primarily of willow and tamarisk.

At the Dolores River, a large release of *D. carinulata* was made in 2004 at a site next to the confluence with the Colorado River, and a smaller release was made in August 2006 approximately 12 km upstream from the town of Gateway, Colorado. At San Juan River, a large release of *D. carinulata* was made in 2007 on the upstream bound of our study site in the town of Bluff, Utah (fig. 1), and another apparent release was made within the vicinity of Paiute Farms, Utah, at the upper extent of Lake Powell and the San Juan River's termination into the lake. Although this release was informal and undocumented, tamarisk defoliation was first detected at this location in 2008 (Meng and others, 2012).
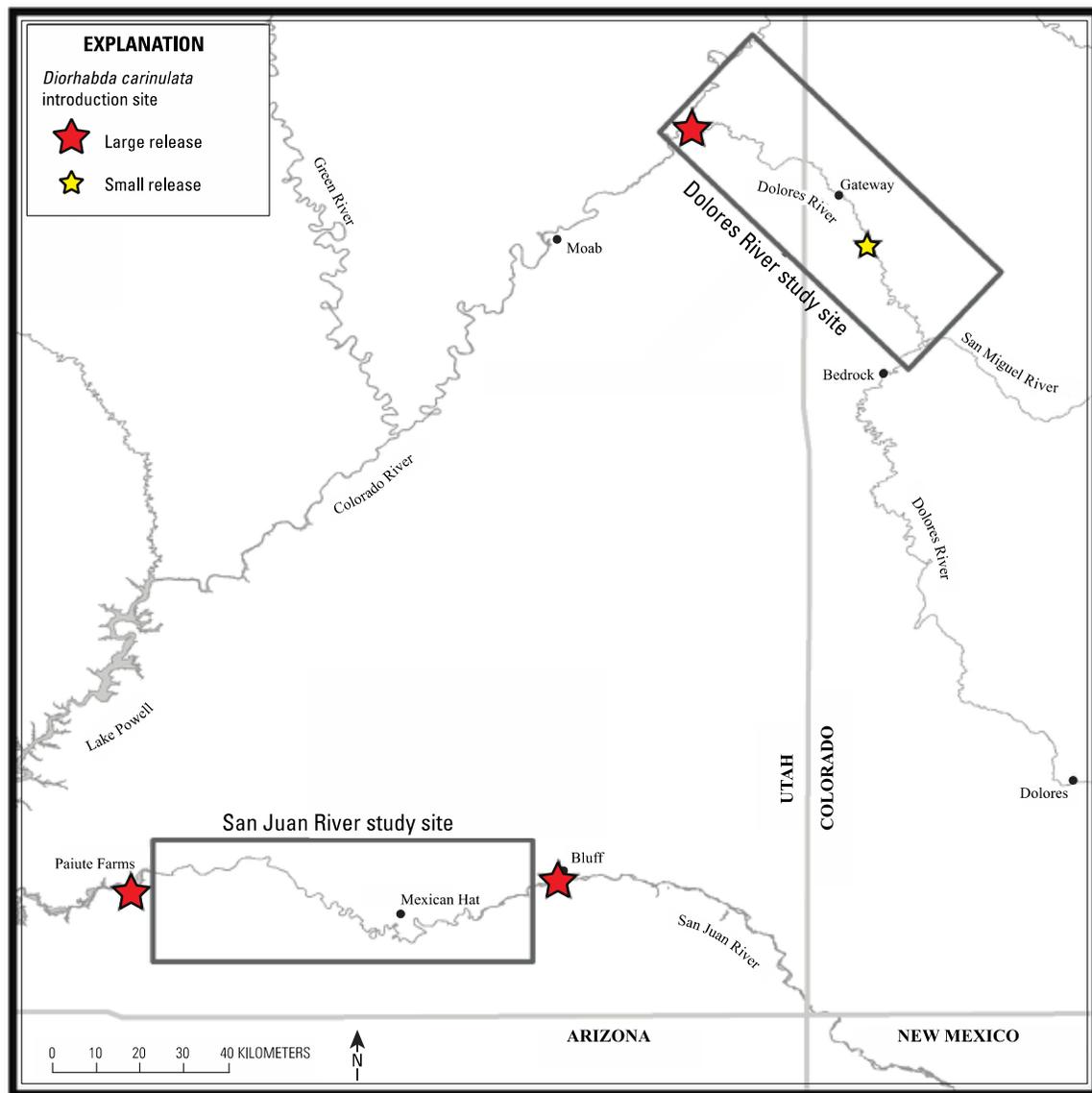
Figure 1. Map of the Colorado, San Juan, San Miguel, and Dolores Rivers in Utah and Colorado, showing locations of study sites on the Dolores and San Juan Rivers. Locations of *Diorhabda carinulata* release sites are marked with stars.

Survey Techniques

On the Dolores River, we surveyed at Bedrock, Colo., as well as from where the river is joined by the San Miguel River downstream to its confluence with the Colorado River (fig. 1). We sampled Bedrock in June 2008 and 2009 and along the river corridor during three periods: August 13–15, 2008; May 18–22, 2009; and May 31–June 3, 2010. We surveyed the San Juan River from Bluff, Utah, downstream to Clay Hills Crossing, ~6 km upstream from Paiute Farms, during July 25–30, 2010. Along both rivers, we used a sweep net to recorded beetle numbers every 1.5 km and collected estimates of tree phenology and plant condition by direct observation.

Data collected along the Dolores River involved 20 sweeps in tamarisk canopies at 1.5 km intervals. In each sweep, we recorded the total number of *D. carinulata* larvae and adults captured. We also visually estimated the average defoliation level of tamarisk within ~100 m of each beetle sampling site. We distinguished defoliation levels as high (70–100 percent), medium (40–60 percent), low (10–30 percent), or absent (0 percent). Data collection along the San Juan River differed; here, we made 25 sweeps in the tamarisk canopies at 1.5-km intervals and recorded defoliation levels in continuous increments of 10 percent. All surveys were conducted as part of a larger monitoring program to map the distribution of *D. carinulata* across the Colorado Plateau region.

Results

Dolores River

After its 2004 release at the junction of the Colorado and Dolores Rivers, *D. carinulata* spread slowly up the Dolores River drainage and reached the confluence with the San Miguel River (km 105) in late 2008. The beetle population at Gateway, Colo., did not achieve high densities and was assimilated by the more rapidly growing population of *D. carinulata* that expanded upstream from the Colorado River confluence in 2007–8.

Defoliation Levels—At Bedrock, Colo. (Dolores River km 156), in early June 2008, beetles were not detected, and tamarisk canopy cover was almost complete (87 percent) for 100 sampled trees. By late June, 64 percent of the tamarisk canopy at this site contained green leaves and 6 percent of the canopy was brown. In July, only 11 percent remained green and 62 percent of the canopy had turned brown from beetle defoliation, indicating that beetles had reached the vicinity of Dolores River km 150 by mid-2008. In August, we observed high (average 97 percent) defoliation levels along the entire Dolores River study area (fig. 2). Extending from the confluence with the Colorado River upstream to km 68.5, we measured defoliation levels consistently at 100 percent (fig. 2). From the edge of this high-defoliation-level zone upstream to the San Miguel River, defoliation levels averaged 57 percent with no defoliation recorded at only one sampling site. In June 2009, the Bedrock site had only 23 percent green leaves and 42 percent of the canopy had turned brown from beetle damage. Defoliation was not detected during our May 2010 river survey, but on May 18 at Bedrock, only 9.4 percent leaf cover remained on tamarisk.

Adult beetles—In August 2008, within the high-defoliation-level zone on the Dolores River (km 0 to ~70), we found only two adult beetles within the first 28.5 km. We found small groups of adult beetles extending upriver another 38.5 km to the end of the completely defoliated zone (fig. 2). Just beyond km 68.5, we noted a large increase in the number of adult beetles at the edge of the high-defoliation-level zone. From that point upstream to the confluence with the San Miguel River, we recorded only a few adult beetles. In May 2009, adult beetles again appeared along only the upper part of our Dolores River study area, but in larger numbers than we found in August 2008 (fig. 3). We detected small numbers of beetles from the Colorado River confluence upstream to km 36, with few aggregations and small numbers of adult beetles extending upstream to km 62. Numbers of adult beetles increased rapidly beginning at km 63 upstream from the Colorado River, and larger numbers were found continuously from that point upstream to the San Miguel River. The largest numbers of adult beetles were recorded between 70 and 82 km upstream from the Colorado River (fig. 3). In May 2010, we noted a large shift in the distribution of adult beetles along the Dolores River. Most of the *D. carinulata* population

had moved downstream to 59 km upstream from the Colorado River confluence, where they had been absent in our May 2009 survey (fig. 3). High numbers of adult beetles were found in the first 35 km upstream from the Colorado River, with peak numbers between km 37 and 58 (fig. 3). Farther upstream to the San Miguel confluence (km 105), where adult beetles were abundant the previous May, beetle numbers were greatly reduced, and we recorded only a few aggregations.

   Beetle larvae—During August 2008, we found only one larva within the 68.5 km length of the lower Dolores River high-defoliation-level zone (fig. 2*B*). Farther upstream in partially defoliated areas, we found larger numbers of larvae all the way to the San Miguel River confluence. Generally, more *D. carinulata* were present in the partially defoliated vegetation zone. We recorded only one larva during our May 2009 survey, as beetles had only recently emerged from overwintering and the first-generation larvae had not yet emerged. Our May 2010 survey was also early in the season, and we found only small numbers of larvae, all within the first 28 km upstream from the Colorado River confluence.
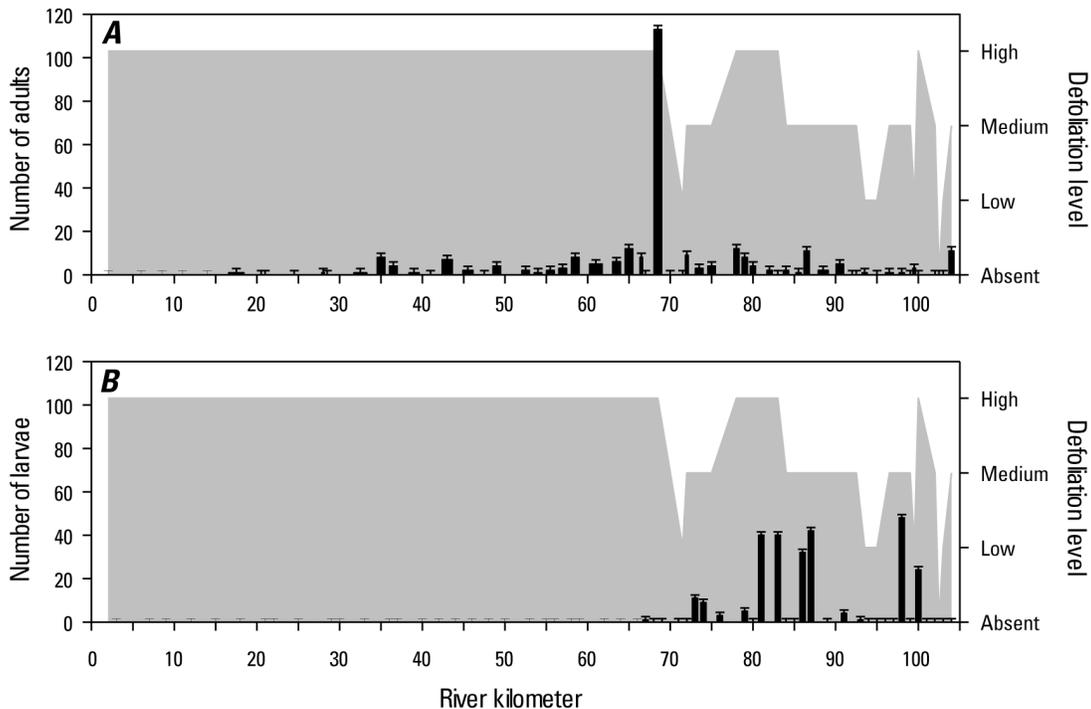
Figure 2.   Distribution of *Diorhabda carinulata* adults (*A*, black bars) and larvae (*B*, black bars) and resulting tamarisk defoliation (gray area) along the Dolores River between the confluences of the Colorado River (river kilometer 0) and the San Miguel River (river kilometer 104) in August 2008.

San Juan River

   Defoliation levels—Along the San Juan River in 2010, we found high-defoliation-level zones extending into our study area from upstream and downstream locations (fig. 4). From Bluff, Utah, defoliation levels were consistently 100 percent downriver for >32 km. From that point downstream, defoliation levels decreased and were mostly low for another 55 km. At ~90 km downstream of Bluff, defoliation levels rose moderately for 30 km, then increased to almost 100 percent for another 13 km, at which point our sampling ended at Clay Hills Crossing, Utah.

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Adult beetles—Adult beetles were found at low abundance levels throughout all reaches of the San Juan River in 2010 with the exception of two spikes at km 34 and km 133 downstream of Bluff (fig. 4*A*). The pattern of adult beetle numbers was consistently low throughout all defoliation zones except for the transition zones where defoliation rates decreased ($r^2 = 0.0127$; fig. 4*A*).

Beetle larvae—We did not detect any larvae in the 32 km downstream from Bluff, where tamarisk was 100 percent defoliated, except for one record of 7 individuals 8 km downriver (fig. 4*B*). We then found larger numbers of larvae from km 32 to 117.5 downstream from Bluff; numbers generally peaked between km 79 and 90 downstream (fig. 4*B*). Numbers of larvae declined markedly at 119 km downstream from Bluff and few larvae were found from there downriver to Clay Hills Crossing. On the San Juan River, we found little relation between larvae numbers and defoliation rates ($r^2 = 0.429$), but the pattern of larvae abundance was generally inverse to defoliation level (fig. 4*B*).
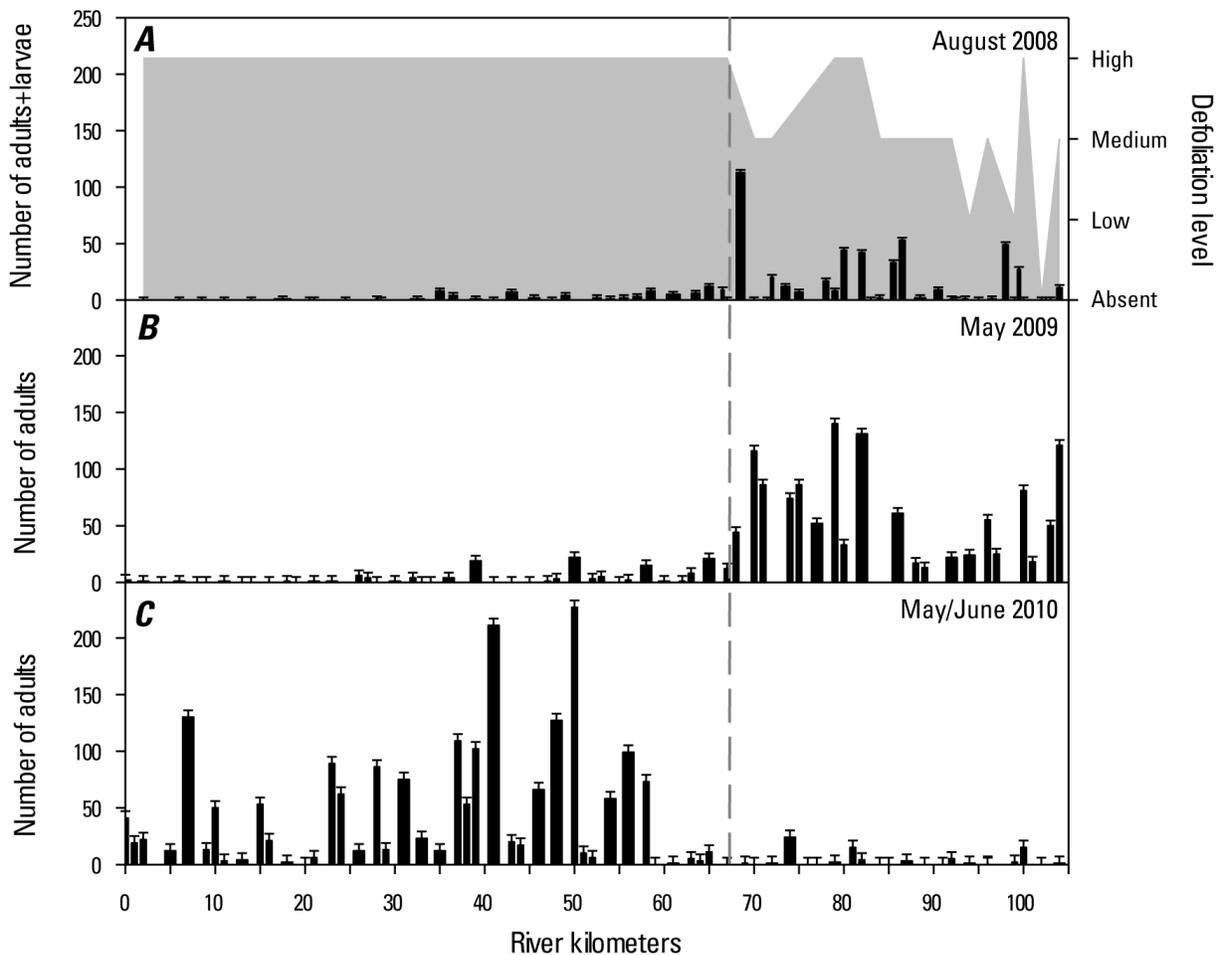
Figure 3. Comparative distributions of *Diorhabda carinulata* adults (black bars) recorded along the Dolores River in 2008–10. Gray area in *A* marks tamarisk defoliation. Gray dashed line denotes boundary between areas of cohesive high and moderate defoliation levels in August 2008 (*A*). The legacy of this high-defoliation-level zone is visible in the distribution of the adult population in 2009 (*B*) and 2010 (*C*).

Discussion

The patterns of *D. carinulata* abundance and tamarisk defoliation level that we found on the Dolores and San Juan Rivers were largely a product of the locations of initial beetle releases, coupled with the degree of tamarisk defoliation and annual beetle-movement patterns. The *D. carinulata* population introduced at the confluence of the Dolores and Colorado Rivers in 2004 began to expand up the Dolores River in 2006. By early 2008, this population had expanded upriver far enough to assimilate the smaller population introduced in 2006 at the Gateway site, but it had not yet reached Bedrock, Colo. As *D. carinulata* populations continued to spread in 2008, the first- and second-generation larvae completely defoliated tamarisk from the Colorado River confluence upstream to km 68.5. After these larvae pupated and reached adulthood, beetles moved upstream to areas where green tamarisk was more available, as we observed adults and new larvae only in areas from km 68.5 to 104 upstream of the Colorado River. Additionally, defoliation was recorded at the Bedrock site (km 156) by July 2008.

At the time of our August 2008 Dolores River survey, >50 percent of adult beetles would likely have already begun to enter reproductive diapause, limiting further dispersal and reproduction, and resulting in adult beetles seeking nearby overwintering sites in the leaf litter (Bean and others, 2007a, b; Bean and others, 2012). We infer that the spatial distribution of adults and larvae found in our August 2008 survey was representative of adult beetles that would overwinter that year and emerge from overwintering at that site in spring 2009. In fact, the adults that we recorded in May 2009 were distributed in a pattern similar to that of the adults and larvae that were present in August 2008 (fig. 3). Thus, the first generation of larvae in 2009 likely were also established in the same areas where adult beetles were found in May 2009. As these larvae developed, food resources would have rapidly depleted in that area, eventually forcing the beetle population to emigrate to where green tamarisk foliage was available, such as along the previously abandoned stretch of the Dolores River from km 0 to 60. In May 2010, adult beetles were distributed from km 0 to 60, with numbers declining in the river stretch upstream. Hultine and others (2010a) described smaller beetle numbers and peak defoliation occurring later in summer 2009 relative to 2008 on the Dolores River, 16 km upstream from the Colorado River confluence. This observation suggests that beetles emerged from overwintering at that site in 2008, leading to early defoliation with the first generation of larvae, whereas the smaller numbers of beetles and later defoliation in 2009 were due to gradual immigration of the *D. carinulata* population back to the site later in the summer.

Displacement of the *D. carinulata* population due to resource depletion also occurred on the San Juan River in 2010. The beetle population, expanding from its introduction site in Bluff, Utah, completely used all the tamarisk leaf resources from Bluff to 32 km downstream (100-percent defoliation) and forced emigration to areas farther downriver. Simultaneously, we observed that the population expanding upriver from the Paiute Farms, Utah, introduction site, had heavily defoliated tamarisk from Clay Hills Crossing, Utah, to 13 km upstream. As this population emigrated farther upriver, it soon converged with the population expanding downriver from Bluff, resulting in complete colonization of the river corridor (fig. 4).

Where *D. carinulata* achieve locally high population densities, we found that they completely defoliate stands of tamarisk and then vacate the area, probably in search of new food resources (that is, green tamarisk leaves). This pattern was consistent at all of our study sites. The high level of tamarisk defoliation along the Dolores River in 2008 and along the San Juan River in 2010 effectively led to the beetles' temporary desertion of those areas, in turn affecting the spatial distribution and colonization patterns of beetle abundance in the future (for example,

in 2009 and 2010 along the Dolores River). Cossé and others (2005) also found that the ability of this species to reach high population densities, possibly as a result of an aggregation pheromone, can lead to rapid and complete utilization of its food resource, apparently causing emigration of almost the entire resident beetle population after complete tamarisk defoliation. The movement of *D. carinulata* from one segment of a river reach to another has been shown by Nagler and others (2014) on the Virgin River, where they documented an average beetle-colonization distance of 25 river km per year. At all our study sites we determined that this recolonization distance averaged 50 river km (range, 35–65 km), twice what Nagler and others (2014) determined on the Virgin River.
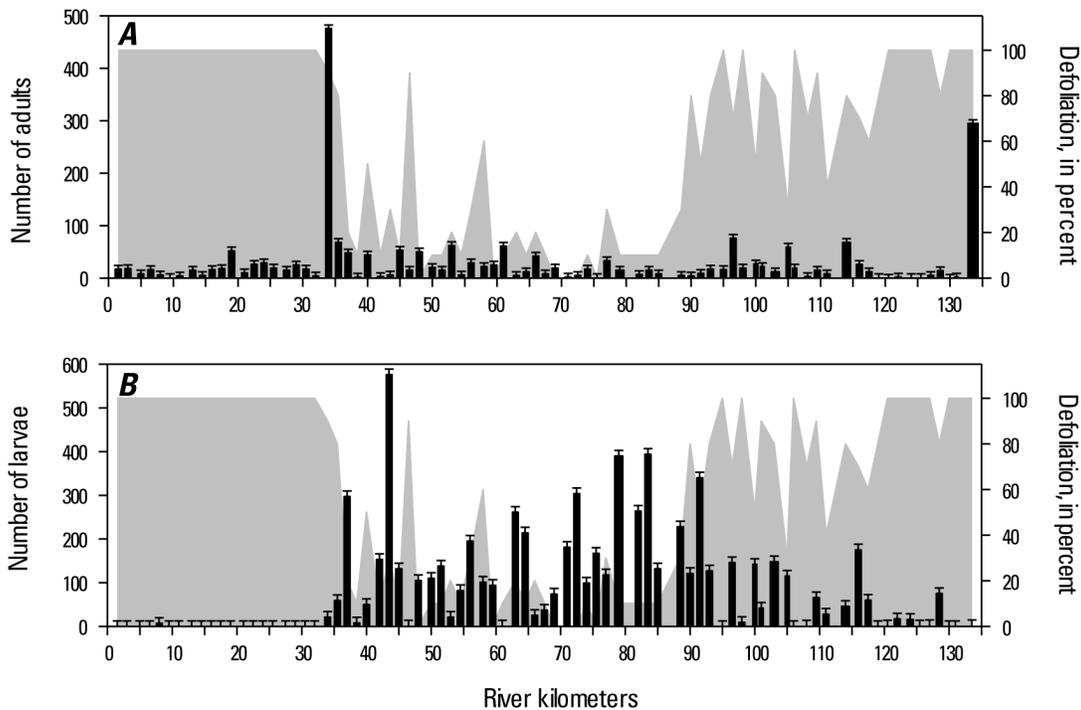
Figure 4. Comparative distributions of *Diorhabda carinulata* adults (*A*, black bars) and larvae (*B*, black bars) and tamarisk defoliation levels (gray area) recorded in late July 2010 along the San Juan River between Bluff, Utah (river kilometer 0), and Clay Hills Crossing, Utah (river kilometer 135).

Spring emergence of overwintering adult *D. carinulata* is linked to temperature, bud burst, and the first appearance of foliage on tamarisk (Lewis and others, 2003). First oviposition by the overwintering generation and the appearance of the first larval generation of the season can be well synchronized in an area when bud burst and temperature rise occur in unison. This synchronization could explain the initial episodic defoliation that Hultine and others (2010a) observed in 2008, when the uniform population emergence owing to temperature rise in spring 2008 led to synchronous establishment of the first larval generation and defoliation of the season, after which adult beetles emigrated out of the site. This pattern explains why, where we found fully green canopies, freshly emerged adult beetles did not need to travel far for food, regardless of the defoliation pattern in the previous year. As the first larval generation grows and feeds, defoliation begins to occur across the colonized area. If the defoliation level becomes intense, mobile adult beetles are forced to emigrate from the defoliated area in search of food resources. Emigration then leads to colonization of new areas and (or) reoccupation of previously

abandoned areas, as we observed in 2010 from river km 0 to 60 on the Dolores River. Thus, the timing of an area's colonization, the beetle population's capacity to fully defoliate an area, and the extent of the beetle population directly influence the time when a site becomes defoliated within a season and over a period of years. Snyder and others (2012) reported similar results in which large-scale defoliation in 2009 was followed by a near-disappearance of the beetle population in 2010 in a study along the Truckee River in Nevada. Snyder and others reported that the peak *D. carinulata* density in 2010 was half the previous year's peak. Although a late-spring freeze earlier that year could have influenced those results, this decrease in density may have been due to large-scale emigration as a result of resource depletion, similar to our findings.

Understanding this pattern of resource depletion and *D. carinulata* population movement are necessary when considering the impact of the beetle on tamarisk habitat and the consequences for other species that live in riparian habitats of the Western United States. For example, the timing of nest building, egg laying, and fledging of bird species may be affected quite differently, depending on when tamarisk defoliation events occur at a site (Sogge and others, 2008; Paxton and others, 2011). If beetles overwinter at a site, that site will be defoliated earlier in the season than where beetles come to occupy midseason after emigrating from another area. Resource managers can take advantage of *D. carinulata* for the suppression of tamarisk, but it is also important to monitor beetle populations to predict the timing of defoliation events. For example, defoliation late in the season, after nesting has occurred, will have less impact on bird species that choose to nest in tamarisk than if defoliation occurs in the middle of the nesting period.

Further studies are necessary to understand the details of this "colonize-defoliate-emigrate" cycle and its long-term effects on tamarisk and other plants and animals in Colorado Plateau ecosystems. When considering the mechanism for which areas are abandoned, it is unclear whether high defoliation levels discourage oviposition by adult *D. carinulata* and encourage dispersal, or if adult beetles lay eggs within high-defoliation-level areas but the newly hatched larvae do not survive. Lewis and others (2003) reported much higher mortality in *D. carinulata* neonate larvae when given suboptimal foliage on which to feed. Future studies could elucidate whether adult *D. carinulata* lay eggs independently of defoliation levels. Additionally, future research can focus on the response of tamarisk plants to defoliation by *D. carinulata*. Tamarisk that is subjected to periodic defoliation may persist, because longer intervals between defoliation events will allow plants to regain lost energy reserves, although it is presently unknown how long this pattern can persist before the tamarisk plant succumbs. Longer term studies would also be useful in understanding the evolving relation among *D. carinulata*, tamarisk, and other plants and animals within the riparian ecosystems of North America as *D. carinulata* move beyond their initial expansion phase.

Conclusion

D. carinulata populations are continuing to spread rapidly across the Colorado Plateau, by an average rate of at least 50 km each year along major river corridors. With these increasing beetle populations, more areas are being subjected to partial and complete tamarisk defoliation in which all available tamarisk leaf matter is being consumed, resulting in subsequent large-scale emigration of *D. carinulata* from the completely defoliated areas. Thus, the lack of food (tamarisk leaves) leads to an abandonment of the defoliated area by adult beetles, whereas partially denuded areas retain beetles that overwinter at that site. We found no *D. carinulata* abandonment of partially defoliated tamarisk areas, although abandonment of completely

defoliated areas lasted at least a year. Adult beetle movement was also influenced by the seasonal timing of emergence and the timing of emigration in relation to the amount of tamarisk leaves available at a given site. Understanding the extent and densities of *D. carinulata* populations throughout the season will be useful to land managers in predicting when and where these intense defoliation events will occur in the following year. Future studies can use our baseline information to better assess the long-term persistence and stability of *D. carinulata* populations and tamarisk density as *D. carinulata* invasions continue to expand across the Colorado Plateau.

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Chapter 2. Utilizing Temperature, Day Length, and *Diorhabda carinulata* Geographic Distribution for Predicting the Intensity of *Tamarix* Species Defoliation

Abstract

We have investigated the spatial dynamics and timing of defoliation of tamarisk (*Tamarix* spp.) by the biological control agent *Diorhabda carinulata* at three sites along the Colorado River and its tributaries. We determined that the location and timing of defoliation were predictable on the basis of (1) abiotic cues for *D. carinulata* activity, (2) spatial distributions and abundances of *D. carinulata* across each study site, and (3) movement of *D. carinulata* as a result of available tamarisk foliage. We found that average spring temperatures >15 °C related to how soon *D. carinulata* began reproducing and defoliation occurred at a study site, leading to variations in voltinism rates of *D. carinulata*. The critical day length for inducing diapause in *D. carinulata* at our study sites was 33–47 minutes shorter than that of populations first released in North America in 2001, suggesting adaptation in response to abiotic cues. We noted a significant positive correlation between the spatial distributions of *D. carinulata* populations in the fall and those of the first generation of larvae in the next spring, suggesting that the areas of defoliation as a result of abundant larval populations could be predicted in advance. We found a significant decrease in *D. carinulata* populations in areas that were 50-percent defoliated relative to those that were 100-percent defoliated, indicating that *D. carinulata* will abandon areas once defoliation levels become high. We also measured that the main *D. carinulata* population area at one study site grew by 19.3±5.6 kilometers (km) and that the overall range of this population at that study site grew by 62.8±5.6 km over 1 year along a linear riparian corridor. These results will enable conservationists to better understand the timing of defoliation events across a landscape and provide a rationale to forecast tamarisk defoliation in areas colonized by *D. carinulata.*

Introduction

Conflicts between differing management strategies are a common source of challenges in the conservation of natural environments (Dunwiddie and others, 2016). The management of nonnative and invasive tamarisk (*Tamarix* spp.) trees in North America has many such challenges (Shafroth and others, 2005; Shafroth and Briggs 2008; Dudley and Bean, 2012). Tamarisk, now one of the most widespread riparian trees in the Western United States (Friedman and others, 2005), has invaded many riparian systems across western North America (Di Tomaso, 1998). In an effort to control tamarisk in the United States, a leaf beetle was introduced in 2001 as a biological control agent (Lewis and others, 2003). Since its release, the biocontrol agent *Diorhabda* spp. (tamarisk beetle) has spread rapidly across much of the Western United States and Mexico (Meng and others, 2012; Jamison and others, 2015; Sanchez-Peña Celso Morales-Reyes and others, 2016), defoliating tamarisk and causing extensive tree mortality (Hultine and others, 2015). Since the release of *Diorhabda* spp., concern has been expressed regarding the impact that tamarisk defoliation will have on wildlife that use tamarisk. Much of this concern has focused on the impact to breeding bird habitat (van Riper and others, 2008), specifically that of *Empidonax traillii extimus* (Southwestern Willow Flycatcher; Sogge and others, 2008; Paxton and others, 2011; Dudley and Bean, 2012). A Federally listed endangered

bird, the Southwestern Willow Flycatcher has been documented to use tamarisk as a nesting substrate (Brown and Trosset, 1989), leaving nests at risk to elevated temperatures, decreased feeding of nestlings, and depredation if defoliation occurs during the breeding season (Sogge and others, 2008; Paxton and others, 2011; Peterson and others, 2015). The effectiveness and low cost associated with using *Diorhabda* spp. as a control agent may highlight it as one of the most economical and sustainable mechanisms for controlling tamarisk at a landscape level (Shafroth and others, 2005). The challenge to utilizing *Diorhabda* spp., however, lies in the inability to control the timing and extent of defoliation events, leaving associated organisms such as the Southwestern Willow Flycatcher at risk of being affected during times of significant life-history events (for example, breeding). With sufficient data on the spatial distribution of *Diorhabda* spp. populations and knowledge of its phenology, the timing of defoliation events may be predictable across a given landscape. If so, such knowledge would allow restoration practitioners to be better informed for making decisions about contrasting conservation and restoration goals.

The ability to predict the seasonal timing of tamarisk defoliation across a given landscape has not yet been demonstrated, even with multiple studies on the phenology of *Diorhabda* spp. (Herrera and others, 2005; Bean and others, 2007a, b; Dalin and others, 2010) and the large amounts of *Diorhabda* spp. distribution data currently being gathered (Sanchez-Peña Celso Morales-Reyes and others, 2016; http://www.tamariskcoalition.org/programs/tamarisk-beetle-maps). The phenologic cycle of *Diorhabda* spp. begins with adult beetles arising from leaf litter in the spring after overwintering, by which time feeding on tamarisk and reproduction soon commence. Emergence from overwintering is likely cued by warmer temperatures, after completion of reproductive diapause by midwinter, like other Chrysomelid beetles (Lewis and others, 2003; Dalin, 2011). As larvae of the first summer generation emerge, they begin to feed on tamarisk foliage, leading to leaf desiccation (Snyder and others, 2010). When larval abundances are high, complete defoliation of a tree's canopy can occur (Dudley and others, 2012). Larval population abundances large enough to defoliate tens of kilometers of river banks have been observed in many regions across Southwestern North America since the introduction of *Diorhabda* spp. in 2001 (Lewis and others, 2003; Meng and others, 2012; Jamison and others, 2015). In North America, *Diorhabda* spp. go through two to six generations before photoperiod cues in the late summer induce diapause (Lewis and others, 2003; Bean and others, 2007b; Milbrath and others, 2007; Dalin and others, 2010). Once in diapause, *Diorhabda* spp. cease to reproduce and disperse, and crawl into the leaf litter to overwinter (Lewis and others, 2003; Bean and others, 2007b). Jamison and others (2015) noted that populations of *Diorhabda carinulata* (northern tamarisk beetle) abandoned areas with high defoliation levels and that the spatial distribution of a beetle population in the fall was similar to that in the following spring. Thus, overconsumption of resources may drive the spatial dynamics of *Diorhabda* spp. populations, whereas environmental cues may dictate seasonal timing and duration.

We decided to investigate how *D. carinulata* biology and the use of its resources affect the timing of defoliation events throughout the year across a broad landscape. Specifically, we sought to determine whether the timing of defoliation events could be predicted by the phenology, abundance, and spatial dynamics of *D. carinulata.* To this end, we monitored three sites of actively colonizing *D. carinulata* populations: one site along the San Juan River and two sites along the Colorado River downstream of Lees Ferry, Ariz. The sites are aligned along an elevational gradient (leading to a temperature cline) within the narrow latitude range ~35°55'–36°50' N (maintaining similar annual day lengths). We monitored each population for a year (spring to spring), recording beetle populations, tamarisk defoliation levels, and the spatial

distribution of each beetle population monthly throughout the active season. We intended to document how *D. carinulata* abundances, spatial dynamics, and phenologic cues determined defoliation events within and between years by looking specifically at (1) how abiotic factors affected the timing and duration of summer activity (including defoliation), as well as affected growth rates; and (2) how the spatial distribution of *D. carinulata* dictated the extent of defoliation, while simultaneously being influenced by degradation of its food resource. Our goals were to determine whether environmental cues affecting the phenology of *D. carinulata* could predict the timing of defoliation and whether spatial dynamics as a result of resource availability predicted the extent of defoliation, within the year and across a landscape.

Methods

Study Sites

We chose three sites at which to conduct our study: the Grand Canyon and Marble Canyon segments of the Colorado River and a segment of the San Juan River (fig. 5). Each study site had *D. carinulata* populations that recently had begun to colonize tamarisk and the length of the river segments at each site varied between 86 and 238 km. Variations in site length were due to logistical constraints and collaborations with associated monitoring programs. The Grand Canyon study site covered 238 km of the Colorado River, from ~16 km upstream from Phantom Ranch, Arizona, at Hance Rapids to Diamond Creek downstream. The Grand Canyon study site (lat 35°45′–36°23′ N) was the lowest elevation (400–750 meters [m] elev) and warmest. The Marble Canyon study site was located along 123 km of the Colorado River, from the boat ramp at Lees Ferry, Ariz., downstream to Hance Rapids (upstream boundary of the Grand Canyon study site). The Marble Canyon study site (lat 36°03′–36°52′ N) is slightly higher in elevation (800–950 m elev) and had slightly cooler temperatures than the Grand Canyon study site. The San Juan study site was located along 86 km of the San Juan River, from 3 km from the base of Navajo Dam in New Mexico downstream to the boat ramp at Kirtland, N. Mex. The San Juan study site (lat 36°40′–36°49′ N) had the highest elevation (1,600–1,700 m elev) and coolest temperatures.

Riparian forests at the San Juan study site were largely composed of thick *Eleagnus angustifolia* (Russian olive) stands, with interspersed patches of tamarisk and varying extents of largely open *Populus deltoides* (cottonwood) galleries, along a wide alluvial plain. Both the Marble Canyon and Grand Canyon study sites are located within deep, confined bedrock canyons (300–1,000 m wide) and are composed of patchy thickets of mostly *Baccharis* spp., *Pluchea serica* (arrowweed), and tamarisk.

Field Methodology

We accessed study sites by raft or kayak and carried out sampling at 1.6- to 4.8-km intervals, depending on the season (winter or summer) and logistical constraints. During the summer months (April–September), we sought to sample at 1.6-km intervals along the river corridor, although logistical issues during each trip sometimes led to sampling at 3.22- to 4.8-km intervals. Each sample included 25 1-m-wide sweeps with a 39-cm-diameter sweep net across five tamarisk canopies. The total numbers of captured *D. carinulata* adults, early-instar larvae, and late-instar larvae (differentiated by the presence of a yellow lateral stripe) were recorded. In addition to sweep samples, one 30-second visual search was made in the tamarisk canopy per sample, in which the number of *D. carinulata* egg clusters were counted. Additionally, the

average defoliation level for the general sampling area (~0.25 square kilometers, km^2) was recorded in 10-percent increments, with 100-percent defoliation equating to the total destruction of all green tamarisk leaves within the sampling area. No sweep netting was done during winter trips (November and February) when beetles were inactive; instead, we collected five 50-gram soil samples of leaf litter with a shovel ~5 m apart under the tamarisk canopies in each sampling area. Collections were spread out on a 12×24-inch tray onsite, and the total number of alive and dead *D. carinulata* adults were counted. In winter, we sampled at 4.8-km intervals along each river.

Beginning in May 2011 (Marble Canyon and Grand Canyon) and June 2011 (San Juan), we sampled at all three study sites monthly through September, when *D. carinulata* reproduction ended. We conducted one winter trip at each study site in winter 2011–12 (November 2011 for Marble Canyon and Grand Canyon and February 2012 for San Juan) to assess the spatial distribution and condition of overwintering *D. carinulata*. In 2012, we visited all three sites one month earlier than in 2011, and twice over two consecutive months, to assess overwintering emergence and establishment of the first summer generation (in April and May for Marble Canyon and Grand Canyon and in May and June for San Juan).
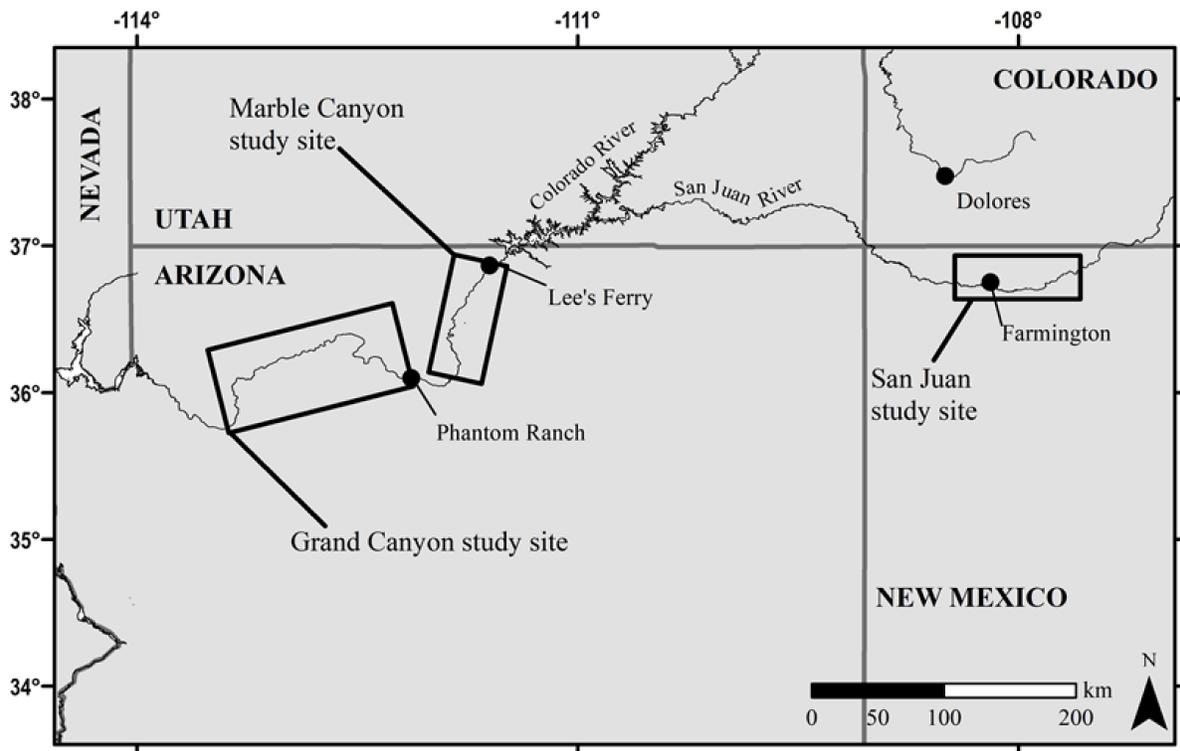
Figure 5. Map of the Colorado and San Juan Rivers in Arizona and New Mexico showing study site locations. All three study sites are located within a similar latitude and along an east-west elevational cline.

Data Analysis

To avoid issues with spatial extent and type I error (Turner and others, 1989), we excluded all sample data from outside the determined *D. carinulata* population range at each study site. The population range was determined to extend across all sample blocks occupied by the main population body within our site boundaries outward (either upstream or downstream) to

the farthest recorded *D. carinulata* observed away from the population during the timeframe of our study. We excluded the area of each study site beyond the farthest recorded *D. carinulata* from our analyses because we considered it too far away from the beetle population to be colonized for the time period of our study. Thus, we analyzed only data from Lees Ferry, Ariz. (km 0), downstream to Nevills Rapid (km 121) at the Marble Canyon study site, and from just below Phantom Ranch, Ariz. (km 145), to Pumpkin Springs (km 343) at the Grand Canyon study site. We observed *D. carinulata* spread across the entire sampling area at the San Juan study site, and so no sample data were excluded.

Because logistical constraints led to some variation in our sampling scheme, we binned and averaged our data in 4.8-km (that is, 3 mi) intervals for use in comparing the spatial distributions of *D. carinulata*, beginning with the farthest upstream sampling location at each study site. These averaged sampling blocks were then used for spatial comparisons in linear and polynomial regressions. For analysis of population statistics (for example, mean life stage numbers), we used only raw, unbinned data as input, ANOVA and T-tests to compare the means, and a critical *p*-value of $p<0.05$ to infer significance of results.

We used the temperature-specific developmental ranges reported in Herrera and others (2005) to estimate the number of *D. carinulata* generations produced at each study site. To do so, we compared Herrera and others' (2005) developmental days with the mean monthly temperature for each survey period, the number of days between surveys, and the life stage(s) in the majority per survey. We used the percentage of samples occupied by *D. carinulata* with eggs to gauge reproduction per survey trip.

To estimate the critical day length for diapause induction, we assumed that 50 percent of the population would enter diapause 13 days after the critical day length (Bean and others, 2007a), and that eggs would stay viable for about a week at our sites in August, depending on temperature (7 days in San Juan and 5 days in Marble Canyon and Grand Canyon). We assumed that population-wide diapause had occurred when the percentage of samples with eggs present decreased to zero.

To gauge *D. carinulata* population growth, we delineated the spatial distribution of each population into one of two categories: (1) the main population body and (2) the dispersal zone. The main population body was the proportion of the area with cohesively high numbers of *D. carinulata* (in all life stages); we delineated its boundary as between the last sample block toward the outer edge of the population in which *D. carinulata* numbers were ≥10 and the previous sample block before occupation. The dispersal zone began at the next sample block after the end of the main population body and ended at the last sample block with *D. carinulata* that had no more than two unoccupied sample blocks between it and the previous occupied sample block (fig. 6).

Data on daily temperatures and day lengths at each study site are detailed in appendix 1.
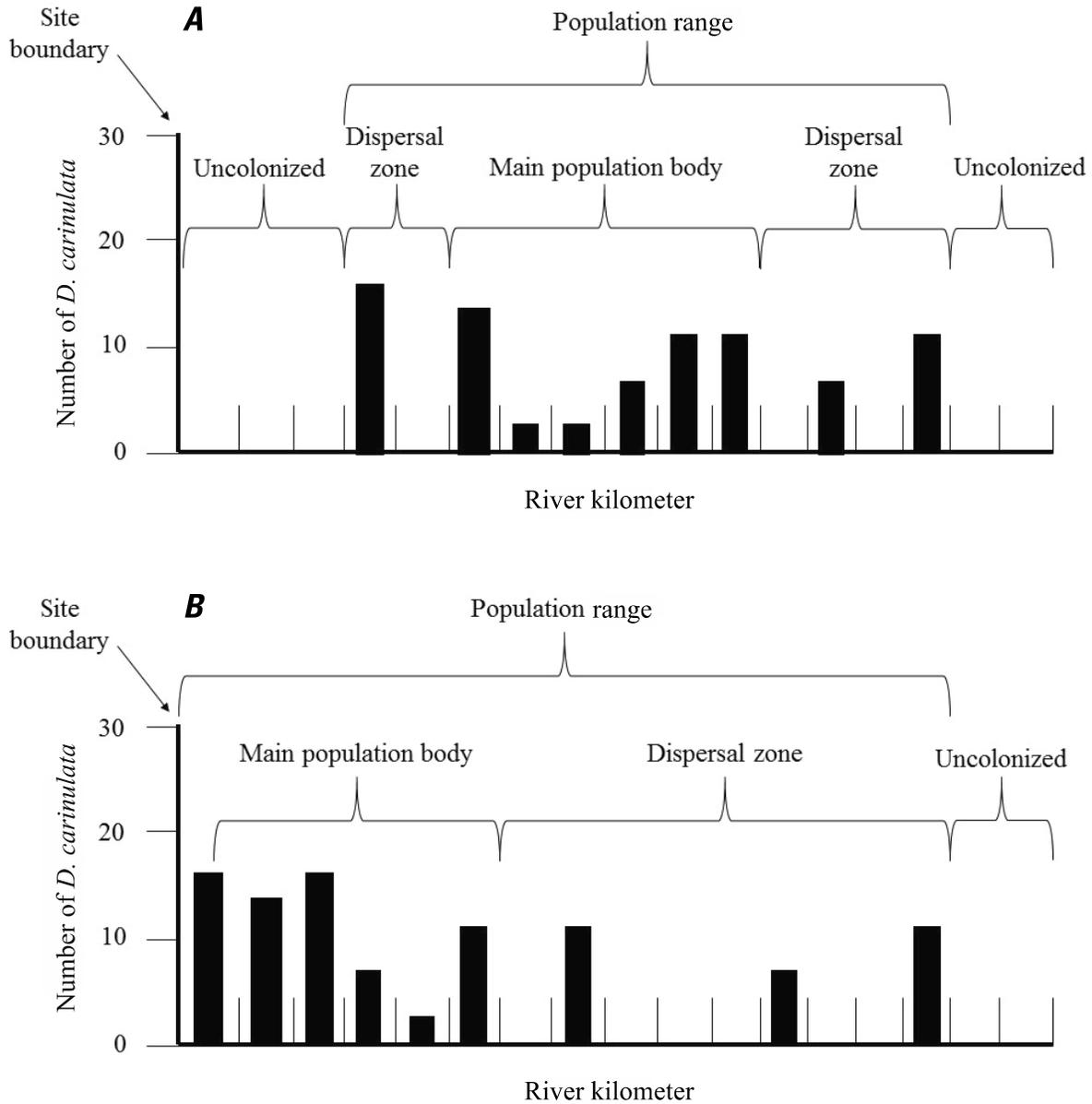
Figure 6. *Diorhabda carinulata* population distributions in 2011 at the (*A*) San Juan and (*B*) Marble Canyon study sites. The total area of the main beetle population, the dispersal zone, and uncolonized regions illustrate how population boundaries are defined within the study sites.

Results

Influence of Abiotic Cues on Seasonal Timing

We determined that *D. carinulata* reproduction began at each site in spring and was associated with rising 7-day-averaged air temperatures of 16–24 °C (fig. 7). We estimated that initial population oviposition ranged from April to June at all study sites in both years (fig. 7) and that population-wide oviposition began ~2 weeks earlier in 2012 than in 2011 (fig. 7, table

1). We determined that the timing of initial defoliation varied across our three study sites in relation to the timing of initial reproduction (fig. 8).

Reproductive activity ceased at all three study sites by September, as indicated by the absence of eggs (table 1). We estimate that the critical day length that would lead >50 percent of the *D. carinulata* population to enter diapause 13 days later (Bean and others, 2007a) was between 13 hours 52 minutes and 14 hours 6 minutes at the three study sites, for two reasons. First, >50 percent of the population had ceased reproducing at the Grand Canyon study site before our August 17–23 surveys, as evidenced by the absence of eggs in samples occupied by *D. carinulata*. Thus, the critical day length would have occurred at least 13 days before August 17 at the Grand Canyon study site, when day lengths were 13 hours 52 minutes. Second, our last survey trip, during which we observed no change in the number of sites occupied by *D. carinulata* with eggs, was at the Marble Canyon study site from August 10–16. Recognizing that eggs stay viable for 5 days at 30 °C (mean temperature at the Grand Canyon for those dates was 33 °C; Herrera and others, 2005), we deduce that 100 percent of the population had not entered diapause by at least August 11 (5 days earlier than the last date of our surveys) and so, the critical day length would have to be less than that determined 13 days earlier at the Marble Canyon study site (14 hours 6 minutes). Owing to the range in day lengths based on latitudes across our study area, we concur that the date range in 2011 within which >50 percent of each beetle population would have been in diapause would have been between August 9 and 19.

Because of the differences in the timing of initial oviposition at each study site in spring and the synchronous cessation of reproduction by September, each study site differed in the total duration of summer activity in 2011, limiting the number of new summer generations of *D. carinulata* to two at the San Juan study site and to three at the Marble Canyon and Grand Canyon study sites (table 1).

Table 1. *Diorhabda carinulata* population per sampling period at the San Juan, Marble Canyon, and Grand Canyon study sites.

[Abundances for each life stage are from the sum of all samples per survey period; percentage of the total of all life stages is in parentheses. Egg values are the percentage of samples with *D. carinulata* present in which eggs were found. OW = overwintering beetles]

		2011					2012	
San Juan								
	Dates		6/8–6/9	7/10–7/12	8/1–8/2	8/31–9/2	5/5–5/12	6/8–6/10
	Sample size (n)		49	42	41	43	39	41
OW generation	Adults		155 (95%)				495 (100%)	126 (7%)
	Eggs		38%	10%			10%	23%
First generation	Early larvae		8 (5%)	27 (11%)			0	1,202 (70%)
	Late larvae			69 (27%)			0	383 (22%)
	Adults			159 (62%)	715 (82%)			
	Eggs				17%	0%		
Second generation	Early larvae				110 (13%)	29 (3%)		
	Late larvae				43 (5%)	120 (14%)		
	Adults					699 (82%)		
Marble Canyon								
	Dates	5/16–5/21	6/13–6/17	7/8–7/11	8/10–8/16	9/3–9/10	4/18–4/24	5/13–5/17
	Sample size (n)	66	46	31	36	66	69	46
OW generation	Adults	223 (9%)					280 (99%)	68 (4%)
	Eggs	73%					0%	21%
First generation	Early larvae	2357 (91%)	27 (4%)				2 (1%)	962 (57%)
	Late larvae	3 (0.1%)	418 (58%)					672 (39%)
	Adults		272 (38%)	238 (30%)				
	Eggs		10%	26%				
Second generation	Early larvae			269 (34%)				
	Late larvae			275 (35%)				
	Adults				446 (40%)			
	Eggs				29%	0%		
Third generation	Early larvae				324 (30%)	0		
	Late larvae				334 (30%)	0		
	Adults					136 (100%)		
Grand Canyon								
	Dates	5/21–5/28	6/17–6/20	7/11–7/15	8/17–8/23	9/11–9/18	4/25–5/2	5/17–5/22
	Sample size (n)	104	55	56	86	86	112	70
OW generation	Adults	59 (2%)					201 (21%)	
	Eggs	37%					27%	8%
First generation	Early larvae	1,100 (32%)					689 (72%)	58 (4%)
	Late larvae	2,268 (66%)					71 (7%)	337 (23%)
	Adults		730 (47%)					1,063 (73%)

		2011			2012
		Grand Canyon			
Second generation	Eggs	38%			
	Early larvae	754 (49%)	221 (12%)		
	Late larvae	64 (4%)	229 (12%)		
	Adults		1,435 (76%)		
Third generation	Eggs	37%	3%	0%	
	Early larvae		208 (12%)	1 (5%)	
	Late larvae		316 (18%)	1 (5%)	
	Adults		1,272 (70%)	20 (90%)	
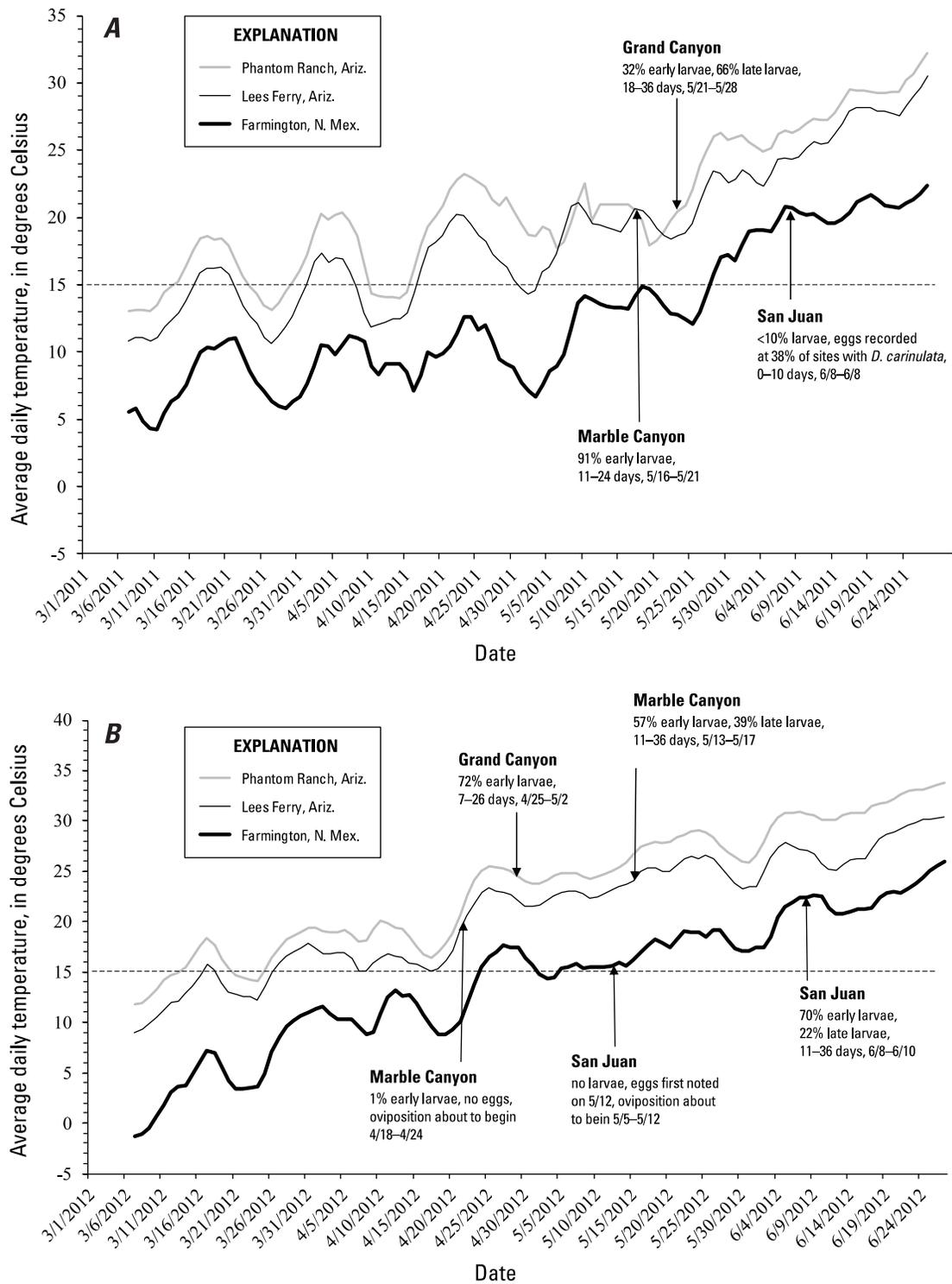
Figure 7. Average daily temperatures at study sites in the Colorado River basin, with timing of initial reproductive activity in 2011 (*A*) and 2012 (*B*). Arrows denote sampling trips, with percentage of population in a larval stage presented along with estimated number of days since initial population-wide oviposition and dates of survey trip, respectively. Developmental day estimates are based on data of Herrera and others (2005).
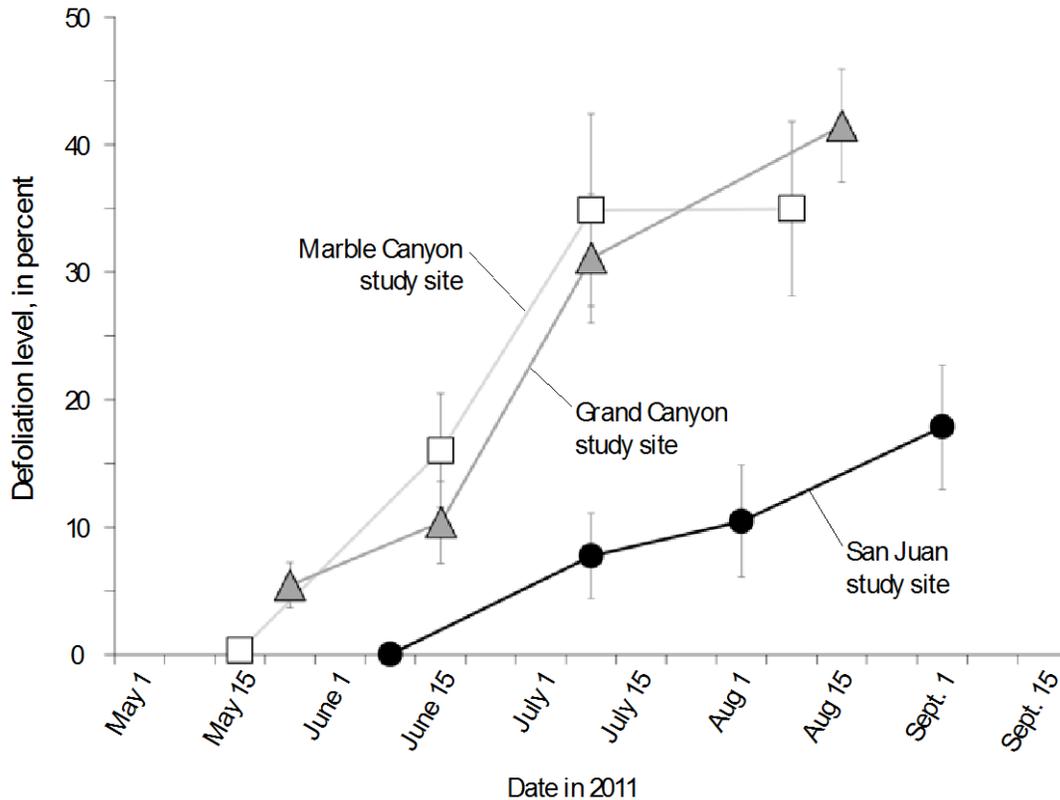
Figure 8. Mean defoliation levels at the Marble Canyon (white squares), Grand Canyon (gray triangles), and San Juan (black circles) study sites in the Colorado River basin in 2011.

Spatial Dynamics of *D. carinulata* and Defoliation

We found a significant positive correlation between the distribution of the entire *D. carinulata* population in fall 2011 and spring 2012 at all three study sites (San Juan: June × September $r^2 = 0.25$, $p < 0.05$; Marble Canyon: May × August, $r^2 = 0.33$, $p < 0.05$; Grand Canyon: April × August, $r^2 = 0.14$, $p < 0.05$; fig. 9). The distribution of first-summer-generation larvae in 2012 also significantly correlated with the distribution of the populations of larvae and adult beetles in the previous fall before overwintering (San Juan: June larvae × (September adults + larvae), $r^2 = 0.22$, $p < 0.05$; Marble Canyon: May larvae × (August adults + larvae), $r^2 = 0.27$, $p < 0.05$; Grand Canyon: April larvae × (August adults + larvae), $r^2 = 0.12$, $p < 0.05$).

We noted significant positive linear correlation between the relative abundances of first-generation larvae and defoliation levels 1 month later at all three of our study sites (Marble Canyon: June defoliation × May larvae, $r^2 = 0.629$, $p < 0.001$ and July defoliation × June larvae, $r^2 = 0.190$, $p < 0.042$; Grand Canyon: June defoliation × May larvae, $r^2 = 0.329$, $p < 0.05$; San Juan: July defoliation × June larvae, $r^2 = 0.714$, $p < 0.05$ and August defoliation × July larvae, $r^2 = 0.689$, $p < 0.05$; fig. 10). The relation between *D. carinulata* population and midsummer defoliation level was better fitted to a quadratic bell curve, where *D. carinulata* larvae and adult beetles became less abundant at defoliation levels >50 percent (fig. 11). The mean number of larvae per sample with 100-percent defoliation was 0.42±0.16 (1 standard deviation, σ), and the mean number of larvae per sample with 50-percent defoliation was 46±16.61 (1σ). All sample blocks with >90 percent defoliation were devoid of larvae during the defoliation period (fig. 12).
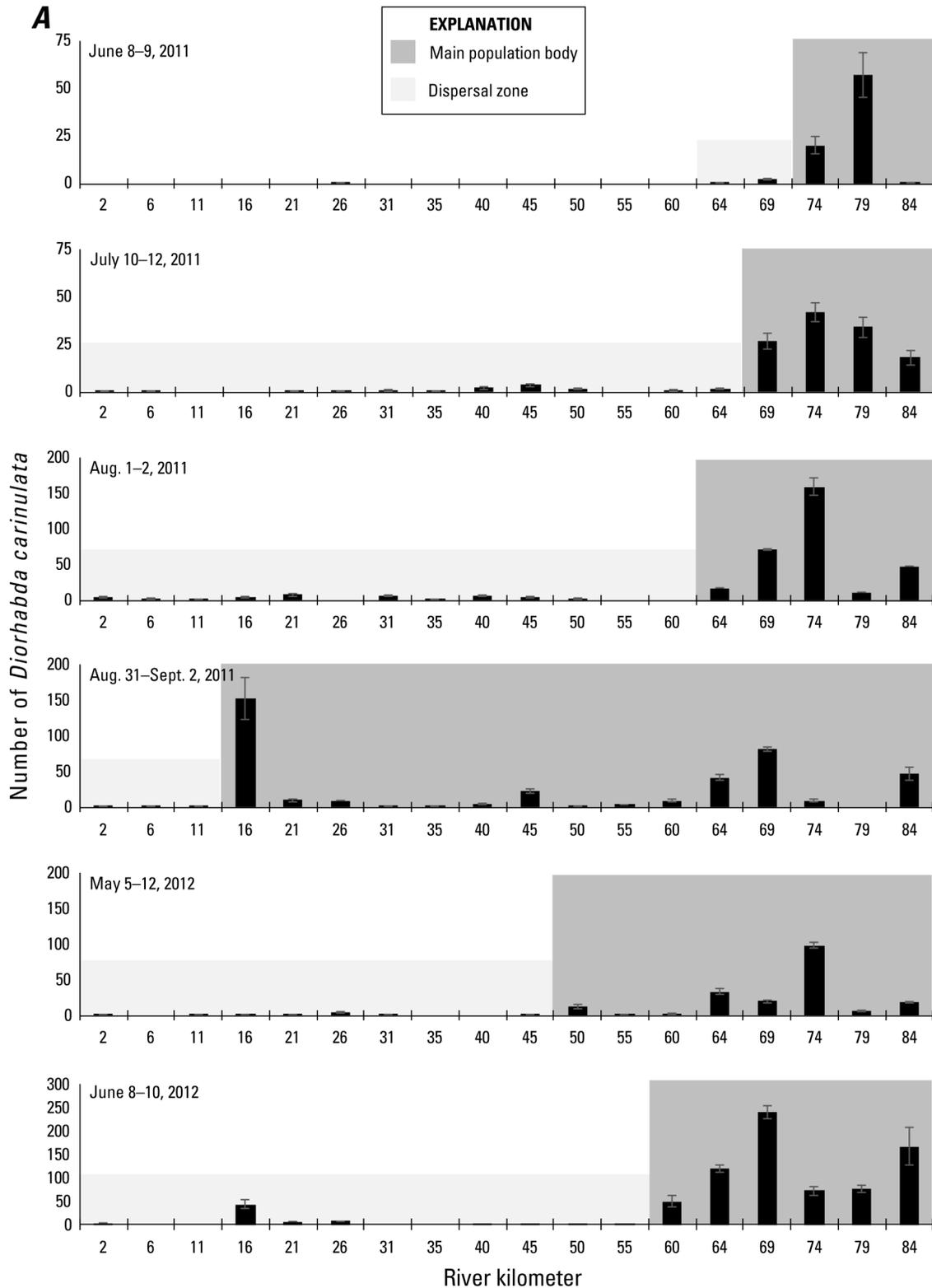
Figure 9. Monthly distributions of *Diorhabda carinulata* along the San Juan River near Farmington, New Mexico (*A*), along the Colorado River in Marble Canyon (*B*), and in the Grand Canyon, Arizona (*C*), with main population bodies (dark gray areas) and dispersal zones (light gray areas) used for analysis highlighted. Error bars denote the standard error for each sampling point.

B

EXPLANATION

Main population body

Dispersal zone

May 16–21, 2011

June 13–17, 2011

July 8–11, 2011

Aug. 10–16, 2011

April 18–24, 2012

May 13–17, 2012

Number of *Diorhabda carinulata*

River kilometer
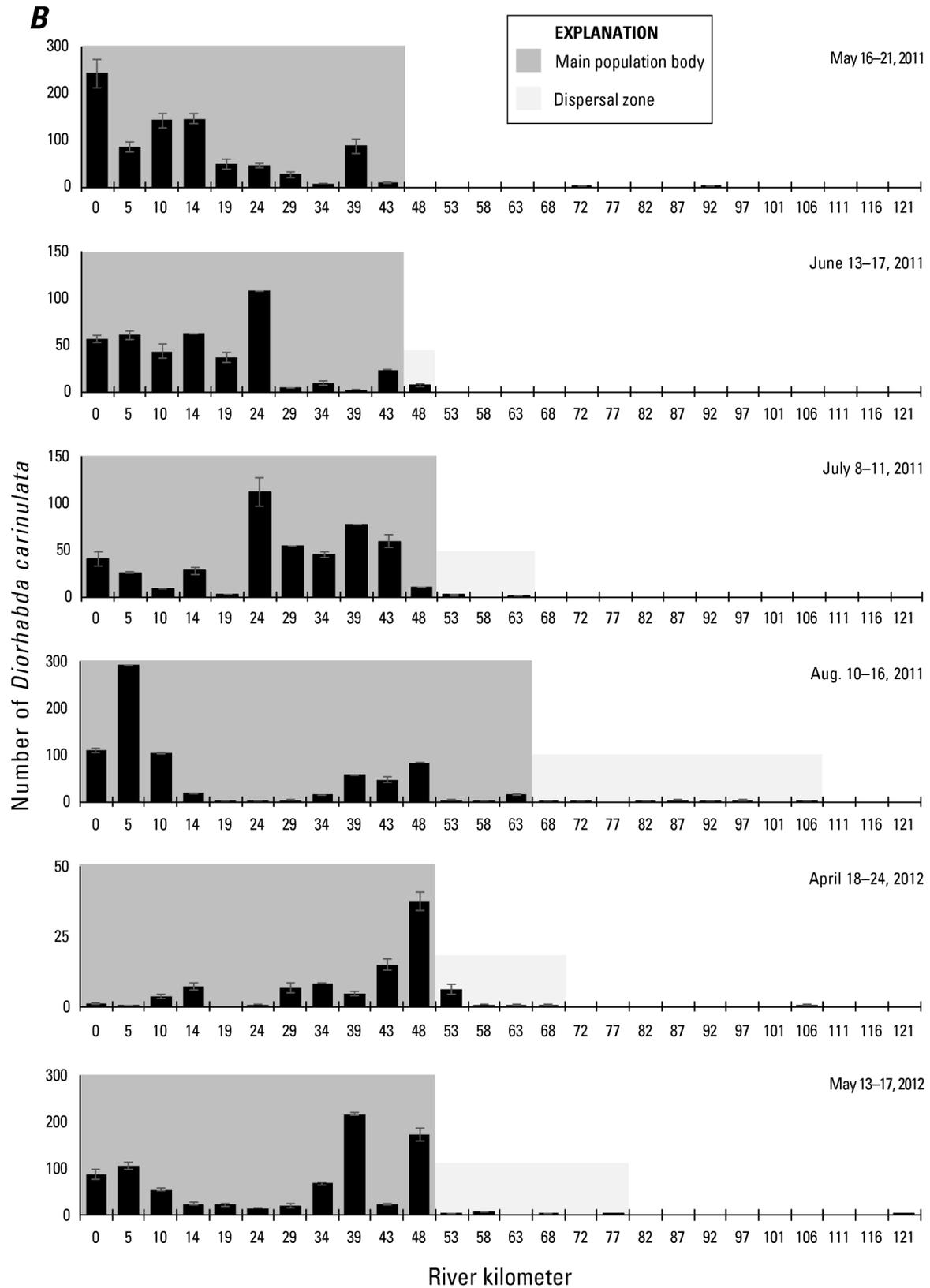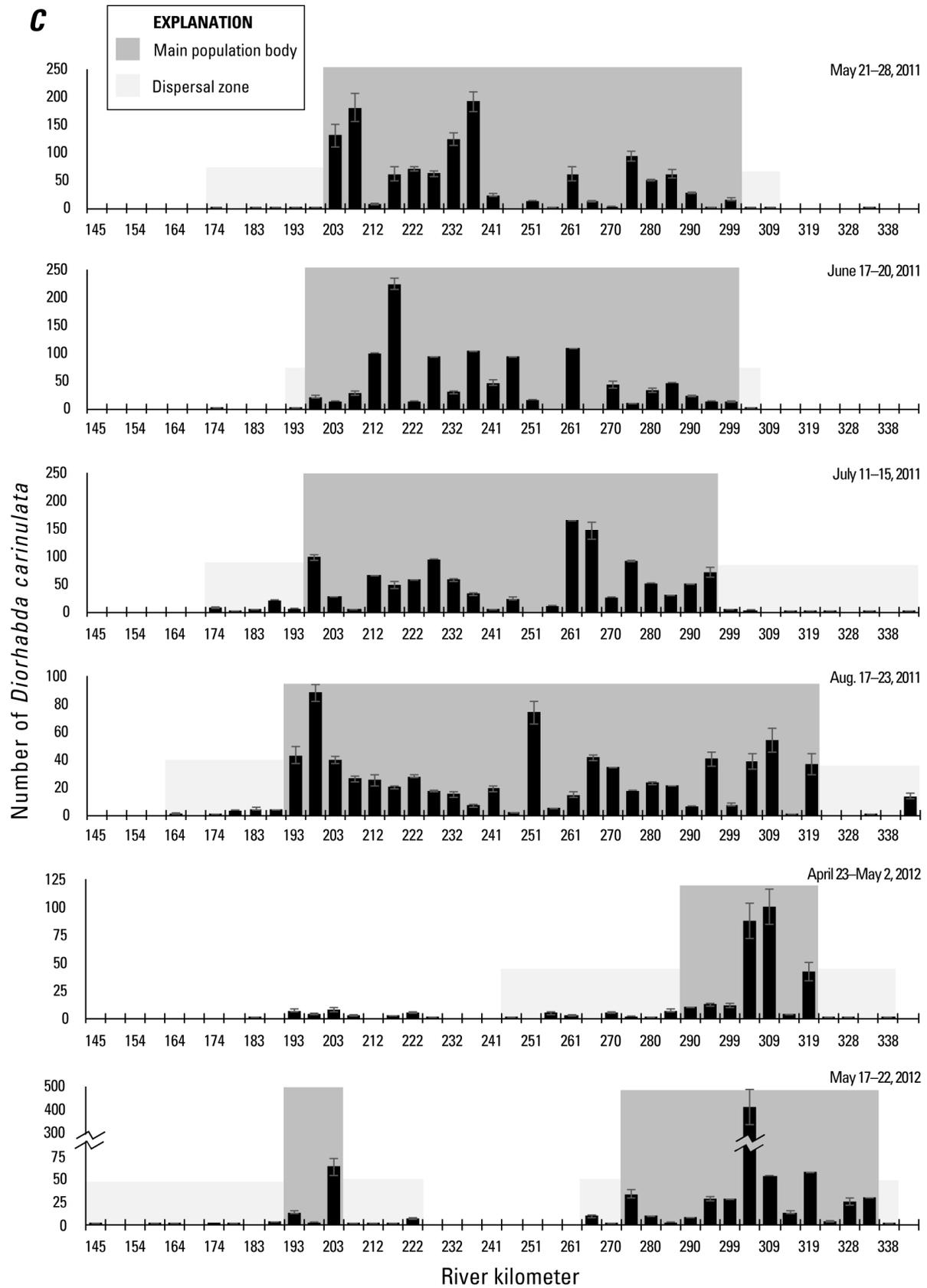
Figure 9.—Continued

Figure 9.—Continued

The dynamics of *D. carinulata* movement based on defoliation levels were most clearly observed at the Marble Canyon study site, where after completely defoliating the first 19 km of the study site, the larval population shifted downstream out of the ≥90-percent defoliated area (fig. 12*B*). In response, tamarisk began to sprout new leaves in the areas where larvae were absent, prompting the beetles to repopulate the upper part of the site by August, once substantial refoliation of tamarisk had occurred (fig. 12*B*).

The sizes of the main population body and the dispersal zone increased at all study sites in 2011, with the upstream side of the Grand Canyon population exhibiting the smallest expansion (table 2). We attribute the beetle population increase at the San Juan study site (which went all the way to our study-site boundary) to immigration into the river corridor from the surrounding areas. During unrelated surveys and monitoring in 2011, we observed that our study site had become encompassed by a larger *D. carinulata* population surrounding the San Juan River corridor, with higher defoliation levels observed than that recorded at our study site. Both the Marble Canyon and Grand Canyon study sites were excluded from such influences, owing to their geologic and geographic isolation.
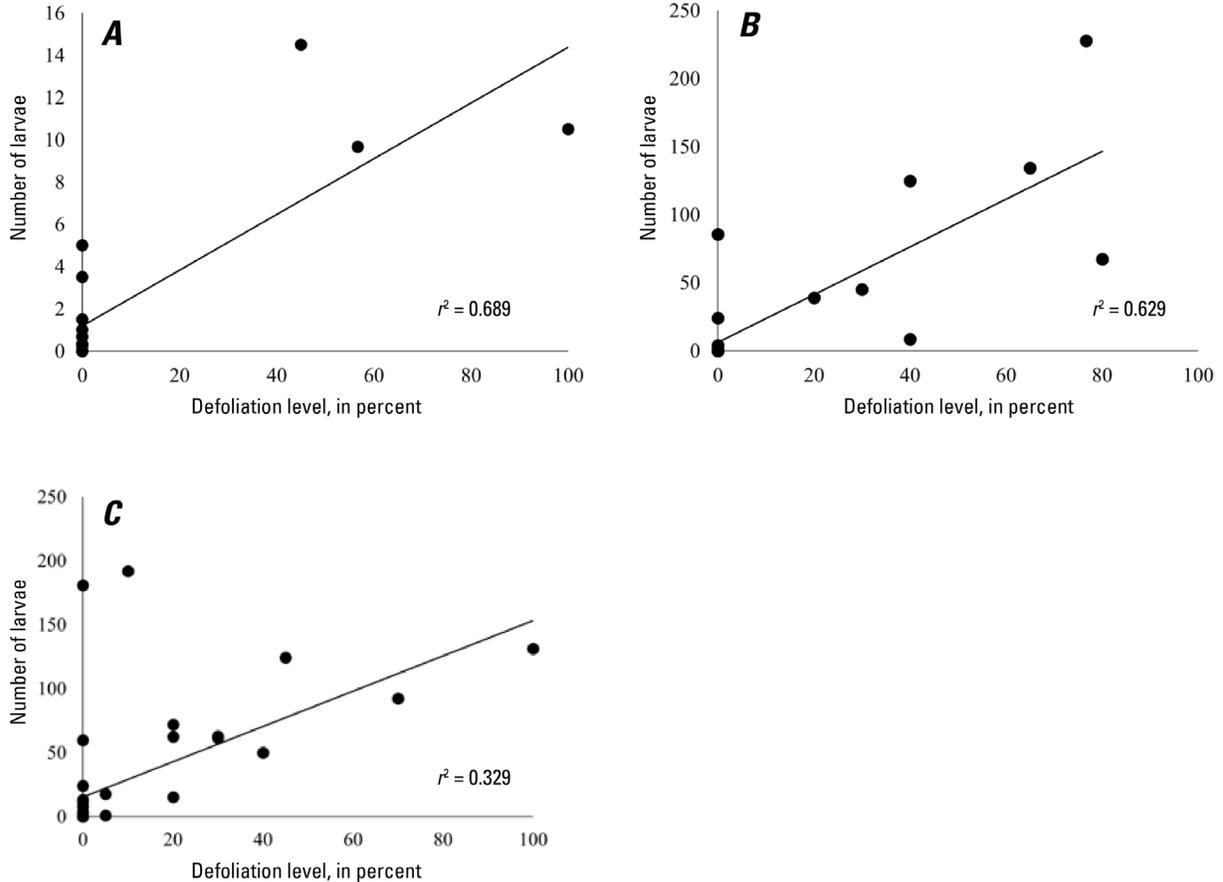
Figure 10. Number of first-summer-generation larvae versus defoliation level one month later at study sites in the Colorado River basin in 2011. *A*, San Juan study site, July–August (r^2=0.689, p<0.05). *B*, Marble Canyon study site, May–June (r^2=0.629, p<0.05). *C*, Grand Canyon study site, May–June (r^2=0.329, p<0.05). r^2 values describe the regression line fit, p values describe the significance.
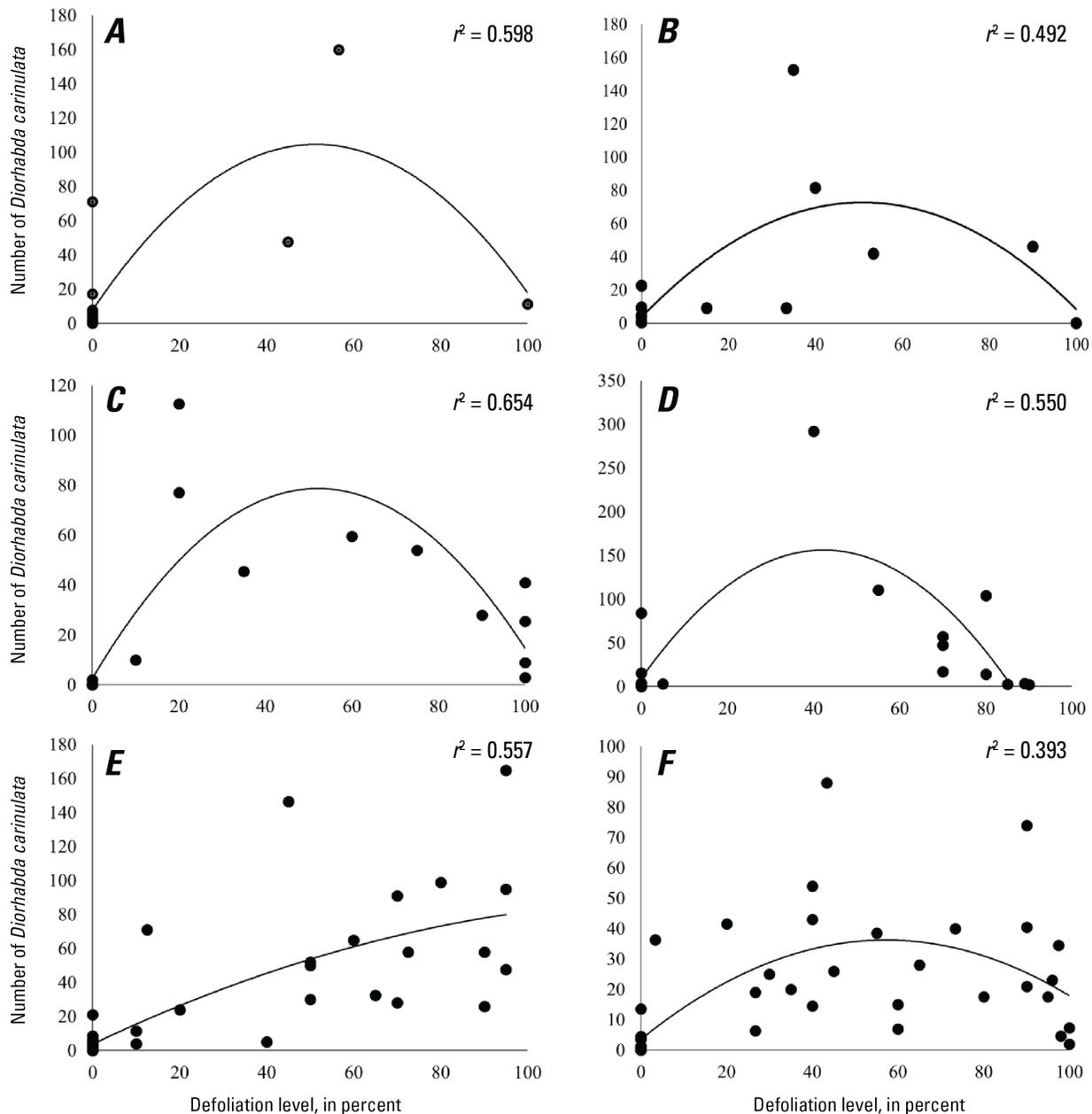
Figure 11. Number of *Diorhabda carinulata* versus defoliation level at study sites in the Colorado River basin midsummer 2011. *A*, San Juan study site, August (r^2=0.598, p<0.05). *B*, San Juan study site, September (r^2=0.492, p<0.05). *C*, Marble Canyon study site, July (r^2=0.654, p<0.05). *D*, Marble Canyon study site, August (r^2=0.550, p<0.05). *E*, Grand Canyon study site, July (r^2=0.557, p<0.05). *F*, Grand Canyon study site, August (r^2=0.393, p<0.05). r^2 values describe the regression line fit, p values describe the significance.

No significant difference in the mean number of *D. carinulata* per sample from May to August 2011 was noted at either the Marble Canyon study site (*F* [Analysis of variance F value] = 1.32, *df* [degrees of freedom] = 3,168, *p* = 0.27) or the Grand Canyon site (*F* = 1.00, *df* = 3,279, *p* = 0.39; fig. 13). Mean numbers of *D. carinulata* per sample in September were

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significantly lower at both study sites, suggesting that overwintering had begun to occur (Marble Canyon: $F = 4.47$, $df = 4,230$, $p <0.05$; Grand Canyon: $F = 7.03$, $df = 4,359$, $p <0.05$; figs. 9B, C). At the San Juan study site, mean numbers of *D. carinulata* per sample differed significantly from June to September 2011 ($F = 3.20$, $df = 3,187$, $p <0.05$; fig. 13), as mean numbers greatly increased in August and September. From May to August, no significant difference was noted in the mean numbers of *D. carinulata* per sample at the Marble Canyon study site relative to the Grand Canyon study site (May: $F = 0.09$, $df = 1$ [Marble Canyon study site] and 155 [Grand Canyon study site], $p = 0.76$; June: $F = 2.65$, $df = 1$ and 95, $p = 0.11$; July: $F = 1.03$, $df = 1$ and 84, $p = 0.31$; August: $F = 1.67$, $df = 1$ and 114, $p = 0.2$). Comparatively, at the San Juan study site, significantly lower mean numbers of *D. carinulata* per sample were noted in June and July in comparison with the other study sites, but not in August (June: $F = 7.48$, $df = 2$ and 146, $p <0.05$; July: $F = 7.05$, $df = 2$ and 131, $p <0.05$; August: $F = 1.04$, $df = 2$ and 157, $p = 0.35$; fig. 13).

Comparing the mean number of *D. carinulata* per sample during the last month of activity (Marble Canyon and Grand Canyon: August surveys; San Juan: September surveys), and the first month of activity with abundant larvae, we found no significant difference at either the San Juan or Marble Canyon study sites (Marble Canyon, August 2011 × May 2012: t statistic (t) $= 1.99$, $df = 76$, $p = 0.67$; San Juan, September 2011 × June 2012: $t = 1.99$, $df = 73$, $p = 0.15$; fig. 9), but a significant difference in the mean number of *D. carinulata* per sample in August 2011 relative to both April and May 2012 at the Grand Canyon study site (August 2011 × April 2012: $t = 1.97$, $df = 196$, $p <0.05$; August 2011 × May 2012: $t = 1.97$, $df =146$, $p <0.05$; fig. 9). We noted a significant difference only when comparing the August mean to the May mean, when a large outlier was removed for May (outlier=838 *D. carinulata*, May mean without outlier=8.99±2.46 *D. carinulata*). Overwintering mortality was higher at the Grand Canyon study site relative to the other two study sites (table 3), disproportional to what we would expect in comparison with the other two study sites, although the difference was not quite significant ($F = 2.51$, $df = 2$ and 64, $p = 0.09$).

Table 2. Linear movement of *Diorhabda carinulata* population boundaries from May to August (Marble Canyon and Grand Canyon study sites) and from June to September 2011 (San Juan study site).

[All distances ±5.6 kilometers (km)]

	Linear expansion of population zones in 2011 (km)	
	Main population body	Dispersal zone
Marble Canyon (downstream)	19.3	62.8
Grand Canyon (upstream)	9.7	9.7
Grand Canyon (downstream)	19.3	33.8
San Juan (upstream)[1]	57.9	62.8
Mean	26.6	42.2

[1]Results at the San Juan study site were confounded by immigration from a nearby population. Both the edge of the main population body and the dispersal zone continued beyond our study boundary.

Table 3. Collections of live and dead *Diorhabda carinulata* in leaf litter at the San Juan, Marble Canyon, and Grand Canyon study sites in the Colorado River basin in winter 2011–12.

Study site	Live	Percent of total live	Dead	Percent of total dead
San Juan	49	98	1	2
Marble Canyon	33	94	2	6
Grand Canyon	59	77	18	23
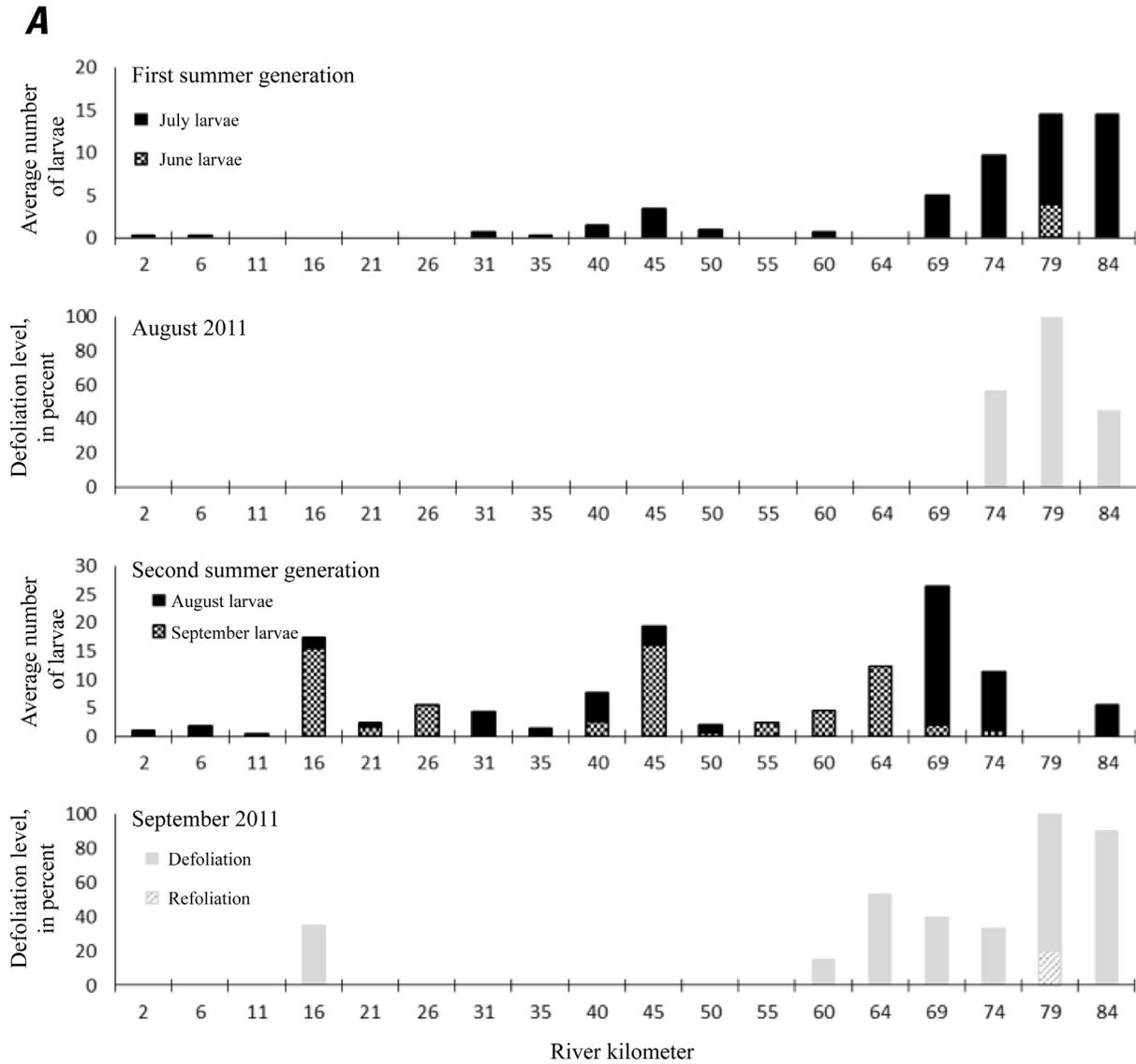
Figure 12. Spatial distributions of *Diorhabda carinulata* larvae and respective defoliation levels along the San Juan River near Farmington, New Mexico (*A*), along the Colorado River in Marble Canyon (*B*), and the Grand Canyon (*C*). Spatial distribution of defoliation levels at start of year correlates with that of average number of first-summer-generation larvae. In contrast, spatial distribution of average numbers of second- and third-summer-generation larvae correlates with that of higher defoliation levels, with larvae not recorded in areas >90-percent defoliated.

Figure 12.—Continued

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c

First summer generation
May 2011

Defoliation
June 2011

Second summer generation
June and July 2011

Defoliation
July 2011

Third summer generation
August 2011

Defoliation
August 2011

River kilometer

Figure 12.—Continued

36
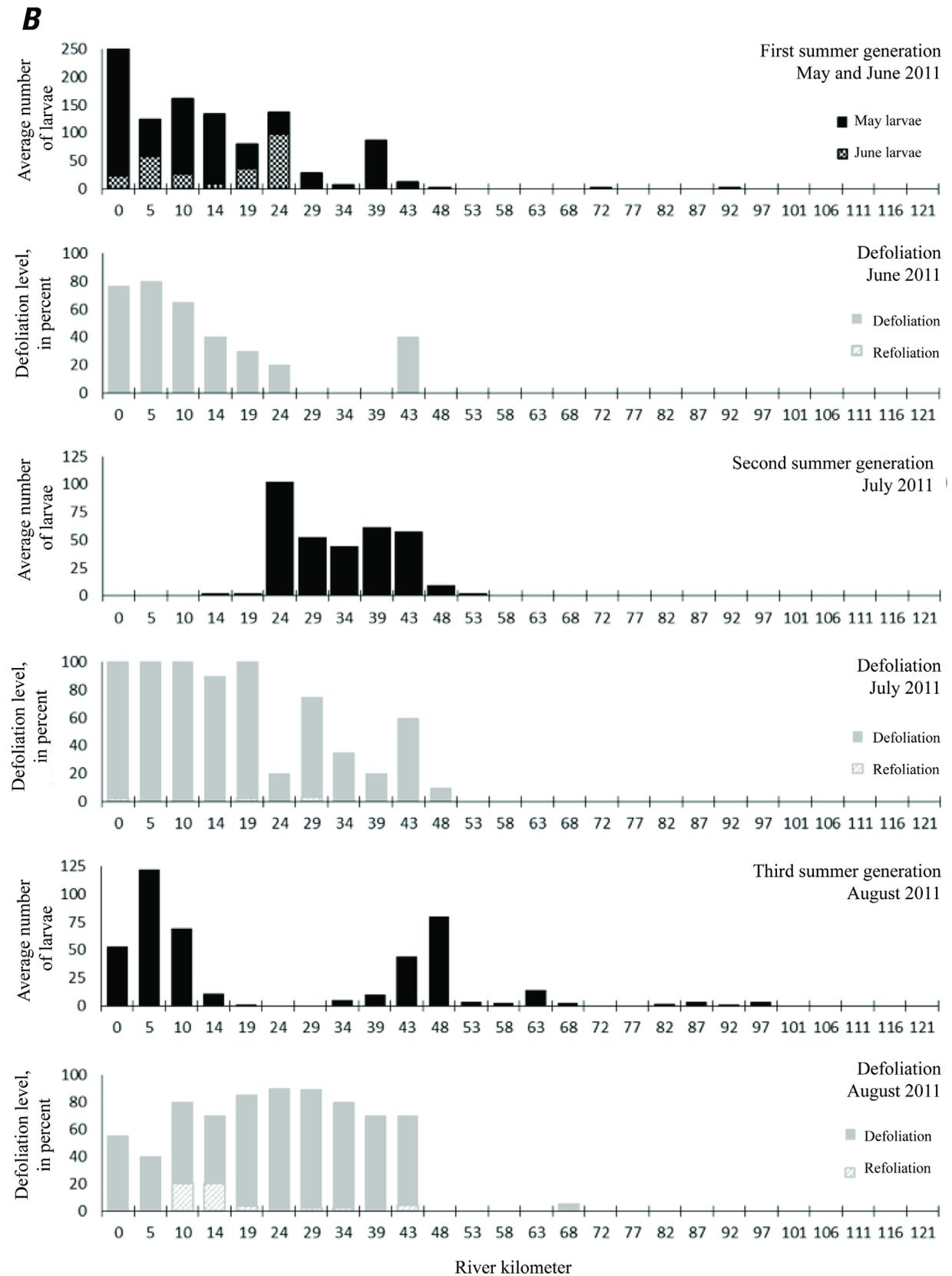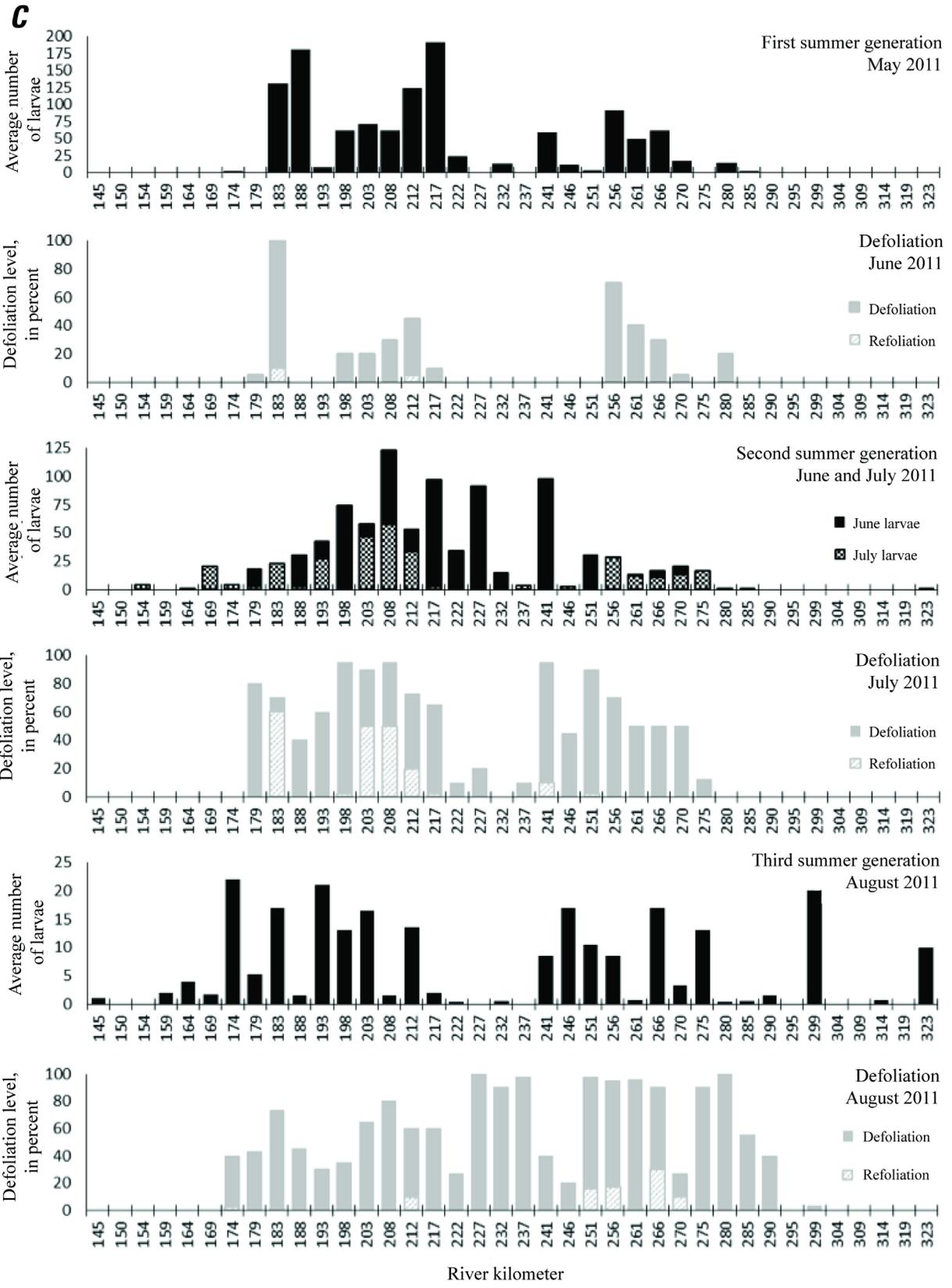
Discussion

Influence of Abiotic Cues on Seasonal Timing

We found 7-day-averaged daily temperatures of 16–24 °C to be good predictors of the start of seasonal activity, directly correlated with how soon defoliation could occur in a given area. Herrera and others (2005) reported 100 percent mortality of all immature life stages, including eggs at 15 °C but full development at 20 °C. Together, our results suggest that ambient spring temperatures >15 °C control how early eggs of the first summer generation can be established and develop into larvae that will produce the first defoliation of the year. In areas where *D. carinulata* populations were high enough in our study, observable defoliation occurred within 1 month of the establishment of the first summer generation, spatially correlated with the relative abundance of larvae of that generation. At the Grand Canyon and Marble Canyon study sites, larger *D. carinulata* populations, coupled with earlier spring temperatures >15 °C, resulted in defoliation occurring as early as late May and mid-June, respectively. In contrast, the San Juan study site had a lower *D. carinulata* population at the start of the season and temperatures did not allow for defoliation until mid-May, resulting in lower mean defoliation levels later than at the other two study sites.

Reproductive diapause occurred within the same two weeks of mid-August at all three study sites, ending dispersal and reproduction. Bean and others (2007a) initially reported the critical day length for *D. carinulata* populations across western North America to be ~14 hours 39 minutes, with >50 percent of the population entering reproductive diapause 13 days after the critical day length was reached. Bean and others (2012) refined these estimates, reporting that the critical day length for *D. carinulata* had changed across populations in North America 7 years after initial releases occurred. On the basis of our results, we estimate a critical day length for our study sites of somewhere between 13 hours 52 minutes and 14 hours 6 minutes, suggesting a critical day length for *D. carinulata* populations 33 to 47 minutes shorter than that of populations first introduced into North America in 2001.

Because the *D. carinulata* population at each of our study sites entered reproductive diapause within the same timeframe but differed in when they first became active, owing to spring temperatures, we noted a difference in how many new generations were produced in 2011. The "environmental container" of spring temperatures and fall day lengths in limiting voltinism rates has also been shown to occur in other leaf beetles (Dalin, 2011). Owing to the earlier arrival of warmer temperatures at the Marble Canyon and Grand Canyon study sites, an entire extra generation developed in comparison with the San Juan study site. As summer activity began as early as it did in 2012 compared to 2011, a fourth generation of *D. carinulata* might have occurred at the Grand Canyon study site in 2012. Differences in voltinism rates as a product of abiotic cues may significantly affect the growth rate of a population to defoliating levels. Although the hotter climates farther south from our study sites in the Mojave and Sonoran Deserts may allow earlier emergence of *D. carinulata* from overwintering, shortened day lengths due to the more southerly latitudes may also induce an earlier overwintering in the summer, thus still limiting this species to three or four generations. Comparatively, other species of *Diorhabda,* such as *D. sublineata* and *D. elongata,* may, in fact, be better suited for regions farther south of our study sites, because their biogeographic heritage is more similar to that of the lower deserts of North America (Tracy and Robbins, 2009).
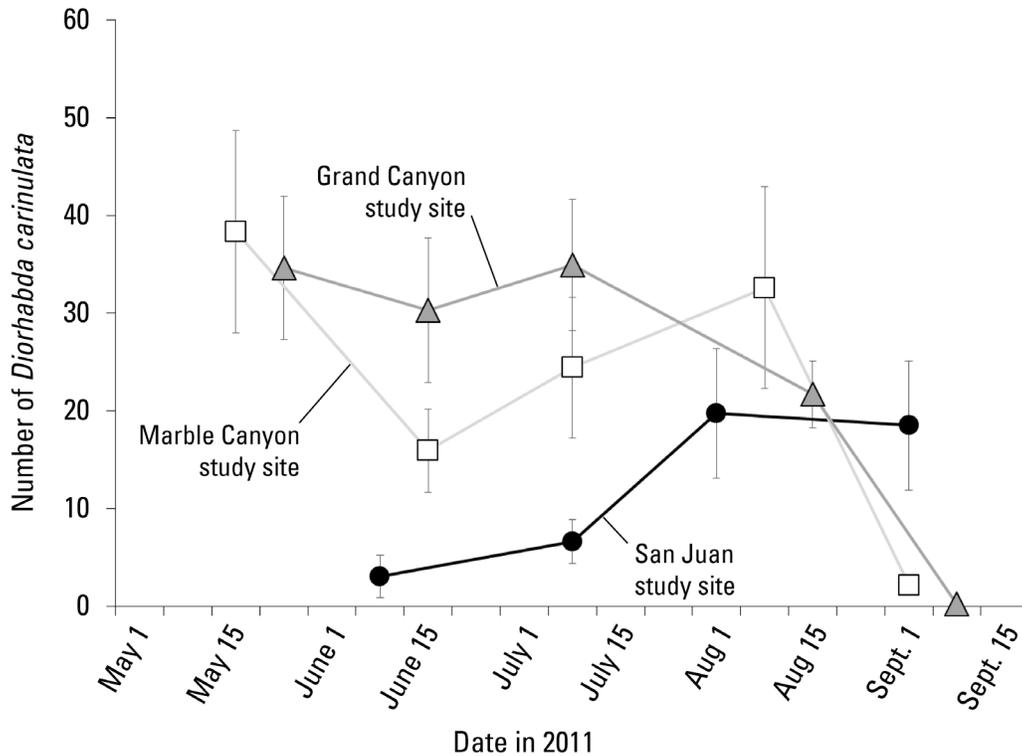
Figure 13. Mean sample abundance of *Diorhabda carinulata* per monthly survey at the Marble Canyon (white squares), Grand Canyon (gray triangles), and San Juan (black circles) study sites in the Colorado River basin in 2011.

Spatial Dynamics of *D. carinulata* and Defoliation

Across our study area, we observed that *D. carinulata* populations declined once defoliation levels rose high enough to dissuade further establishment by *D. carinulata*. We recorded nearly a hundredfold difference between the mean numbers of *D. carinulata* in areas of 50-percent versus 100-percent defoliation (46 ± 16.61 [1σ] and 0.42 ± 0.16 [1σ], respectively). At the Marble Canyon study site, >90 percent defoliation was spread over the first 19 km of the river in July and was completely deserted by the second summer generation of larvae. Jamison and others (2015) reported the desertion of a large (>60 km long) defoliation zone along the Dolores River by *D. carinulata*, suggesting that beetles readily leave areas when food resources disappear. Our results complement Jamison and others' (2015) findings that areas will be abandoned when the defoliation level reaches >90 percent and may not be recolonized for ≥1 year. Interannual variation in tamarisk defoliation levels have been reported in other studies as well (Hultine and others, 2010; Pattison and others, 2011; Nagler and others, 2012; Snyder and others, 2012), where *D. carinulata* populations decrease in the year(s) after a substantial season of defoliation. We suggest that this effect is likely due to emigration of beetles out of highly defoliated areas.

Snyder and others (2010) reported that leaf desiccation is a product of uncontrolled water loss through destroyed cells from beetle feeding and that feeding leads to inflated leaf loss more than would be expected. Although they detected no signs of chemical communication to initiate such a reaction in tamarisk, they proposed that exaggerated leaf loss may be an evolutionary reaction to herbivory, in which trees prematurely lose leaves to deprive beetles of an already-

small food bank. Hudgeons and others (2007) reported that root carbohydrate reserves of tamarisk did not significantly differ between control trees and tamarisk defoliated for only 1 month, and that only extended periods of time (months to years) led to a significant reduction in defoliation. Tamarisk may have evolved to lose leaves to desiccation rapidly after intense feeding occurs so that herbivores may move on quicker, allowing trees the chance to return to normality sooner. We observed heavily defoliated areas to be both abandoned and rapidly refoliated within 1 month after herbivory ceased. Rapid refoliation of tamarisk after defoliation by *D. carinulata* has also been noted by other workers (Nagler and others, 2012; Snyder and others, 2012).

As *D. carinulata* emigrate from defoliated areas, dispersal appears to correlate in its rise with that of the increase in defoliation levels. The record for farthest dispersed *D. carinulata* was for one adult found 43 km from the main population body and 13 km from the nearest other beetle at the isolated Marble Canyon study site. Although the Marble Canyon and San Juan study sites had a similar level of expansion of both the main population body and the dispersal zones, we believe that our results were confounded at the San Juan study site by immigration into the site from a greater regional population. *D. carinulata* population at the San Juan study site significantly increased as soon as the first summer generation of larvae pupated altogether into winged adults by the start of August 2011. This observation would support our notion that the *D. carinulata* population increase at this study site in August and September was a result of immigration as winged adults of the first summer generation could finally disperse out of other defoliated areas into the river corridor where we sampled.

Owing to the open topography of the San Juan study site, *D. carinulata* population movement there would have been less inhibited than within the deeply entrenched canyons of the Marble Canyon and Grand Canyon study sites. On the basis of surveys outside the dates of this study, we observed that both Marble Canyon and Grand Canyon study sites would have lacked much influence from surrounding *D. carinulata* populations, owing to the sparseness of tamarisk across the areas surrounding those canyons. As a result, these two study sites were more topographically and geographically isolated from other *D. carinulata* populations than the San Juan study site. We believe that the combination of topography, geographic isolation, average temperature, and day length all affected the population dynamics that we observed during our study. The San Juan study site, which had the smallest *D. carinulata* population, also had the largest increase in population size, owing to the geography and topography of the study site. Because the San Juan study site was the coldest, with the shortest active season, only two new summer generations occurred there. In contrast, the Marble Canyon study site produced three new summer generations, had the most cohesive population movement of all the study sites, and exhibited the same patterns of other large colonizing *D. carinulata* populations reported elsewhere (Jamison and others, 2015). Although the Marble Canyon study site had a lower rate of population expansion than the San Juan study site, the mean abundance of *D. carinulata* was consistently higher there than at the San Juan study site. Comparatively, the Grand Canyon study site was the warmest, resulting in almost four new summer generations. Population movement there differed from that at the Marble Canyon study site in that it was less cohesive and more scattered. Additionally, we observed significant mortality in the winter of 2011–12 at the Grand Canyon study site, resulting in a significantly reduced *D. carinulata* population in the following spring.

We attribute the decline and lack of expansion in the *D. carinulata* population at the Grand Canyon study site to the geology and habitat suitability of the study site, in which riparian

vegetation and tamarisk are generally sparse in various parts of the canyon. We noted an observable boundary in the middle of the Grand Canyon at km 246 that appeared to divide the *D. carinulata* population in two. This boundary occurs along a geologic stretch of canyon called the Muav Gorge (km 227–280), a very narrow and deep-walled part of the canyon in which vegetation in riparian zones is less abundant. We believe that the geologic setting of the Muav Gorge and that of the canyon at the upstream side of the Grand Canyon study site significantly affected the increase and expansion of the *D. carinulata* population upstream of km 285 in the Grand Canyon. The relative scarcity of tamarisk may explain why we observed a disproportionate number of dead overwintering beetles relative to what we would have expected. Out of the 18 dead *D. carinulata* found in winter in the Grand Canyon study site, 13 were within the Muav Gorge, and 4 others near the upstream boundary of the study site. Bean and others (2007b) described how *D. carinulata* procure fat bodies upon induction into diapause, for fueling metabolic activity throughout overwintering. It is reasonable to suggest that in areas of high defoliation and sparse tamarisk, finding sufficient foliage to feed and sequester fat bodies before overwintering may be a challenge. The mean abundances of *D. carinulata* at the Grand Canyon study site in April and May 2012 were significantly lower than in August 2011, suggesting two important points: (1) resource scarcity (whether due to defoliation or scarcity of tamarisk) may influence the overwintering mortality rates of *D. carinulata*; and (2) winter mortality will significantly lower the *D. carinulata* population, decreasing the defoliation potential of the first-summer-generation larvae in the following spring.

   We noted a significant correlation between the spatial distribution of each population in fall 2011 and spring 2012. Because we would not expect the distribution of a population to move over the winter (barring mortality), the spatial correlation between the population in the fall and spring is useful for forecasting the location of high-abundance first-summer-generation larvae in the next year. Because of this correlation, as well as that between the abundance of first-summer-generation larvae and the intensity level of the first defoliation of the year, the occurrence and location of initial tamarisk defoliation may be predictable 6 months or more before it occurs.

   Although defoliation from first-summer-generation larvae is related to the distribution of the *D. carinulata* population in the proceeding fall, we observed defoliation in the season from second- and third-generation larvae to occur in one of two ways: (1) first-summer-generation larval abundances, and thus initial defoliation, were low enough that second-generation larvae were established within the same area, only intensifying defoliation levels; or (2) first-summer-generation larval abundances were high enough to cause substantial defoliation, and subsequent pupation into the adult stage would cause emigration out into areas with sufficient green foliage to establish the second summer generation, which would then begin to defoliate new areas, or areas with low larval abundances as in the first way. Any third-generation larvae would be established and cause defoliation in the same way, on the basis of abundances and movement of the second summer generation. Thus, the timing of defoliation by the second and later summer generations of larvae will depend on the rate and timing of pupation of each generation, and this defoliation will occur only in areas where defoliation from the previous generation was not too high.

Conclusion

   The management of invasive tamarisk and the conservation of riparian forests in North America is a dynamic situation involving many challenges. Tamarisk, interestingly now in need of protection and conservation in parts of its native Central Asia (Zhang and Zhang, 2012), is

simultaneously spreading in Australia and Argentina (Griffin and others, 1989; Natale and others, 2013). The introduction of *Diorhabda* spp. to North America may be a useful occurrence in which we can study its effectiveness as a biologic control mechanism, while also observing its dynamic interactions with tamarisk. The ability to predict the timing of tamarisk defoliation by *D. carinulata* is useful if we are concerned about the impacts of defoliation on other organisms. Our findings suggest that the synthesis of (1) abiotic cues, (2) spatial distribution of *D. carinulata*, and (3) movement of *D. carinulata* as affected by resource destruction (that is, defoliation) during summer, may permit prediction of when and where defoliation will occur across a given landscape. This information may be useful for planning restoration with regard to other species conservation when considering the potential use and impacts of tamarisk defoliation by *D. carinulata*.

   With regard to the conservation of breeding birds, for example, the timing of initial defoliation by the first-summer-generation larvae as a product of springtime temperature rise is of unique concern. Paxton and others (2011) presented a case concerning tamarisk defoliation as an "ecological trap," whereby breeding birds build nests in tamarisk before the occurrence of defoliation, only to have defoliation occur once they have begun incubating eggs or feeding nestlings, leading to a significant increase in nest failure. To illustrate their concerns, Paxton and others (2011) compared initial tamarisk-defoliation dates at a site near Dolores, Colo. with the timing of Southwestern Willow Flycatcher breeding events in Roosevelt, Ariz. (fig. 1). On the basis of this comparison, they predicted that defoliation would occur after Southwestern Willow Flycatchers began nesting but before fledging their young, so that birds would be led into an ecological trap related to the timing of defoliation and bird phenology. Although the example used by Paxton and others (2011) was purely hypothetical to explain a point of concern, on the basis of our results we would expect a different result if this scenario actually occurred in Roosevelt, Ariz. On the basis of our observed correlation between *D. carinulata* activity and springtime temperature rise, in this scenario we would expect defoliation from first-summer-generation larvae to initially occur in Roosevelt, Ariz., by late April or early May (similar to what occurred at the Grand Canyon study site), during the period in which most Southwestern Willow Flycatchers would have migrated into the area and ≥6 weeks before eggs would be laid (Sogge and others, 1997; Ellis and others, 2009). Thus, we would expect an entirely different outcome, in which defoliation would occur before nesting sites were chosen, giving Southwestern Willow Flycatchers the chance to avoid tamarisk for nesting.

   Comparatively, if this hypothetical scenario were to occur instead in Dolores, Colo., on the basis of our results, two different outcomes could ensue. (1) If *D. carinulata* abundances were too low to noticeably defoliate an area with first-summer-generation larvae, and if defoliating levels were not achieved until the second summer generation, then defoliation would not be expected to occur until early August to mid-August, at which point most Southwestern Willow Flycatchers would have fledglings or be migrating. Conversely (2), if this generation overwintered in high abundances, then we would expect high defoliation levels in the next spring at the height of incubation, just as Paxton and others (2011) suggested. Furthermore, if defoliation levels then were high enough, we would expect the *D. carinulata* population to abandon the area, dispersing in the adult stage to establish the second summer generation in a new area. Because only two new summer generations would be expected in Dolores, Colo., the second summer generation would become the overwintering generation, and as a result the area of initially high defoliation level would be devoid of *D. carinulata* for a whole year until adults of the first summer generation in the following season could finally migrate back around mid-

July. Thus, because our results on defoliation timing are a product of abiotic cues, spatial abundances and dispersal of beetles from overconsumed areas have specific value to the concerns presented by Paxton and others (2011).

Given the continued movement of *D. carinulata* and other more southern adapted *Diorhabda* species (*D. sublineata* and *D. elongata*) into Southwestern Willow Flycatcher critical habitat (Bloodworth and others, 2016), further research is warranted on the adaptability of *D. carinulata* to lower latitudes and on the abiotic restraints governing the timing of activity in *D. sublineata* and *D. elongata*. Because *Diorhabda* spp. will likely colonize tamarisk across the range of the Southwestern Willow Flycatcher, understanding the dynamics of tamarisk defoliation and the response of Southwestern Willow Flycatchers to tamarisk defoliation will be useful for protecting the bird during its reproductive season. Our results provide a rationale by which to understand and predict the variation in the timing of defoliation across a given landscape and may be useful for the conservation of riparian habitats.

Management Implications

- The duration of annual activity of *D. carinulata* will be dictated by rising temperatures in the spring and shortening day lengths in the fall. These abiotic cues will dictate the number of new generations, the timing of initial defoliation, and when *D. carinulata* will disappear and defoliation will cease.
- The abundance of *D. carinulata* in the fall, just before overwintering, will be useful in predicting the location of initial defoliation in the next spring. The timing and location of the first defoliation events of the year can be predicted ≥6 months before.
- If defoliation levels reach >90 percent, *D. carinulata* will emigrate until sufficient green foliage returns. *D. carinulata* may abandon an area for as long as a year.
- The density of tamarisk in an area may limit the size of a *D. carinulata* population, and areas with sparse tamarisk may not allow sustainable levels of *D. carinulata* population.
- Winter mortality may have a large impact on how quickly a *D. carinulata* population can increase defoliation level in the following spring.

Acknowledgments

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Appendix 1. Temperature and Day-Length Data for Study Sites in the Colorado River basin, 2011–12

Temperature Data, 2011–12

Temperature data are from records supplied by the National Oceanic and Atmospheric Administration (NOAA)'s National Environmental Satellite, Data, and Information Service (http://www.ncdc.noaa.gov/cdo-web/search) for the spring months (March 1–June 30) in 2011 and 2012. For the Marble Canyon study site, we used the data from station GHCND:USW00053164 (PAGE 9 WSW AZ US, elev 991.8 m, lat 36.8637° N, long 111.6012° W) in Lees Ferry, Arizona; for the Grand Canyon study site, we used the data from station GHCND:USC00026471 (PHANTOM RANCH AZ US, elev 771.1 m, lat 36.1383° N, long 112.0958° W) in Phantom Ranch, Arizona; and for the San Juan study site, we used the data from station GHCND:USC00293142 (FARMINGTON AG SCIENCE CNT NM US, elev 1,714.5 m, lat 36.6897° N, long 108.3086° W) in Farmington, New Mexico. Dates are listed in "yyyymmdd" format; T_{max} and T_{min}, maximum and minimum temperature, respectively, on each day.

Temperature Data for the Marble Canyon Study Site from Lees Ferry, Ariz., 2011

Date	T_{max}	T_{min}
20110301	15.5	0.4
20110302	18.4	2.7
20110303	20.6	5
20110304	16.9	7.3
20110305	18	1.5
20110306	17.2	4.3
20110307	15.6	7.5
20110308	14.8	5.3
20110309	17.3	2.9
20110310	19.5	3.6
20110311	22.8	4.1
20110312	24.8	6.3
20110313	20.7	8
20110314	23.8	6.7
20110315	24.1	8.9
20110316	27.2	8.5
20110317	23.5	13.6
20110318	23.9	7.7
20110319	22.1	9.7
20110320	19.3	9.9

Date	T_{max}	T_{min}
20110321	17.7	4.8
20110322	13.6	3.2
20110323	17.1	2.1
20110324	18.6	7.3
20110325	18.3	6.1
20110326	11.3	5.8
20110327	20.1	2.7
20110328	23.3	7.1
20110329	17.7	8.1
20110330	24.2	6.5
20110331	28.6	14.6
20110401	29.8	9.7
20110402	31.3	10.4
20110403	23	8.3
20110404	17.3	4.1
20110405	25.9	4.7
20110406	20.2	9.8
20110407	22	6.9
20110408	16.9	6.8
20110409	11.2	3.8
20110410	15.8	1.8
20110411	19.5	3.2
20110412	24.8	8.5
20110413	24.5	8.7
20110414	19.9	9.4
20110415	21.4	8.3
20110416	27.8	7.6
20110417	31	11.8
20110418	28.3	16.6
20110419	27.1	10.5
20110420	28.8	11.7
20110421	28.4	14.4
20110422	24.5	13.8
20110423	21.7	13.6
20110424	23.4	11
20110425	24.7	8.3
20110426	20	11.1
20110427	19.5	7.2
20110428	28.7	6.5
20110429	23.9	8.6
20110430	15.5	6.3
20110501	17.6	8.1

Date	T_{max}	T_{min}
20110502	20.7	6.7
20110503	28.2	6.3
20110504	30	15.5
20110505	29	11.9
20110506	33.5	12.3
20110507	33.3	15.5
20110508	30.8	18.8
20110509	21.2	10.2
20110510	16.8	7.9
20110511	21.3	12.6
20110512	28.9	9.3
20110513	29.7	13.8
20110514	30.5	15.5
20110515	30.8	16.9
20110516	26.3	16.2
20110517	24.4	13.3
20110518	19.5	12.7
20110519	19.3	11.4
20110520	22.5	10
20110521	28.1	9.5
20110522	30.7	13.5
20110523	29	17
20110524	26	14.7
20110525	29.4	12.9
20110526	32.7	18.3
20110527	35.5	15.6
20110528	35.6	17.7
20110529	28	13.2
20110530	24.8	11.9
20110531	33.1	10.3
20110601	33.4	19.1
20110602	30.2	16.8
20110603	29.7	13.4
20110604	35.6	13.2
20110605	37.5	15.4
20110606	33.7	18.5
20110607	31.6	14.5
20110608	33.1	16.4
20110609	33.6	16.2
20110610	35.5	17.4
20110611	35	19.4
20110612	34.5	17.3

Date	T_{max}	T_{min}
20110613	34.8	17.5
20110614	37.1	19
20110615	39.1	20.5
20110616	38	25.9
20110617	33.1	22.4
20110618	36.3	18.5
20110619	31.3	20.6
20110620	31.4	18.5
20110621	35.1	20.8
20110622	39	18.4
20110623	40.8	21.1
20110624	40.7	25.5
20110625	40.5	23.3
20110626	39.6	21.4
20110627	41.6	19.7
20110628	41.3	22.5
20110629	40.7	28.7
20110630	34.9	26.5

Temperature Data for the Marble Canyon Study Site from Lees Ferry, Ariz., 2012

Date	T_{max}	T_{min}
20120301	12.7	2.2
20120302	10.6	1.8
20120303	12.8	0.2
20120304	17.1	0.8
20120305	19	1.4
20120306	24.3	4.3
20120307	13.4	4.5
20120308	16.8	4.5
20120309	17.5	1.5
20120310	18.5	3.1
20120311	22.8	4
20120312	21.9	10.9
20120313	25.5	4.7
20120314	22.7	5.5
20120315	25	6.6
20120316	26.4	6.6
20120317	23.4	14.8
20120318	15.2	3.8

Date	T_{max}	T_{min}
20120319	11.2	2.9
20120320	14.2	4
20120321	20.1	4.1
20120322	23.9	5.1
20120323	26.6	6.8
20120324	25.4	9
20120325	26.2	11.3
20120326	21.3	12.3
20120327	22.7	7.7
20120328	26.3	7.5
20120329	25.6	10.4
20120330	28.1	9.1
20120331	30.3	11.1
20120401	20.1	10.5
20120402	18.4	7.7
20120403	22.7	7.9
20120404	26.9	7.9
20120405	26.1	10.1
20120406	18.4	10.3
20120407	20.3	4
20120408	25.4	4.9
20120409	29.6	7.7
20120410	29.9	9.2
20120411	25.9	12.2
20120412	20.4	12
20120413	17.8	10.2
20120414	12.9	4
20120415	21.2	7.1
20120416	22.9	9.5
20120417	26.5	8.7
20120418	30.5	10.2
20120419	30.1	14.9
20120420	28.2	13.7
20120421	31.7	12.7
20120422	34.1	13.8
20120423	35.1	15.3
20120424	34.7	15.7
20120425	27.6	18.8
20120426	24.8	15.5
20120427	26.2	13.9

Date	T_{max}	T_{min}
20120428	25.4	16.5
20120429	25.1	14.9
20120430	30.9	11.2
20120501	31.5	17.9
20120502	29.6	19.2
20120503	31.8	14.4
20120504	33.1	14.2
20120505	29.3	16.2
20120506	27.1	15.7
20120507	25.7	16.1
20120508	27.5	17.5
20120509	29.9	13.5
20120510	34.4	14.1
20120511	33.3	17.7
20120512	32.6	17.6
20120513	32.5	15.8
20120514	31.4	14.1
20120515	35.5	14.3
20120516	34.5	21.4
20120517	37.4	16.2
20120518	31	20.4
20120519	28.9	16.1
20120520	33.7	14.5
20120521	38	15.6
20120522	38.3	20.7
20120523	35.6	23.7
20120524	32.4	19.1
20120525	32.8	22.6
20120526	23.4	17
20120527	26.2	11.9
20120528	29.2	12.5
20120529	34.5	13.6
20120530	35	16.2
20120531	35.8	19.4
20120601	38.3	19.5
20120602	39.4	22.4
20120603	39.7	21.8
20120604	38.4	21.9
20120605	35.7	22.8
20120606	33.6	19.2

Date	T_{max}	T_{min}
20120607	34.5	18.3
20120608	38	18.9
20120609	38	22.1
20120610	30.5	17.8
20120611	33.6	17.4
20120612	37.8	16.9
20120613	38.4	18.1
20120614	38	21.6
20120615	37.2	22.6
20120616	38.4	20.3
20120617	40.1	20.6
20120618	40	24.6
20120619	40.2	20.9
20120620	38.2	26.1
20120621	42.5	20.8
20120622	40.6	23.5
20120623	41	20.8
20120624	41.3	22.5
20120625	40.3	25.6
20120626	39.9	23.3
20120627	40.3	25
20120628	40.6	25.1
20120629	41.3	25
20120630	41.7	24.5

Temperature Data for the Grand Canyon Study Site from Phantom Ranch, Ariz., 2011

Date	T_{max}	T_{min}
20110301	17.8	1.7
20110302	19.4	3.9
20110303	22.8	6.7
20110304	21.1	5.6
20110305	21.1	3.9
20110306	22.2	5.6
20110307	21.1	9.4
20110308	15.6	5
20110309	20.6	3.3
20110310	22.2	6.1
20110311	26.7	6.1
20110312	27.2	10.6

Date	T_{max}	T_{min}
20110313	25.6	8.9
20110314	25.6	9.4
20110315	26.7	11.1
20110316	28.3	11.1
20110317	26.7	13.9
20110318	26.1	8.9
20110319	26.1	8.9
20110320	22.8	12.2
20110321	20.6	7.2
20110322	16.1	5.6
20110323	20	3.9
20110324	20	9.4
20110325	18.3	9.4
20110326	16.7	6.1
20110327	22.2	7.8
20110328	25.6	10
20110329	22.2	11.1
20110330	25.6	8.3
20110331	29.4	12.2
20110401	32.2	11.7
20110402	33.3	12.2
20110403	31.7	17.8
20110404	21.1	8.9
20110405	30.6	7.8
20110406	25	11.1
20110407	23.9	9.4
20110408	20	7.2
20110409	11.7	3.9
20110410	16.1	4.4
20110411	22.8	5
20110412	26.7	9.4
20110413	26.7	10
20110414	21.7	10
20110415	25.6	7.8
20110416	29.4	9.4
20110417	33.9	12.8
20110418	29.4	17.2
20110419	30.6	16.7
20110420	31.7	16.1
20110421	30	18.3
20110422	29.4	13.9
20110423	26.7	18.3

Date	T_{max}	T_{min}
20110424	27.2	15.6
20110425	27.8	15
20110426	26.1	16.1
20110427	25	9.4
20110428	32.2	10
20110429	31.7	19.4
20110430	23.3	8.3
20110501	20	8.3
20110502	25	7.2
20110503	31.1	8.9
20110504	32.8	12.2
20110511	25.6	13.9
20110512	31.7	12.8
20110517	25.6	13.9
20110518	23.3	11.1
20110519	23.9	9.4
20110520	26.1	12.8
20110521	31.1	11.7
20110522	32.8	15.6
20110523	30.6	18.3
20110524	30.6	15.6
20110525	35	16.1
20110526	35.6	21.7
20110527	38.3	17.2
20110528	36.7	20
20110529	32.2	20.6
20110530	27.2	13.9
20110531	36.1	12.8
20110601	35.6	17.8
20110602	32.8	16.7
20110603	33.9	16.7
20110604	37.2	15.6
20110605	38.9	17.2
20110606	36.1	19.4
20110607	36.1	16.1
20110608	34.4	17.2
20110609	35.6	16.7
20110610	38.9	18.3
20110611	36.7	21.1
20110612	36.1	18.9
20110613	37.2	17.8
20110614	39.4	20.6

Date	T_{max}	T_{min}
20110615	42.2	20.6
20110616	39.4	26.1
20110617	34.4	21.7
20110618	38.9	18.9
20110619	35.6	18.3
20110620	35.6	18.3
20110621	39.4	19.4
20110622	43.9	20.6
20110623	43.3	22.8
20110624	42.8	25
20110625	41.7	22.8
20110626	41.7	23.3
20110627	43.3	21.1
20110628	43.3	23.9
20110629	40.6	30
20110630	38.3	25.6

Temperature Data for the Grand Canyon Study Site from Phantom Ranch, Ariz., 2012

Date	T_{max}	T_{min}
20120301	16.1	5.6
20120302	13.9	3.3
20120303	16.7	1.1
20120304	21.1	2.8
20120305	22.2	3.9
20120306	25.6	6.7
20120307	21.7	5
20120308	19.4	3.3
20120309	21.1	4.4
20120310	21.7	7.8
20120311	26.7	8.9
20120312	25.6	8.3
20120313	27.8	7.2
20120314	26.7	8.3
20120315	27.8	9.4
20120316	29.4	10.6
20120317	25.6	14.4
20120318	20	5.6
20120319	11.1	4.4
20120320	16.1	5
20120321	21.7	5

Date	T_{max}	T_{min}
20120322	26.1	6.7
20120323	28.3	9.4
20120324	27.8	10.6
20120325	27.8	12.2
20120326	23.9	9.4
20120327	26.7	8.3
20120328	27.8	10.6
20120329	27.8	10.6
20120330	28.9	12.2
20120331	31.7	13.9
20120401	27.8	11.7
20120402	19.4	8.9
20120403	23.9	9.4
20120404	28.9	10.6
20120405	27.2	13.9
20120406	22.2	12.8
20120407	26.1	9.4
20120408	30	10.6
20120409	33.3	11.1
20120410	33.3	12.2
20120411	21.1	14.4
20120412	22.8	12.8
20120413	20	13.3
20120414	17.2	6.7
20120415	20.6	7.2
20120416	25	8.3
20120417	30	10
20120418	32.2	12.2
20120419	32.2	13.9
20120420	32.2	15
20120421	36.1	14.4
20120422	38.3	16.1
20120423	37.8	17.2
20120424	36.7	16.7
20120425	30	20
20120426	27.8	17.8
20120427	28.3	17.2
20120428	28.9	17.2
20120429	30.6	16.7
20120430	33.9	13.9
20120501	32.2	18.3
20120502	32.2	17.8

Date	T_{max}	T_{min}
20120503	33.3	17.2
20120504	35	16.1
20120505	34.4	16.1
20120506	31.1	16.1
20120507	31.1	15.6
20120508	31.1	15.6
20120509	32.2	13.9
20120510	36.1	17.8
20120511	36.7	18.3
20120512	36.7	17.8
20120513	35.6	17.8
20120514	36.1	16.7
20120515	38.9	19.4
20120516	37.2	19.4
20120517	39.4	18.3
20120518	33.3	23.9
20120519	34.4	18.9
20120520	37.8	16.7
20120521	40.6	18.9
20120522	40.6	21.1
20120523	39.4	22.2
20120524	36.7	22.2
20120525	32.8	21.7
20120526	29.4	17.8
20120527	28.9	13.9
20120528	34.4	15
20120529	37.8	17.2
20120530	37.8	17.8
20120531	40	17.8
20120601	43.3	21.1
20120602	41.7	23.9
20120603	41.7	22.2
20120604	40	22.2
20120605	37.8	23.3
20120606	37.8	18.9
20120607	39.4	20
20120608	40	21.1
20120609	39.4	23.3
20120610	36.7	22.2
20120611	39.4	22.8
20120612	40.6	20
20120613	41.1	21.1

Date	T_{max}	T_{min}
20120614	40.6	22.8
20120615	39.4	21.7
20120616	41.7	21.7
20120617	42.2	25
20120618	41.7	25
20120619	42.2	20
20120620	43.3	22.8
20120621	44.4	25
20120622	42.2	24.4
20120623	42.2	22.2
20120624	42.8	25
20120625	41.7	27.8
20120626	40.6	26.1
20120627	42.2	26.1
20120628	42.2	27.8
20120629	43.9	27.2
20120630	43.9	26.1

Temperature Data for the San Juan Study Site from Farmington, N. Mex., 2011

Date	T_{max}	T_{min}
20110301	10.6	-6.7
20110302	15	0
20110303	16.7	1.7
20110304	16.7	0
20110305	11.1	-6.7
20110306	12.2	-3.3
20110307	10	0.6
20110308	8.9	-1.7
20110309	6.1	-4.4
20110310	12.2	-1.7
20110311	15.6	0.6
20110312	19.4	2.2
20110313	18.9	1.7
20110314	15.6	0.6
20110315	18.3	0
20110316	18.9	1.1
20110317	22.8	3.9
20110318	20.6	1.1
20110319	18.9	1.7
20110320	20.6	3.9

Date	T_{max}	T_{min}
20110321	16.1	5
20110322	19.4	0
20110323	8.9	-5
20110324	12.8	-3.3
20110325	13.3	-3.9
20110326	15	-3.3
20110327	13.3	0
20110328	15.6	0.6
20110329	17.8	-1.1
20110330	13.9	-2.2
20110331	15.6	-1.7
20110401	21.1	2.8
20110402	23.3	6.1
20110403	26.1	9.4
20110404	18.9	-3.9
20110405	11.7	-3.9
20110406	21.1	0.6
20110407	18.9	4.4
20110408	17.2	3.9
20110409	20.6	6.1
20110410	15	-6.1
20110411	10	-3.3
20110412	15.6	3.3
20110413	21.1	1.1
20110414	20.6	2.2
20110415	13.3	-0.6
20110416	7.8	-0.6
20110417	20.6	4.4
20110418	24.4	6.1
20110419	8.9	5.6
20110420	20	6.1
20110421	23.3	6.7
20110422	23.3	2.8
20110423	19.4	5
20110424	18.9	5.6
20110425	13.9	3.3
20110426	15.6	3.9
20110427	11.7	-1.1
20110428	11.7	-1.7
20110429	19.4	1.7
20110430	22.8	-2.2
20110501	11.1	-2.2

Date	T_{max}	T_{min}
20110502	11.7	-3.3
20110503	13.9	0
20110504	20.6	2.2
20110505	23.3	1.1
20110506	22.8	3.3
20110507	26.7	5.6
20110508	27.8	7.2
20110509	26.1	10
20110510	19.4	2.2
20110511	16.1	2.8
20110512	16.1	3.3
20110513	21.1	2.8
20110514	25	6.1
20110515	26.7	8.9
20110516	26.7	7.8
20110517	25.6	10
20110518	20.6	7.8
20110519	13.9	3.3
20110520	12.2	4.4
20110521	17.2	3.3
20110522	19.4	7.8
20110523	23.9	8.9
20110524	23.9	7.8
20110525	18.9	4.4
20110526	21.7	7.2
20110527	26.7	9.4
20110528	27.2	13.9
20110529	30.6	14.4
20110530	28.9	5.6
20110531	18.9	6.7
20110601	28.9	10.6
20110602	30	13.3
20110603	29.4	8.9
20110604	28.3	11.7
20110605	31.1	13.3
20110606	32.2	13.9
20110607	31.7	8.3
20110608	27.2	10
20110609	30.6	8.9
20110610	26.7	8.9
20110611	28.3	12.2
20110612	30	10

Date	T_{max}	T_{min}
20110613	28.9	12.8
20110614	30	10
20110615	29.4	10.6
20110616	32.2	14.4
20110617	32.2	14.4
20110618	29.4	15
20110619	30	13.3
20110620	28.9	8.9
20110621	25.6	7.8
20110622	28.3	10.6
20110623	31.7	13.9
20110624	35	16.1
20110625	33.3	15
20110626	33.3	15.6
20110627	33.3	13.3
20110628	35	18.9
20110629	33.9	18.9
20110630	35.6	18.9

Temperature Data for the San Juan Study Site from Farmington, N. Mex., 2012

Date	T_{max}	T_{min}
20120301	8.9	-3.3
20120302	9.4	-6.1
20120303	11.7	-10.6
20120304	3.3	-6.7
20120305	10	-2.2
20120306	15.6	-1.1
20120307	17.2	2.2
20120308	9.4	-2.2
20120309	10	-4.4
20120310	10.6	-3.3
20120311	8.9	-2.2
20120312	16.1	-1.1
20120313	15.6	0
20120314	19.4	0
20120315	18.3	0
20120317	21.1	2.8
20120318	20	3.3
20120319	7.2	-5
20120320	2.2	-5

Date	T_{max}	T_{min}
20120321	14.4	-4.4
20120322	20	-3.9
20120323	19.4	-3.3
20120324	22.8	2.8
20120325	22.8	6.7
20120326	22.8	5
20120327	20.6	-0.6
20120329	22.2	3.3
20120330	20.6	2.2
20120331	22.2	2.8
20120401	25.6	6.1
20120402	22.8	0.6
20120403	8.3	-1.1
20120404	15	-2.2
20120405	20	0.6
20120406	20.6	3.3
20120407	18.3	-3.9
20120408	17.8	2.8
20120409	23.3	3.3
20120410	25.6	7.8
20120411	26.7	8.9
20120412	26.1	4.4
20120413	16.1	0
20120414	13.9	2.2
20120415	10	-1.1
20120416	13.3	-2.8
20120417	15.6	1.1
20120418	21.1	3.9
20120419	23.3	6.1
20120420	20.6	2.8
20120421	22.8	3.9
20120422	26.7	7.8
20120423	27.8	9.4
20120424	28.9	11.1
20120425	29.4	10
20120426	25.6	10.6
20120427	26.7	6.1
20120428	20	3.9
20120430	21.7	3.3
20120501	23.9	7.2
20120502	23.9	5
20120503	24.4	6.1

Date	T_{max}	T_{min}
20120504	26.1	7.8
20120505	27.8	7.8
20120506	25.6	5.6
20120507	24.4	6.1
20120508	22.2	2.8
20120509	21.7	7.8
20120510	23.3	7.2
20120511	26.7	7.2
20120512	27.8	9.4
20120513	25.6	10.6
20120514	22.8	3.9
20120515	23.3	9.4
20120516	28.3	12.8
20120517	28.3	10.6
20120518	28.9	13.3
20120519	26.7	6.7
20120520	23.3	6.7
20120521	27.2	10
20120522	30.6	12.8
20120523	30.6	10
20120524	30	7.8
20120525	24.4	11.7
20120526	29.4	13.3
20120527	27.8	2.8
20120528	20	2.8
20120529	23.3	8.3
20120530	28.9	8.3
20120531	28.3	9.4
20120601	30.6	11.7
20120602	27.8	14.4
20120603	32.2	13.3
20120604	32.2	17.2
20120605	33.3	13.3
20120606	31.7	11.7
20120607	31.1	12.2
20120608	30.6	12.2
20120609	32.2	12.8
20120610	31.1	13.3
20120611	25.6	7.2
20120612	28.9	10
20120613	31.7	12.8
20120614	33.3	12.8

Date	T_{max}	T_{min}
20120615	31.7	13.9
20120616	31.7	13.9
20120617	31.7	14.4
20120618	32.8	13.9
20120619	32.8	12.8
20120620	32.2	14.4
20120621	31.7	12.2
20120622	35	17.2
20120623	36.1	16.1
20120624	36.1	18.3
20120625	36.7	18.9
20120626	35	16.7
20120627	34.4	18.3

Day-Length Data, 2011

Day lengths are from the U.S. Naval Observatory sunrise/sunset tables (http://aa.usno.navy.mil).

Day Lengths for the Marble Canyon Study Site from Lees Ferry, Ariz., 2011

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              o  ,    o  ,            LEE'S FERRY, AZ         Astronomical Applications Dept.
Location: W111 35, N36 51             Universal Time         U. S. Naval Observatory
                                                             Washington, DC  20392-5420

                              Duration of Daylight for 2011

Day   Jan.   Feb.   Mar.   Apr.   May    June   July   Aug.   Sep.   Oct.   Nov.   Dec.

      h  m   h  m   h  m   h  m   h  m   h  m   h  m   h  m   h  m   h  m   h  m   h  m
01    09:41  10:22  11:22  12:35  13:41  14:30  14:39  14:02  12:59  11:50  10:40  09:50
02    09:41  10:24  11:24  12:38  13:43  14:31  14:38  14:01  12:57  11:48  10:38  09:49
03    09:42  10:26  11:27  12:40  13:45  14:32  14:38  13:59  12:55  11:45  10:36  09:48
04    09:43  10:28  11:29  12:42  13:47  14:33  14:37  13:57  12:52  11:43  10:34  09:47
05    09:44  10:30  11:31  12:45  13:49  14:34  14:36  13:55  12:50  11:41  10:32  09:46
06    09:44  10:32  11:34  12:47  13:51  14:35  14:36  13:53  12:48  11:38  10:30  09:45
07    09:45  10:34  11:36  12:49  13:53  14:36  14:35  13:51  12:46  11:36  10:28  09:44
08    09:46  10:36  11:38  12:51  13:55  14:36  14:34  13:50  12:43  11:34  10:26  09:43
09    09:47  10:38  11:41  12:54  13:57  14:37  14:33  13:48  12:41  11:31  10:24  09:42
10    09:48  10:40  11:43  12:56  13:59  14:38  14:32  13:46  12:39  11:29  10:22  09:42
11    09:49  10:42  11:46  12:58  14:00  14:38  14:31  13:44  12:37  11:27  10:21  09:41
12    09:50  10:44  11:48  13:01  14:02  14:39  14:30  13:42  12:34  11:25  10:19  09:40
13    09:52  10:46  11:50  13:03  14:04  14:39  14:29  13:40  12:32  11:22  10:17  09:40
14    09:53  10:48  11:53  13:05  14:06  14:40  14:28  13:38  12:30  11:20  10:15  09:39
15    09:54  10:51  11:55  13:07  14:07  14:40  14:27  13:36  12:27  11:18  10:13  09:39
16    09:55  10:53  11:57  13:10  14:09  14:40  14:26  13:34  12:25  11:15  10:12  09:39
17    09:57  10:55  12:00  13:12  14:11  14:41  14:25  13:32  12:23  11:13  10:10  09:38
18    09:58  10:57  12:02  13:14  14:12  14:41  14:23  13:30  12:20  11:11  10:08  09:38
19    10:00  10:59  12:05  13:16  14:14  14:41  14:22  13:27  12:18  11:09  10:07  09:38
20    10:01  11:02  12:07  13:18  14:15  14:41  14:21  13:25  12:16  11:06  10:05  09:38
21    10:03  11:04  12:09  13:21  14:17  14:41  14:20  13:23  12:13  11:04  10:03  09:38
22    10:04  11:06  12:12  13:23  14:18  14:41  14:18  13:21  12:11  11:02  10:02  09:38
23    10:06  11:08  12:14  13:25  14:20  14:41  14:17  13:19  12:09  11:00  10:00  09:38
24    10:08  11:11  12:16  13:27  14:21  14:41  14:15  13:17  12:06  10:58  09:59  09:38
25    10:09  11:13  12:19  13:29  14:22  14:41  14:14  13:15  12:04  10:55  09:58  09:38
26    10:11  11:15  12:21  13:31  14:24  14:41  14:12  13:12  12:02  10:53  09:56  09:38
27    10:13  11:17  12:23  13:33  14:25  14:40  14:11  13:10  11:59  10:51  09:55  09:38
28    10:14  11:20  12:26  13:35  14:26  14:40  14:09  13:08  11:57  10:49  09:54  09:39
29    10:16         12:28  13:37  14:27  14:40  14:07  13:06  11:55  10:47  09:52  09:39
30    10:18         12:31  13:39  14:28  14:39  14:06  13:04  11:52  10:45  09:51  09:39
31    10:20         12:33         14:29         14:04  13:01         10:42         09:40
```

Day Lengths for the Grand Canyon Study Site from Phantom Ranch, Ariz., 2011

```
                 o   ,    o  ,              PHANTOM RANCH, AZ          Astronomical Applications Dept.
    Location: W112 08, N36 05                 Universal Time           U. S. Naval Observatory
                                                                       Washington, DC  20392-5420


                                        Duration of Daylight for 2011
```

Day	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m
01	09:45	10:25	11:23	12:34	13:39	14:26	14:34	13:59	12:58	11:50	10:43	09:54
02	09:45	10:27	11:26	12:37	13:41	14:27	14:34	13:57	12:56	11:48	10:41	09:53
03	09:46	10:28	11:28	12:39	13:43	14:28	14:33	13:56	12:53	11:46	10:39	09:52
04	09:47	10:30	11:30	12:41	13:45	14:29	14:33	13:54	12:51	11:44	10:37	09:51
05	09:48	10:32	11:32	12:43	13:46	14:30	14:32	13:52	12:49	11:41	10:35	09:50
06	09:48	10:34	11:35	12:46	13:48	14:31	14:31	13:50	12:47	11:39	10:33	09:49
07	09:49	10:36	11:37	12:48	13:50	14:31	14:31	13:48	12:45	11:37	10:31	09:48
08	09:50	10:38	11:39	12:50	13:52	14:32	14:30	13:47	12:42	11:35	10:29	09:47
09	09:51	10:40	11:42	12:52	13:54	14:33	14:29	13:45	12:40	11:32	10:27	09:47
10	09:52	10:42	11:44	12:55	13:55	14:33	14:28	13:43	12:38	11:30	10:25	09:46
11	09:53	10:44	11:46	12:57	13:57	14:34	14:27	13:41	12:36	11:28	10:24	09:45
12	09:54	10:46	11:48	12:59	13:59	14:34	14:26	13:39	12:33	11:26	10:22	09:45
13	09:55	10:48	11:51	13:01	14:01	14:35	14:25	13:37	12:31	11:23	10:20	09:44
14	09:57	10:51	11:53	13:03	14:02	14:35	14:24	13:35	12:29	11:21	10:18	09:44
15	09:58	10:53	11:55	13:06	14:04	14:36	14:23	13:33	12:27	11:19	10:17	09:43
16	09:59	10:55	11:58	13:08	14:06	14:36	14:22	13:31	12:24	11:17	10:15	09:43
17	10:01	10:57	12:00	13:10	14:07	14:36	14:21	13:29	12:22	11:15	10:13	09:43
18	10:02	10:59	12:02	13:12	14:09	14:36	14:20	13:27	12:20	11:12	10:12	09:42
19	10:03	11:01	12:05	13:14	14:10	14:37	14:18	13:25	12:18	11:10	10:10	09:42
20	10:05	11:03	12:07	13:16	14:12	14:37	14:17	13:23	12:15	11:08	10:08	09:42
21	10:06	11:06	12:09	13:18	14:13	14:37	14:16	13:21	12:11	11:06	10:07	09:42
22	10:08	11:08	12:11	13:21	14:14	14:37	14:14	13:19	12:11	11:04	10:05	09:42
23	10:09	11:10	12:14	13:23	14:16	14:37	14:13	13:17	12:09	11:02	10:04	09:42
24	10:11	11:12	12:16	13:25	14:17	14:37	14:12	13:15	12:06	10:59	10:03	09:42
25	10:12	11:14	12:18	13:27	14:18	14:36	14:10	13:13	12:04	10:57	10:01	09:42
26	10:14	11:17	12:21	13:29	14:20	14:36	14:09	13:11	12:02	10:55	10:00	09:42
27	10:16	11:19	12:23	13:31	14:21	14:36	14:07	13:08	11:59	10:53	09:59	09:43
28	10:18	11:21	12:25	13:33	14:22	14:36	14:05	13:06	11:57	10:51	09:57	09:43
29	10:19		12:28	13:35	14:23	14:35	14:04	13:04	11:55	10:49	09:56	09:43
30	10:21		12:30	13:37	14:24	14:35	14:02	13:02	11:53	10:47	09:55	09:44
31	10:23		12:32		14:25		14:01	13:00		10:45		09:44

Day Lengths for the San Juan Study Site from Farmington, N. Mex., 2011

```
                    o   ,    o   ,              FARMINGTON, NM          Astronomical Applications Dept.
Location: W108 12, N36 42                       Universal Time          U. S. Naval Observatory
                                                                        Washington, DC  20392-5420

                                      Duration of Daylight for 2011

Day   Jan.    Feb.    Mar.    Apr.    May     June    July    Aug.    Sep.    Oct.    Nov.    Dec.

      h  m    h  m    h  m    h  m    h  m    h  m    h  m    h  m    h  m    h  m    h  m    h  m
01    09:42   10:22   11:22   12:35   13:41   14:30   14:38   14:02   12:59   11:50   10:41   09:51
02    09:42   10:24   11:25   12:37   13:43   14:31   14:37   14:00   12:57   11:48   10:39   09:49
03    09:43   10:26   11:27   12:40   13:45   14:32   14:37   13:58   12:54   11:45   10:37   09:48
04    09:44   10:28   11:29   12:42   13:47   14:32   14:36   13:56   12:52   11:43   10:35   09:47
05    09:44   10:30   11:32   12:44   13:49   14:33   14:36   13:55   12:50   11:41   10:33   09:47
06    09:45   10:32   11:34   12:47   13:51   14:34   14:35   13:53   12:48   11:39   10:31   09:46
07    09:46   10:34   11:36   12:49   13:53   14:35   14:34   13:51   12:45   11:36   10:29   09:45
08    09:47   10:36   11:39   12:51   13:54   14:36   14:33   13:49   12:43   11:34   10:27   09:44
09    09:48   10:38   11:41   12:53   13:56   14:36   14:32   13:47   12:41   11:32   10:25   09:43
10    09:49   10:40   11:43   12:56   13:58   14:37   14:31   13:45   12:39   11:29   10:23   09:43
11    09:50   10:42   11:46   12:58   14:00   14:37   14:31   13:43   12:36   11:27   10:21   09:42
12    09:51   10:44   11:48   13:00   14:02   14:38   14:30   13:41   12:34   11:25   10:19   09:42
13    09:52   10:47   11:50   13:03   14:03   14:38   14:29   13:39   12:32   11:22   10:18   09:41
14    09:54   10:49   11:53   13:05   14:05   14:39   14:27   13:37   12:29   11:20   10:16   09:41
15    09:55   10:51   11:55   13:07   14:07   14:39   14:26   13:35   12:27   11:18   10:14   09:40
16    09:56   10:53   11:57   13:09   14:08   14:39   14:25   13:33   12:25   11:16   10:12   09:40
17    09:58   10:55   12:00   13:11   14:10   14:40   14:24   13:31   12:23   11:13   10:11   09:40
18    09:59   10:57   12:02   13:14   14:11   14:40   14:23   13:29   12:20   11:11   10:09   09:39
19    10:00   11:00   12:05   13:16   14:13   14:40   14:21   13:27   12:18   11:09   10:07   09:39
20    10:02   11:02   12:07   13:18   14:15   14:40   14:20   13:25   12:16   11:07   10:06   09:39
21    10:03   11:04   12:09   13:20   14:16   14:40   14:19   13:23   12:13   11:05   10:04   09:39
22    10:05   11:06   12:12   13:22   14:17   14:40   14:17   13:21   12:11   11:02   10:02   09:38
23    10:07   11:09   12:14   13:24   14:19   14:40   14:16   13:19   12:09   11:00   10:01   09:38
24    10:08   11:11   12:16   13:27   14:20   14:40   14:14   13:16   12:06   10:58   09:59   09:39
25    10:10   11:13   12:19   13:29   14:21   14:40   14:13   13:14   12:04   10:56   09:58   09:39
26    10:12   11:15   12:21   13:31   14:23   14:40   14:11   13:12   12:02   10:54   09:57   09:39
27    10:13   11:18   12:23   13:33   14:24   14:39   14:10   13:10   11:59   10:51   09:55   09:39
28    10:15   11:20   12:26   13:35   14:25   14:39   14:08   13:08   11:57   10:49   09:54   09:40
29    10:17           12:28   13:37   14:26   14:39   14:07   13:06   11:55   10:47   09:53   09:40
30    10:19           12:30   13:39   14:28   14:38   14:05   13:03   11:52   10:45   09:52   09:40
31    10:20           12:33           14:29           14:03   13:01           10:43           09:41
```