

THE EFFECTS OF BIRD AND BAT ARTHROPOD PREDATION ON SAPLING
BLACK COTTONWOODS IN THE CONTEXT OF RESTORATION

by

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ABSTRACT

THE EFFECTS OF BIRD AND BAT ARTHROPOD PREDATION ON SAPLING BLACK COTTONWOODS IN THE CONTEXT OF RESTORATION

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Phytophagous arthropod consumption by birds and bats has been shown to initiate top-down cascading effects that reduce plant damage or accelerate plant growth in terrestrial ecosystems. Birds and bats attracted to ecological restoration sites can potentially contribute to ecosystem functioning by reducing herbivore-caused plant damage and indirectly facilitating plant growth. I examined tri-trophic interactions between birds and bats, arthropods, and sapling black cottonwoods (*Populus balsamifera* ssp. *trichocarpa*) along two recovering tributary streams of Mono Lake, California, USA. I used mesh enclosures over saplings to remove the direct effects of bird and bat predation on arthropods dwelling on black cottonwoods, and I compared arthropod density and biomass, herbivore-caused foliage damage, and shoot growth between predator-free saplings and paired control saplings to which birds and bats had foraging access. Avian foraging surveys conducted in the riparian vegetation along the streams revealed that 49 percent of foraging attacks were made in black cottonwoods compared to other substrates but that only four percent of black cottonwood foraging attacks occurred in saplings comparable in height to experimental saplings. Contrary to predictions, neither total arthropod biomass or density, nor any arthropod foraging functional group (i.e., herbivores, predators and parasites, leaf chewers) differed between enclosure saplings and controls. It followed that bird and bat exclusion did not significantly influence herbivore-caused leaf damage or sapling shoot growth. Arthropod densities on

sapling black cottonwoods were lower than has been reported by researchers who found bird-initiated species-level trophic cascades on other plants in the Salicaceae family.

Further, I found no evidence that birds and bats preferentially consumed predaceous or herbivorous arthropods, or that intratrophic arthropod predation attenuated vertebrate predation effects. It appears that birds and bats do not indirectly reduce foliage damage or facilitate black cottonwood sapling growth in the context of riparian ecosystem restoration when herbivore loads are low.

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INTRODUCTION

As predators, pollinators, and seed dispersers, birds and bats contribute ecological services that can facilitate plant growth, reproduction, and recolonization (Cleveland et al. 2006, Muscarella and Fleming 2007, Whelan et al. 2008, Wenny et al. 2011). In particular, herbivorous arthropod consumption by birds and leaf-gleaning bats has been demonstrated to initiate top-down ecological effects that reduce plant damage and improve plant growth in terrestrial ecosystems (Whelan et al. 2008, Mooney et al. 2010, Mäntylä et al. 2011). Through experiments in which insectivorous birds and/or foliage-gleaning bats were either excluded from plants (e.g., Altegrim et al. 1989, Kalka et al. 2008, Kellermann et al. 2008, Böhm et al. 2011), or increased in density near plants (e.g., Sanz 2001), researchers have demonstrated cascading effects in which birds or bats consume herbivorous arthropods and reduce herbivore-caused plant damage. Through similar experimental means, researchers have also demonstrated species-level trophic cascades (*sensu* Polis 1999) in which bird and bat predation not only reduces plant damage, but also can indirectly increase plant growth (e.g., Sipura 1999, Mazia et al. 2009, Bridgeland et al. 2010). Marquis and Whelan (1994) were the first to experimentally link bird predation of herbivores to improved biomass productivity in a plant species (*Quercus alba*). They further suggested that because of this demonstrated intertrophic relationship, bird declines could have widespread negative implications for forest productivity (Whelan and Marquis 1995).

Ecologists have variously argued that trophic cascades are idiosyncratic in their strength and occurrence across ecosystems (Polis et al. 2000) or conversely that trophic

cascades are much more ubiquitous and important in their role as ecosystem stabilizers than previously recognized (Terborgh and Estes 2010). While recent meta-analyses suggest that cascading effects of bird or bat predation on reducing plant damage is strong and widespread, fewer studies have investigated effects on plant growth and their cumulative results are variable (95% confidence intervals on growth effect sizes in meta-analyses overlap zero, Mooney et al. 2010, Mäntylä et al. 2011). Strong et al. (2000) and Sekercioglu (2006) suggested that multiple studies using a variety of plant species in different ecosystems are needed to assess the generality of the bird-herbivore-plant interaction. Indeed, prior to the significant finding of Marquis and Whelan (1994), ecologists found that top-down effects of bird predation reduced leaf-chewing arthropod abundance, but did not cascade to changes in leaf tissue chemistry in sagebrush (*Artemisia tridentata*) (Wiens et al. 1979) or to increased grassland cover (Bock et al. 1992). Further, recent research continues to provide conflicting results even as experimental spatial and temporal variability is incorporated: across three years and three elevations, Schwenk et al. (2010), found no significant bird predation effects on plant damage, or shoot growth in sapling sugar maples (*Acer pensylvanicum*) whereas Böhm et al. (2011) found that bird and bat predation greatly reduced herbivory in sapling and mature oaks (*Quercus robur*) across study sites.

The large body of experimental and theoretical research on trophic cascades has classical theoretical roots in a proposal by Hairston et al. (1960), later termed the “green world” hypothesis (Polis 1999). This work provided a simplified framework in which to study the complexity of food webs by grouping species of similar feeding strategies into

discrete trophic levels, and provided a top-down explanation for “why the world is green” in which predators suppress herbivores and plant growth is indirectly unleashed (Hairston et al. 1960, Oksanen et al. 1981). Plants and “green” ecosystems are also regulated by bottom-up effects exerted by light and temperature and the availability of water and nutrients – factors perhaps poorly described by simplified trophic levels (Polis and Strong 1996, Polis 1999). Additionally, food webs are often more complex than hierarchical trophic levels imply and they can, for example, be influenced strongly by intratrophic competition within predators and herbivores, or chemical defenses of the plants themselves (Polis 1999, Ohgushi et al. 2009). The relative importance of top-down versus bottom-up regulation of terrestrial ecosystems has been long debated (e.g., Hairston et al. 1960, Murdoch 1966, Pace et al. 1999, Polis 1999), but it appears generally accepted that top-down and bottom-up forces are complementary (Terborgh and Estes 2010), and their relative roles can vary with heterogeneity across or within systems (Hunter and Price 1992). The question for ecologists remains: under what interacting biotic and abiotic conditions do trophic cascades occur (Hunter and Price 1992, Shurin et al. 2010)?

The investigation of bird and bat initiated trophic cascades in the context of ecological restoration is especially relevant because the goal of many restoration projects is to efficiently re-establish the biotic community and to restore ecological functioning (SERI 2004). Ecological functioning is rather loosely defined but can mean a system’s ability to sequester and transform energy and nutrients (e.g., through inter-trophic food webs) and a resiliency to natural environmental fluctuations (Palmer et al. 1997, SERI

2004). Determining the mechanisms through which species contribute to ecosystem functioning has the potential of maximizing restoration success (Palmer et al. 1997, Lindell 2008). By consuming herbivorous arthropods, birds and bats attracted to ecosystems undergoing restoration can potentially contribute to ecosystem functioning by reducing herbivore-caused plant damage and indirectly facilitating plant growth. Further, some of the strongest trophic links between bird and bat predation and plant growth occur when herbivorous insect out-breaks occur or folivore damage is highest (e.g., Mazia et al. 2009, Bridgeland et al. 2010), suggesting that bird and bat predation can contribute to ecosystem resiliency. Previous studies have examined the cascading effects of reptilian or mammalian consumers on plant growth in restoring ecosystems experimentally (Van Zandt et al. 2005) and observationally (Beschta and Ripple 2010). Studies have additionally investigated effects of bird-dispersed seeds on seedling establishment in recovering landscapes (e.g., Robinson and Handle 1993, Holl 1998). To my knowledge, however, researchers have not explicitly studied the indirect effects of bird and bat predation on plant growth in human-restored habitats.

I considered one potential mechanism by which birds and bats contribute to ecosystem functioning in the context of restoration by examining tri-trophic interactions between birds and bats, arthropods, and sapling black cottonwoods (*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & A. Gray) Brayshaw) along two tributary streams of Mono Lake, California. Here, cottonwoods and the riparian breeding bird community are recovering after water flows were re-established following decades of diversions (Stine et al. 1984, USDA 2001, Heath et al. 2006a, Heath et al. 2006b, McBain and Trush Inc. and

Ross Taylor and Assoc. 2010). I hypothesized that bird and bat predation initiates a top-down species level trophic cascade in which arthropod and foliage damage reductions are sufficient to accelerate black cottonwood shoot growth. I removed the direct effects of bird and bat predation on black cottonwood-dwelling-arthropods via mesh enclosures placed over saplings, and I compared arthropod density and biomass, foliage damage, and shoot growth between predator-free saplings and paired control saplings to which birds and bats had foraging access. I predicted that enclosed saplings would have higher arthropod densities and biomass, higher arthropod-inflicted leaf damage and less shoot growth than control saplings. I further predicted that the abundance of bird species that foraged on black cottonwood would be spatially correlated with the magnitude of treatment effects.

MATERIALS AND METHODS

Study Area

This study was conducted along the lower reaches of two tributaries of Mono Lake, Mono County, California, USA: Lee Vining Creek and Mill Creek (1944 – 2030 m, 38° 2'23"N, 119° 9'23.86"W - 37°57'9.67"N, 119° 7'3"W). The streams have the capacity to carry approximately 6,200 and 2,500 hectare-meters of water per year respectively and when unrestricted represent about half of Mono Lake's gauged inflow (Stine et al. 1984). Riparian vegetation along the streams is recovering from decades of cumulative ecological damage caused by water diversions beginning as early as the 1850's, water impoundments and livestock grazing (Stine et al. 1984, Stine 1995). Active restoration has taken place on Lee Vining Creek since the early 1990's (e.g., some plantings, channel openings and large woody debris placement), but the majority of the restoration has been passive (namely returning minimum requirement water flows since 1985 and the cessation of livestock grazing (CSWRCB 1994, McBain & Trush Inc. and Ross Taylor & Assoc. 2010)). Mill Creek is not actively being restored, but periodic water releases since the early 1960's, the cessation of livestock grazing since the mid 1980's, and reductions in diversions for irrigation since the late 1990's have resulted in the regeneration of some riparian vegetation (Stine 1995, USDA 2001), and plans are underway to return a higher percentage of its diverted water flows (SCE 2004).

Stream vegetation is generally characterized as Great Basin cottonwood-willow riparian forest consisting primarily of remnant mature and sapling black cottonwoods, mixed willow shrub (*Salix exigua*, *S. lucida*, *S. lutea*, *S. lasiolepis*), remnant mature and

seedling Jeffrey pine (*Pinus jeffreyi*), and Woods' rose (*Rosa woodsii*). As a legacy of several decades of complete water diversions, stream floodplains also retain extensive patches of big sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) shrubs which otherwise characterize much of the streams' adjacent landscape. Along both streams, vegetation changes as elevation increases: downstream sections are deltaic and are comprised mostly of willow, while upstream canopies are characterized by mature pines, some aspen (*P. tremuloides*) and greater tree species richness. Black cottonwoods are present in varying densities and age classes throughout.

Experimental Sapling Selection and Exclosure Construction

I used avian point count stations randomly located during a previous study (Heath and Ballard 2003) as starting points for experimental sapling selection. Starting points were linearly spaced ca. 250 m apart, along the lowest 3.25 and 4.75 km reaches of Lee Vining Creek and Mill Creek, respectively. On each creek, the first point was located 50 m upstream from Mono Lake and the final upstream point was placed at approximately 2070 m in elevation where the canyons narrowed and increased in slope and where a state highway crossed both streams. Because of a sharp bend in Mill Creek, the number of creek kilometers between the initial and final point were greater along Mill Creek than along Lee Vining Creek, and thus more points were placed on Mill Creek. In July 2009, I chose cottonwood saplings using a matched pair design in which pairs were located within 50 m of starting points. I used height criteria alone (150 – 250 cm) to select one sapling nearest the starting point and completed the pair by selecting the next nearest

sapling of similar form, distance to water and overhead shading (mean \pm 1 SD distance between final pair members was 9.31 ± 8.45 m). I then randomly assigned one member of each pair as a control sapling and the other as an exclosure sapling. I initially selected 30 pairs of saplings, however two pairs on Lee Vining Creek were damaged due to high stream flows destroying an exclosure and mortality of unknown cause; thus a total of 56 saplings in 28 pairs were used for the experiment (11 pairs on Lee Vining Creek, 17 on Mill Creek). Mean sapling height at time of selection was 180 ± 31 cm, and mean approximate sapling age, based on counts of terminal budscars in 2010, was 7 ± 2.5 (range 3 – 14 years). All saplings were pre-reproductive during the time of the experiment.

Between March 12 and April 17, 2010 (i.e., prior to cottonwood bud break occurring the first three weeks of May) I placed rectangular cages, constructed with 19 mm diameter polyvinyl chloride (PVC) pipe and wrapped with transparent nylon gill netting, around the 28 exclosure saplings leaving room for vertical and horizontal shoot extension within the netting. I used 25 mm square mesh (Nylon Net Company N202C, Memphis TN, USA), which was in the mid-range of mesh sizes used by previous studies that demonstrated significant bird or bat predation effects (e.g., 16 mm^2 - 38 mm^2 , Sipura 1999, Marquis and Whelan 1994, respectively). I secured netting to PVC pipes with zip ties and Snap Clamps™ (Circo Innovations, Grass Valley, CA, USA) and net bottoms to the ground with creek stones. Though I observed an orange-crowned warbler (*Oreothlypis celata*) successfully enter and leave an exclosure on one occasion, no other birds or bats were observed in exclosures, and I assumed that most individual

insectivorous birds and foliage-gleaning bats were successfully excluded. I did not observe lizards inside exclosures, but the mesh size would have allowed entry of the common lizard species within the study area (e.g., *Sceloporus occidentalis*, *S. graciosus*, *Elgaria coerulea*). I also assumed that most arthropods associated with black cottonwood were able to enter through the netting. For example, I observed larvae of the largest adult winged phytophagous arthropod in the area (*Papilio rutulus*, 90 – 120 mm wingspan) on both control and exclosure saplings, and I observed several individuals of other Lepidoptera families easily enter by landing on the mesh and entering with closed wings. The exclosures did not otherwise appear to dissuade birds from foraging within close vicinity to the saplings (i.e., on nearby control saplings); on several occasions I observed birds foraging from foliage within 1m of exclosures. I did not directly measure netting effects on saplings or environmental conditions within exclosures, but previous studies using similar exclosure construction found no netting effects on temperature and humidity (Kellerman et al. 2008) and negligible effects on leaf photosynthetic rate (Bridgeland et al. 2010).

Avian and Bat Surveys

To describe proportional use of substrates by foraging birds, I conducted instantaneous sampling foraging surveys (Altmann 1974, Bell et al. 1994, Hejl et al. 1994). I sampled linear transects encompassing all sapling pairs on both creeks. The entire 8.5 km was sampled once per month during May through August 2010, and shorter transect sections of both creeks were sampled one additional time in late June or early

July. Surveys were typically completed between 0630 and 1100. I moved slowly and continuously in a relatively straight line between sapling pairs, scanning all vegetation within view. When I detected a bird, I began counting in seconds and at the five second mark, I recorded the behavior, species and height of the bird and the species and height of the prey substrate into an audio recording device. Using definitions provided by Remsen and Robinson (1994), I categorized bird behaviors as “search” (movements used to search for food or substrates that hide food), “attack” (the moment when prey is sighted to when a capture attempt is made), or “other”. Individuals recorded as searching were further observed until they left the substrate, and attack behaviors observed during this time (or just before the 5 second mark) were noted. To maintain independence of observations within a survey, only information on the first individual detected within a flock was recorded and I distinguished individuals using simultaneous singing or plumage dimorphism when possible. Otherwise, I only recorded data for an individual if the same species had not been recorded within 30 m or for the previous ten minutes. I performed all surveys with the exception of one June survey on Lee Vining Creek which was performed by a different qualified observer.

To index avian insectivore abundance and species composition around sapling pairs throughout the experimental period, I performed variable circular plot point counts (Bibby et al. 2000) at all sapling pair locations three times during peak territorial behavior (June), and once during local peak landbird migration (late May), peak fledging period (mid-July), and mid-August post-breeding dispersal (avian phenology based on 1998-2005 PRBO unpublished data, SKH personal observation). During 5-minute counts,

I stood at the same point location and recorded all individuals seen or heard, and determined distances to all observations with a Leica Laser RangefinderTM. Mean experimental sapling distance to point count locations was 12.22 ± 7.78 m. Detections within 50 m of observer, summed for each point and survey combination, were used as an index of bird abundance for analyses. At this 50 m cut-off, I assumed probability of detection was similar among sapling pairs and I performed all surveys to eliminate differences in observer bias; I further presumed that indices at this scale provide a useful measure of avian abundance (Johnson 2008). When comparing 2010 data to previous years' abundance indices, I used only two June surveys since only June surveys were conducted prior to 2010. This time period corresponded to the peak of territorial behavior (i.e., singing males) within the study area (PRBO unpublished data, SKH personal observation).

To compare timing of bird egg hatch, nestling fledge, bird abundance and fluctuations in arthropod biomass, I used data from 2000-2005 gathered by monitoring bird nests during previous research within the same study areas on Lee Vining Creek and Mill Creek (see Heath et al. 2006a, Heath et al. 2006b). Nest searching plots ($n = 2$ for each creek) encompassed 65% of the sapling transect area on each creek. For each of the six years in the dataset, I tallied the number of nests hatched and fledged from all four nest searching plots combined within 15 weekly time periods May 1 – August 15, for 20 of the 24 species I observed foraging from black cottonwoods in 2010. No nests were found for the remaining four species either because they were transient species that did not breed within the study area or because the species did not build their own nests (i.e.,

Brown-headed Cowbirds, *Molothrus ater*). I present mean numbers of nests hatched and fledged (mean of six years) for each week.

Bats can reduce vegetation-dwelling arthropods more significantly than birds (Kalka et al. 2008, Williams-Guillen et al. 2008), and foliage-gleaning is an important feeding strategy for bats in both temperate and tropical regions (Wilson 1973). Thus, to determine the presence and frequency of detection of cottonwood associated bat species within the study area, I conducted passive acoustic surveys using one automated ultrasonic detector (Pettersson D240X, Pettersson Elektronik, Uppsala, Sweden) and an mp3 data recorder (iriver iFP-800) capable of capturing the quietest of bat echolocation calls within a 20 m sphere of the device (Ahlen and Baagoe 1999). When triggered by bat echolocation calls, the detector downloaded 1.7 second samples of stored ultrasound as 17 second time-expanded samples to the recorder. I deployed the detector and recorder 1.5 – 0.5 hours before dusk and collected them the following afternoon; battery power for both devices allowed for dusk to dawn recordings but since time stamps were not attached to mp3 files, I could not confirm the number of recording hours per night. I attached the detector and recorder to the top of a 2.5 m pole and placed the device within 50 m of sapling pairs, near cottonwood patch edges or under mature cottonwood canopies, choosing areas under the canopies that were adequate for bat movement. I placed the device at distances from vegetation (ca. 1 m) that would minimize both the obstruction of bat flyways and echoes from vegetative surfaces (Weller and Zabel 2002). I placed the device for two or three consecutive nights at each location, for a total of 12 locations and 34 nights divided evenly between Lee Vining Creek and Mill Creek;

sampling a site for at least eight nights is recommended to reduce biased estimates of bat activity (Hayes 1997). I began recording June 7, 2010 and spaced recording nights evenly throughout the remainder of the experimental period (five to six nights in June, six in July, five to six in August for each creek), thus I likely missed species that may have seasonally moved through the area in April or May (e.g., western red bats (*Lasiurus borevillii*) or hoary bats (*L. cinereus*), J. Szewczak personal communication). Recorded echolocation calls were analyzed using SonoBat™ (version 3.02; SonoBat, Arcata, CA, USA) and automated species identifications were confirmed through visual inspection of sonograms by a qualified biologist with knowledge of Western US bat echolocation call characteristics (J. Szewczak, Humboldt State University). Whether or not an echolocation call was identified to species, the software categorized it as a low or high frequency (kHz) bat call. Since individual bats were not discernable, 17 second segments identified as high or low frequency calls were considered bat passes and were tallied for each recording night (i.e., one detector for one night); I assumed that recordings extended from dusk to dawn during at least one of the recording nights per location and from the two or three recording nights at one location I calculated the maximum number of bat passes per location as an index of bat activity.

Arthropod Surveys

To quantify arthropod biomass and density on saplings, I non-destructively counted all exposed arthropods and concealment structures (i.e., arthropod-constructed leaf folds, rolls, ties, galls and leaf cases) on exclosure and control saplings four times between May 22 and August 15, 2010. I did not count the dead mother shells of

oystershell scales (*Lepidosaphes ulmi*), but was prepared to count live nymphs or other crawler scales if present. I performed counts on the saplings in the same order during every survey so that surveys were spaced 21-26 days apart for each sapling. I inspected branches, stems and both sides of all leaves for arthropods and concealment structures and counted leaves with a tally counter. I identified all arthropods at least to order, and to family when possible, using a combination of consistent morphospecies identification codes in the field accompanied by photographs and voucher specimens collected from nearby saplings. I measured the first individual of each morphospecies encountered to the nearest millimeter and tallied individuals by size and morphospecies accordingly, creating a new tally within the same morphospecies if a new size group was encountered and measured. I counted one leaf fold, roll, tie or gall for each leaf when present, though leaves may have had several folds or galls per leaf. I performed all arthropod counts, measurements and morphospecies identifications and verbally transmitted these to an assistant who recorded the data. I calculated (dry-weight) biomass (mg) from length measurements using published parameter estimates for length-weight regressions for all orders, some families, and adult, nymph and larval life stages that I encountered (Model 1; Rogers et al. 1977, Sample et al. 1993). I further placed exposed arthropods into three non-mutually exclusive functional groups that reflected their different feeding strategies: 1) herbivores were adult, larval and nymph moths and butterflies (Lepidoptera), sawflies (Pamphiliidae, Tenthredinidae), larval and adult striped willow leaf beetle (*Disonycha alternata*), and phytophagous families of true bugs (Hemiptera) and thrips (Thysanoptera), 2) leaf-chewers, a subset of herbivores, were larval moths, butterflies and

sawflies and larval and adult striped willow leaf beetle, and 3) predators/parasitoids were adult, larval and nymph spiders (Araneae), mites (Acari), lacewings (Neuroptera), assassin bugs (Reduviidae), predatory thrips (Aeolothripidae), wasps (Apocrita), ladybug beetles and larvae (Coccinellidae), and larval hoverflies (Syrphidae). It is possible that my non-destructive sampling technique disproportionately underrepresented fast flying or hopping arthropods that flee upon disturbance or arthropods invisible to the naked eye. However, nearly all studies investigating the cascading effects of birds and bats also used this non-destructive sampling method and thus the arthropod counts and biomass estimates in this study are comparable to others (see reviews by Mooney et al. 2010, Mäntylä 2011). To provide a snapshot of which arthropods were dwelling within leaf folds, on July 10, 2010 (i.e., at the peak of arthropod abundance), I haphazardly sampled silk-fastened leaf folds from thirty non-experimental cottonwood saplings on each creek (stratified into upper, middle and lower stream sections) for a total of 60 leaf folds from 60 saplings. Leaf folds were opened and the contents identified and counted.

Sapling Growth Measurements

The production of biomass on black cottonwood saplings can be estimated effectively by measuring leader shoots, and since growth is indeterminate from bud break until leaves abscise, variation in biomass can be attributed to factors within that year's growing season (Sigurdsson 2001). From September 4 - 8, 2010 (prior to leaf senescence) I measured new shoot elongation on all saplings from the previous year's apical budscar to the base of the current year's apical bud. I also measured 2009 shoot elongation (i.e., prior to exclosure placement) on all saplings to serve as a pre-treatment growth

comparison. Sixteen leader shoots with at least two years of elongation were randomly selected from four cardinal direction quadrats further separated into four vertical sections, so that shoots were measured from all directions and all heights of the sapling. An additional top leader shoot was measured for a maximum total of 17 shoots measured per sapling. Fewer shoots were measured for smaller saplings that did not have shoots in all sixteen sections ($n = 5$ saplings). Mean shoot elongation was calculated for each sapling in each year.

Leaf Damage Assessment

I quantified leaf damage inflicted by leaf chewing, mining, constructing and galling arthropods. After growth measurements were completed, I randomly collected 50 leaves from the same saplings sections from which leader shoots were chosen and placed them in a plant press. In order to reduce leaf selection bias, and the probability of missing chewed leaves for which only petioles remained, I haphazardly chose a leaf from each section and then collected the next leaf (whole, partial, or petiole-only) from the same whirl in a counter-clockwise direction. For each leaf, I used a transparent plastic sheet printed with a 5 mm² dot grid to count the number of dots that overlay chewed, mined, galled or folded sections and calculated their proportion relative to the total number of dots enclosed within the total leaf area outline. If only petioles remained, I assumed the leaf area was 100% chewed by arthropods; early abscission would have left petiole scars, not full petioles (Williams and Whitham 1986). If substantial sections of the leaf were removed, I used similarly sized intact leaves to sketch an outline from which to determine total dot numbers. It is possible that browsing mule deer (*Odocoileus hemionus*) could

have caused leaf damage (e.g., 100% chewed leaves) on control saplings. However, I counted the number of stems with recent browse damage while building and dismantling exclosures, and found low levels of browse damage overall and no evidence of more browse damage on control than on exclosure saplings (control = 0.68 ± 1.22 and exclosure = 0.50 ± 1.11 stems browsed per sapling). Since I did not assess damage caused by insects that use rostra to suck phloem from leaves and stems (e.g., Hemiptera), nor account for premature leaf abscission known to result from petiole gall aphids (*Pemphigus* spp.) in *Populus* (Williams and Whitham 1986), I likely underestimated those types of leaf damage. For each sapling I calculated 1.) frequency of damage (percent of the 50 leaves with each type of damage) and 2.) percent leaf area damage (mean percentage of 50 leaves for each type of damage).

Statistical Analyses

To test effects of bird and bat removal on total arthropod biomass and density on saplings, I fit repeated measures linear mixed effects models (LMM) using restricted maximum likelihood (package ‘nlme’, Pinheiro et al. 2011). The response variable was total arthropod biomass^{-100 leaves} or total arthropod density^{-100 leaves} (natural log-transformed to meet assumptions of normality and homogeneity); fixed effects were treatment (exclosure, control), survey period (May, June, July, August), their interaction, and the blocking factor sapling pair; and the random effect was sapling (repeatedly measured across four survey periods). To select the optimal variance and correlation structures for the models, I used information criteria (AIC values) and Likelihood Ratio Tests on

maximum likelihood fits (LRT; Pinheiro and Bates 2000, Zuur et al. 2009). I used generalized linear models (GLM) to test indirect predator removal effects on frequency of sapling leaf chew damage (quasibinomial errors, logit link), percent leaf area chewed (arcsine square root transformed, Gaussian errors, identity link), and 2010 extension of cottonwood sapling shoots (natural log-transformed, Gaussian errors, identity link). Treatment was the fixed effect and pair was the block in all GLM models and 2009 shoot extension (natural log transformed) was a covariate in the 2010 shoot extension model. Significance of fixed effects terms in LMMs and GLMs were assessed with *F*-tests (Pinheiro and Bates 2000, Zuur et al. 2009). I visually inspected factor-level residual plots to assure that LMMs and GLMs met residual assumptions of homogeneity and normality. To analyze the effect of exclosures on the biomass^{-100 leaves} of arthropod functional groups (i.e., herbivores, leaf chewers and predators and parasitoids), I used a non-parametric repeated-measures approach with pair as a blocking factor (package ‘nparLD’, Noguchi et al. 2011); the approach calculates an ANOVA-type statistic (ATS) which tests for differences in relative treatment effects between groups (Brunner et al. 2002). Since sapling pairs were spread evenly along 8 km of streamside across two creeks, environmental heterogeneity between pairs was expected and the intent of the paired design was to account for this variation among sapling pairs within and between creeks. Preliminary exploratory analysis of data using package ‘lattice’ (Sarkar 2011) and mean and standard deviation summaries across various creek, pair, treatment and survey groupings confirmed that pooling data across creeks was a reasonable approach (Bolker 2008, Zuur et al 2009).

I calculated standardized effect sizes (d) and associated 95% confidence intervals (95% CI) for effects of predator exclusion on total arthropod biomass and density, leaf damage and shoot growth using equations and function scripts provided in Nakagawa and Cuthill (2007) that account for the non-normal error structures, repeated measures, multiple parameters, or between group and residual variance components found in LMMs (Equations 22 & 23) or GLMs (Equation 10). To estimate d for treatment effects on arthropod functional groups and concealment structures I used treatment rank means (averaged across surveys), derived from the non-parametric repeated measures analysis, in lieu of sample means and calculated Hedge's g effect sizes and associated standard errors and 95% CI (Equations 1 & 2, Nakagawa and Cuthill 2007).

All other mean comparisons or correlations were analyzed with permutation tests (K-Sample Permutation Tests or Spearman's Test for Independence respectively, stratified by pair or survey when appropriate) in which P -values were based on 9,999 Monte-Carlo replications (package 'coin', Hothorn et al. 2006, Hothorn et al. 2008). Analyses were performed using program *R* version 2.12.2 (R Development Core Team 2011). Means \pm 1 standard deviation are presented unless otherwise noted.

RESULTS

Bird and Bat Predators

I detected 77 bird species during foraging surveys and point counts; 24 of these attacked prey in black cottonwoods (Table 1), and 49% of observed foraging attacks occurred in black cottonwoods ($n = 188$). Attacks were also observed in willow (18%), in the air (7%), on Jeffrey pine (5%), and 11 other substrates (21%). Yellow warbler (*Dendroica petechia*) was the species most frequently observed foraging from black cottonwoods (45% of black cottonwood foraging attacks, Table 1). Although 37% of attacks made in cottonwoods of any height were made at less than 3 m, only 4% of foraging attacks in cottonwoods were in saplings less than 3 m in total height (i.e., maximum height of the experimental trees). Mean height of cottonwoods from which birds made attacks was 10.6 ± 5.8 m (range 1.5 – 28.0 m). Mean total detections of bird species observed to forage in black cottonwoods did not differ significantly between survey periods (permutation test, $\max T = 2.52$, $P = 0.07$; Figure 1), but differed between sapling pairs ($\max T = 3.58$, $P = 0.02$), with detections ranging from 0.33 ± 0.52 to 8.50 ± 1.37 birds^{-50m} across sapling pairs during any one survey.

Bat detectors and recorders captured high or low frequency (kHz) bat echolocation calls during 28 of the 34 recording nights, for a total of 2,126 bat passes. Mean maximum number of bat passes per site were 134.3 ± 43.0 in June, 63.4 ± 57.4 in

Table 1. Bird species observed attacking prey in black cottonwoods during foraging surveys, percentage of all attacks observed in black cottonwood made by each species ($n = 93$), and mean maximum number of adult and juvenile detections within 5 minutes and 50 m of sapling pair point count stations (maximum of 6 surveys, mean of $n = 28$ pairs \pm 1 SE) at Mono Lake, California, 2010.

Common name	Scientific name	Percentage of black cottonwood attacks	Maximum number of detections
Red-breasted sapsucker	<i>Sphyrapicus ruber</i>	1	0.07 \pm 0.05
Hairy woodpecker	<i>Picoides villosus</i>	4	0.14 \pm 0.07
Red-shafted flicker	<i>Colaptes auratus cafer</i>	1	0.46 \pm 0.12
Dusky flycatcher	<i>Empidonax oberholseri</i>	1	0.11 \pm 0.08
Warbling vireo	<i>Vireo gilvus</i>	4	0.25 \pm 0.10
Mountain chickadee	<i>Poecile gambeli</i>	4	0.21 \pm 0.09
Bushtit	<i>Psaltriparus minimus</i>	1	0.00
House wren	<i>Troglodytes aedon</i>	3	1.11 \pm 0.19
Blue-gray gnatcatcher	<i>Polioptila caerulea</i>	1	0.07 \pm 0.05
American robin	<i>Turdus migratorius</i>	1	0.68 \pm 0.14
Orange-crowned warbler ^a	<i>Oreothlypis celata</i>	2	0.14 \pm 0.08
Yellow warbler	<i>Dendroica petechia</i>	45	1.68 \pm 0.19
Black-and-white warbler ^a	<i>Mniotilta varia</i>	1	0.00
Wilson's warbler ^a	<i>Wilsonia pusilla</i>	3	1.11 \pm 0.27

Table 1. Bird species observed attacking prey in black cottonwoods during foraging surveys, percentage of all attacks observed in black cottonwood made by each species ($n = 93$), and mean maximum number of adult and juvenile detections within 5 minutes and 50 m of sapling pair point count stations (maximum of 6 surveys, mean of $n = 28$ pairs \pm 1 SE) at Mono Lake, California, 2010 (continued).

Common name	Scientific name	Percentage of black cottonwood attacks	Maximum number of detections
Green-tailed towhee	<i>Pipilo chlorurus</i>	4	0.54 ± 0.15
Spotted towhee	<i>Pipilo maculatus</i>	6	1.54 ± 0.20
Brewer's sparrow	<i>Spizella breweri</i>	2	0.50 ± 0.16
Song sparrow	<i>Melospiza melodia</i>	2	1.07 ± 0.19
Western tanager	<i>Piranga ludoviciana</i>	1	0.39 ± 0.14
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	2	0.21 ± 0.09
Brown-headed cowbird	<i>Molothrus ater</i>	1	0.61 ± 0.25
Bullock's oriole	<i>Icterus bullockii</i>	4	0.82 ± 0.16
Cassin's finch	<i>Carpodacus cassinii</i>	1	0.43 ± 0.18
Lesser goldfinch	<i>Carduelis psaltria</i>	1	0.11 ± 0.08

^a All species except these breed regularly within the study area. Wilson's warblers are spring transients, orange-crowned warblers are post-breeding dispersers and occasional breeders, and black-and-white warblers are occasional vagrants to the western U.S. (Gaines 1992, Heath et al. 2006a, Heath et al. 2006b).

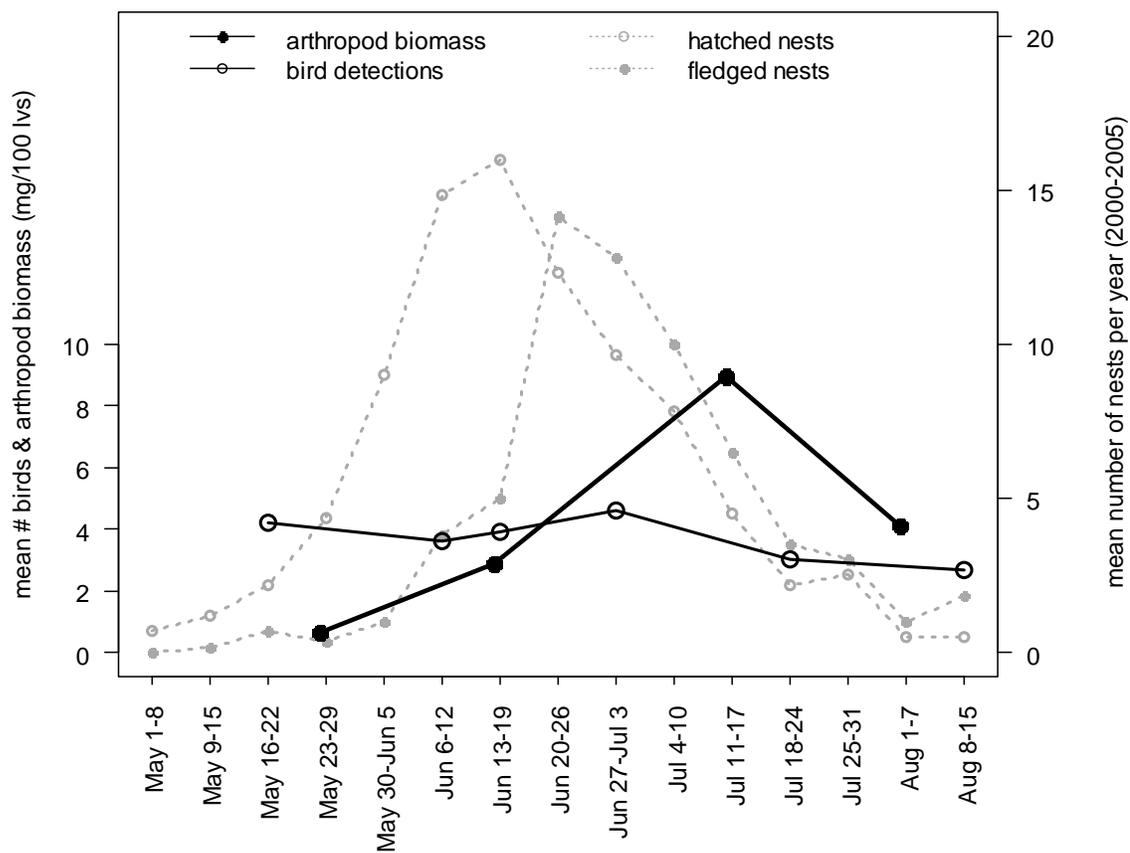


Figure 1. Phenology of cottonwood foraging bird species nesting (2000-2005) and abundance (2010), and cottonwood sapling arthropod biomass (2010) at Mono Lake, California. Mean number of hatched and fledged nests within study area per year ($n = 6$ years), mean adult and juvenile point count detections per sapling pair ($n = 28$), and mean arthropod biomass per control sapling ($n = 28$) for each seven day period. Presented without error bars for graphical clarity.

July, and 126.0 ± 123.1 in August. Of the high or low frequency bat passes, 895 were confidently identified to species and ten bat species were identified within the study area (Table 2). Small-footed myotis (*Myotis ciliolabrum*), little brown bat (*M. lucifiugus*) and long-eared myotis (*M. evotis*) were the most frequently detected species, with 37%, 31% and 23% of identified detections, respectively. The long-eared myotis is a substrate-gleaning (e.g., leaves, trunks) and aerial-hawking bat (Manning and Jones 1989) while the little brown bat captures aerial prey in and around vegetation breaks (Buchler 1976, Fenton and Barclay 1980). Long-eared myotis have distinctive echolocation calls indicating substrate-gleaning or aerial hawking behavior (Faure and Barclay 1994) and both types of calls were recorded in the study area.

Arthropods

I counted 71,652 exposed-feeding adult, nymph and larval arthropods, totaling an estimated 16,536 mg, in 14 orders over four survey periods (Table 3, Appendix A). Aphids (62% of all tallied arthropods, Aphididae) and lace bugs (23%, Tingidae) occurred in the highest densities. The largest contributors to biomass were ants (24%, Formicidae) and adult (14%) and larval (12%) moths and butterflies (Table 3). Leaf folds (69%), leaf galls (12%), petiole galls (12%) and leaf ties (8%) comprised most of the 13,309 leaves with arthropod-constructed shelters counted across the four surveys. Of the 116 arthropods concealed within the 60 leaf fold contents investigated, 57% were

Table 2. Bat species detected with automated ultrasonic detectors placed within 50 m of black cottonwood saplings, and percentage of identified bat passes ($n = 895$) at Mono Lake, California, 2010.

Common name	Scientific name	Percentage of identified bat passes
Big brown bat	<i>Eptesicus fuscus</i>	4
Silver-haired bat	<i>Lasionycteris noctivagans</i>	1
Small-footed myotis	<i>Myotis ciliolabrum</i>	37
California myotis	<i>Myotis californicus</i>	< 1
Hairy-winged myotis	<i>Myotis volans</i>	< 1
Little brown bat	<i>Myotis lucifugus</i>	31
Yuma myotis	<i>Myotis yumanensis</i>	< 1
Long-eared myotis	<i>Myotis evotis</i>	23
Pallid Bat	<i>Antrozous pallidus</i>	< 1
Free-tailed bat	<i>Tadarida brasiliensis</i>	3

Table 3. Percentages of total number and biomass of arthropods encountered across four survey periods on control and exclosure black cottonwood saplings at Mono Lake, California, 2010. All values are percentage of total. Summary statistics for all arthropod group, survey and treatment combinations are provided in Appendix A.

Order Suborder or life stage Family	percentage of total number	percentage of total biomass
Araneae	< 1	6
Acari	< 1	< 1
Ephemeroptera	< 1	3
Odonata	< 1	< 1
Plecoptera	< 1	< 1
Hemiptera	92	28
Heteroptera		
Tingidae	23	9
Auchenorrhyncha	6	8
Sternorrhyncha		
Aphididae	62	10
Thysanoptera	1	< 1
Coleoptera	< 1	4
Neuroptera	< 1	1
Hymenoptera	5	26
Sawfly larvae	< 1	< 1

Table 3. Percentages of total number and biomass of arthropods encountered across four survey periods on control and exclosure black cottonwood saplings at Mono Lake, California, 2010. All values are percentage of total. Summary statistics for all arthropod group, survey and treatment combinations are provided in Appendix A (continued).

Order Suborder or life stage Family	percentage of total number	percentage of total biomass
Sawfly adults	< 1	< 1
Apocrita Formicidae	4	24
Trichoptera	< 1	< 1
Lepidoptera	< 1	26
Larvae	< 1	12
Adults	< 1	14
Mecoptera	< 1	< 1
Diptera	1	3
Order unknown	< 1	< 1

aphids, 23% were butterfly or moth larvae, 9% were ants, 4% were mites, and beetles (Coleoptera), thrips and sawfly larvae comprised the remaining individuals. Total arthropod biomass ($\text{mg}^{-100 \text{ leaves}}$) and total arthropod density varied significantly between survey periods (Figure 2), but exclusion of birds and bats did not significantly increase arthropod biomass or density (Table 4), nor was there a significant interaction between survey period and treatment (Appendix B). Similarly, biomass^{-100 leaves} did not differ between exclosure and control saplings for herbivore, leaf-chewing, or predator and parasitoid arthropod functional groups (Table 4, Figure 3, Appendix C). A sharp peak in leaf-chewing arthropod biomass on exclosure trees in July (Figure 3) was attributed mostly to a group of 27 gray midge (*Nycteola cinereana*) moth larvae on one exclosure sapling which totaled 688 mg and was nearly double the biomass for any other sapling during that survey.

The number of leaves with folds, rolls, ties and leaf cases^{-100 leaves} did not differ between control saplings and exclosure saplings (Table 4). However 95% confidence intervals around the treatment effect did not overlap zero suggesting a trend for more leaves with folds, rolls, ties and leaf cases on control saplings (Table 4, Figure 3). There was no difference in the number of leaf and petiole galls^{-100 leaves} between sapling treatments (Table 4, Appendix C). Neither the total number of cottonwood-foraging-birds (Spearman Correlation Test, $Z = 0.89$, $P = 0.39$) nor yellow warblers (Spearman

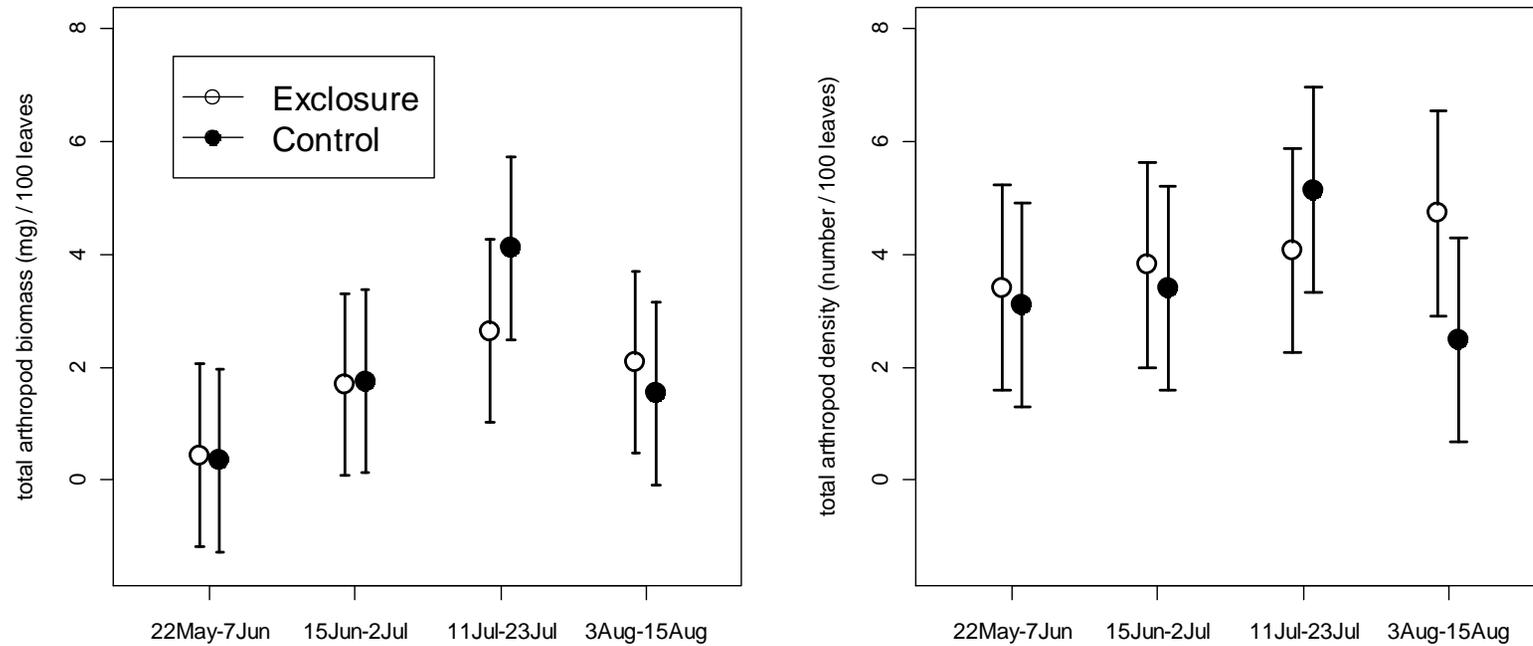


Figure 2. Total arthropod biomass ($\text{mg}^{-100 \text{ leaves}}$) and density $^{-100 \text{ leaves}} \pm 1$ SE on black cottonwood saplings ($n = 28$ for each treatment and survey combination) to which birds and bats did (control) and did not (exclosure) have access at Mono Lake, California, 2010. Back-transformed from LMM natural log-transformed interpolated values, averaged across pairs.

Table 4. Treatment effect results, standardized treatment effect size and 95% confidence intervals for models examining the effects of bird and bat exclusion on total arthropod biomass ($\text{mg}^{-100 \text{ leaves}}$) and density $^{-100 \text{ leaves}}$, functional group biomass ($\text{mg}^{-100 \text{ leaves}}$), frequency of leaf chew damage and leaf area chewed (%), and shoot growth (mm) on black cottonwood saplings at Mono Lake, California, 2010. Full fixed effect model results (pair, survey, treatment and treatment \times survey interaction) presented in Appendices B-D.

Response variable	Treatment effect (control vs. enclosure saplings)				Effect size	
	Test statistic		df	<i>P</i>	(control - enclosure)	Effect size 95% CI
Total arthropod biomass ^a	<i>F</i> ^b	0.79	1, 27	0.38	-0.12	-0.40, 0.15
Total arthropod density ^a	<i>F</i> ^b	0.10	1, 27	0.75	-0.01	-0.26, 0.24
Herbivore biomass	<i>ATS</i> ^c	0.55	1.0	0.46	-0.17	-0.61, 0.26
Leaf-chewer biomass	<i>ATS</i> ^c	0.82	1.0	0.36	-0.22	-0.83, 0.40
Predators & parasitoids biomass	<i>ATS</i> ^c	0.04	1.0	0.85	0.07	-0.74, 0.88
Number of leaf folds, rolls and ties	<i>ATS</i> ^c	2.99	1.0	0.08	0.51	0.08, 0.94

Table 4. Treatment effect results, standardized treatment effect size and 95% confidence intervals for models examining the effects of bird and bat exclusion on total arthropod biomass ($\text{mg}^{-100 \text{ leaves}}$) and density^{-100 leaves}, functional group biomass ($\text{mg}^{-100 \text{ leaves}}$), frequency of leaf chew damage and leaf area chewed (%), and shoot growth (mm) on black cottonwood saplings at Mono Lake, California, 2010. Full fixed effect model results (pair, survey, treatment and treatment \times survey interaction) presented in Appendices B-D (continued).

Response variable	Treatment effect (control vs. enclosure saplings)					
	Test statistic	df	<i>P</i>	Effect size (control - enclosure)	Effect size 95% CI	
Number of leaf and petiole galls	<i>ATS</i> ^c	0.17	1.0	0.68	-0.25	-0.47, -0.03
Frequency of leaf chew damage	<i>F</i> ^d	0.55	1, 27	0.47	0.28	-0.48, 1.04
Percent leaf area chewed ^a	<i>F</i> ^d	2.95	1, 27	0.10	-0.66	-1.43, 0.12
Shoot growth ^a	<i>F</i> ^d	3.17	1, 27	0.09	0.69	-0.10, 1.46

^a Log-transformations were applied to total arthropod and shoot growth data, arcsine square root transformation was applied to leaf area chewed data.

^b Conditional *F*-test statistic from linear mixed effect models.

^c ANOVA-type statistic from non-parametric repeated measures tests.

^d Analysis of deviance *F*- statistic from quasibinomial and Gaussian generalized linear models.

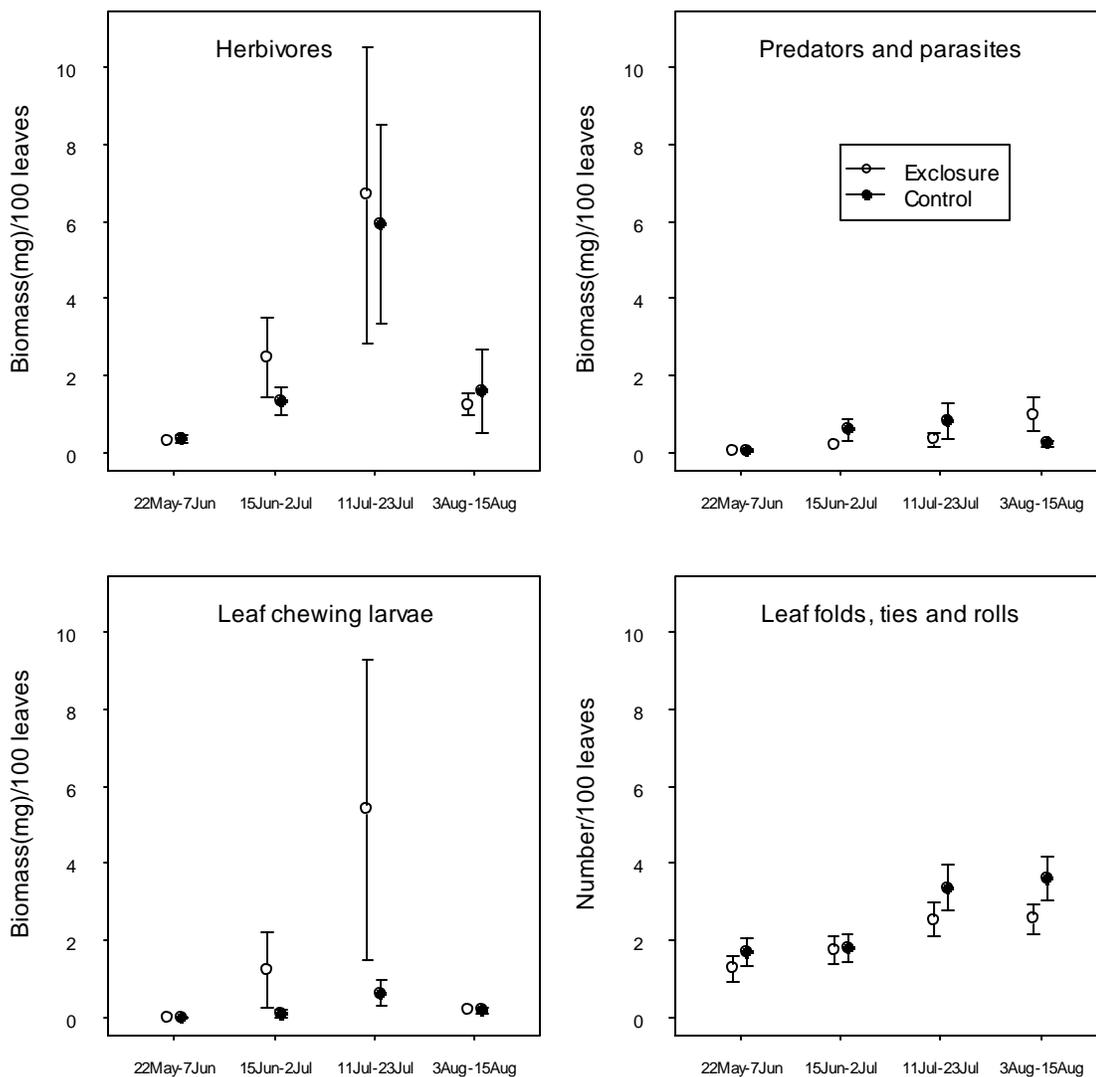


Figure 3. Biomass ($\text{mg}^{-100 \text{ leaves}}$) for arthropod foraging functional groups and number of concealment structures $^{-100 \text{ leaves}}$ (mean ± 1 SE; $n = 28$ for each treatment and survey combination) on black cottonwood saplings to which birds and bats did (control) and did not (exclusion) have access at Mono Lake, California, 2010.

Correlation Test, $Z = 0.67$, $P = 0.51$) was correlated with differences between control and exclosure sapling arthropod biomass.

Predator Exclusion Effects on Herbivory and Shoot Elongation

Herbivore chew holes accounted for 83% of all leaf damage area, followed by leaf folds (7%) and leaf mines (5%). Exclusion of birds and bats did not increase the frequency of leaves with chew damage (Figure 4). Mean percent leaf area chewed was low overall, and though higher on exclosure saplings (control $3.51 \pm 3.69\%$, exclosure $4.76 \pm 3.17\%$), the difference was not significant and 95% confidence intervals on treatment effect size overlapped zero (Table 4).

Finally, 2010 shoot elongation was not significantly different between exclosure and control saplings (Figure 5, Table 4, Appendix D). The shoot extension model improved markedly with pre-treatment (i.e., 2009) shoot elongation included as a covariate (e.g., $\Delta AICc$ between models with and without 2009 growth included as a covariate was 25.90), suggesting that variance in 2010 shoot elongation was largely explained by the location or genetics of individual saplings. Mean sapling shoot elongation in 2010 (12.63 ± 6.63 mm) and 2009 (12.03 ± 8.65 mm) did not differ (permutation test, $Z = -0.608$, $P = 0.55$).

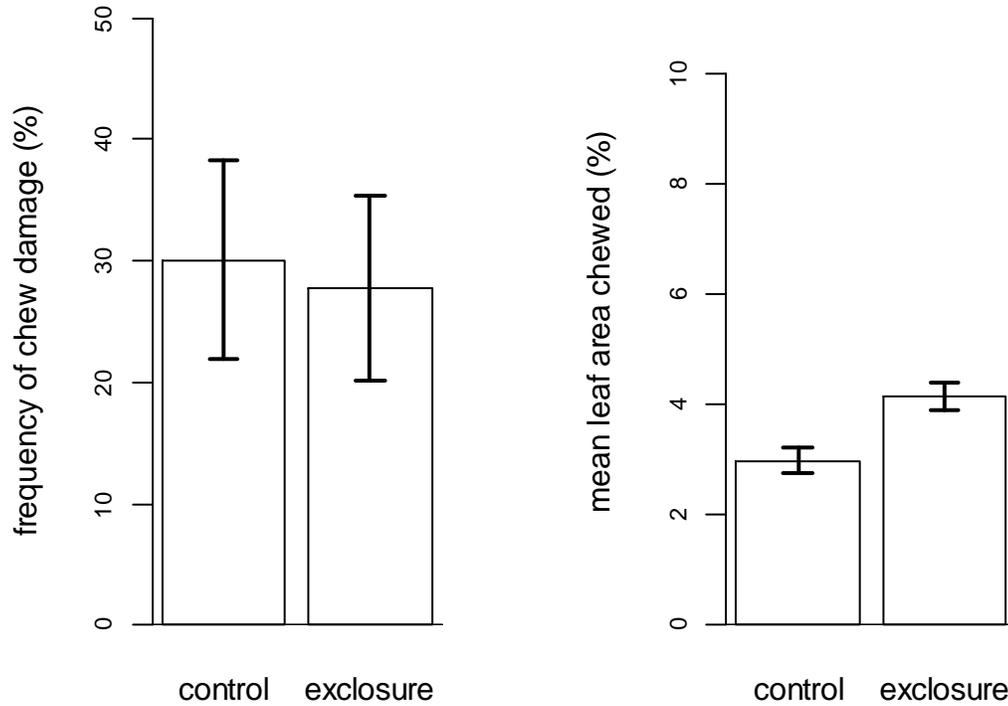


Figure 4. Frequency of chew damaged leaves and percentage leaf area chewed (mean \pm 1 SE) for black cottonwood saplings to which birds and bats did (control) and did not (exclosure) have foraging access at Mono Lake, California, 2010. GLM interpolated means averaged across pairs; values for percent leaf area chewed back-transformed from arcsine square root transformations.

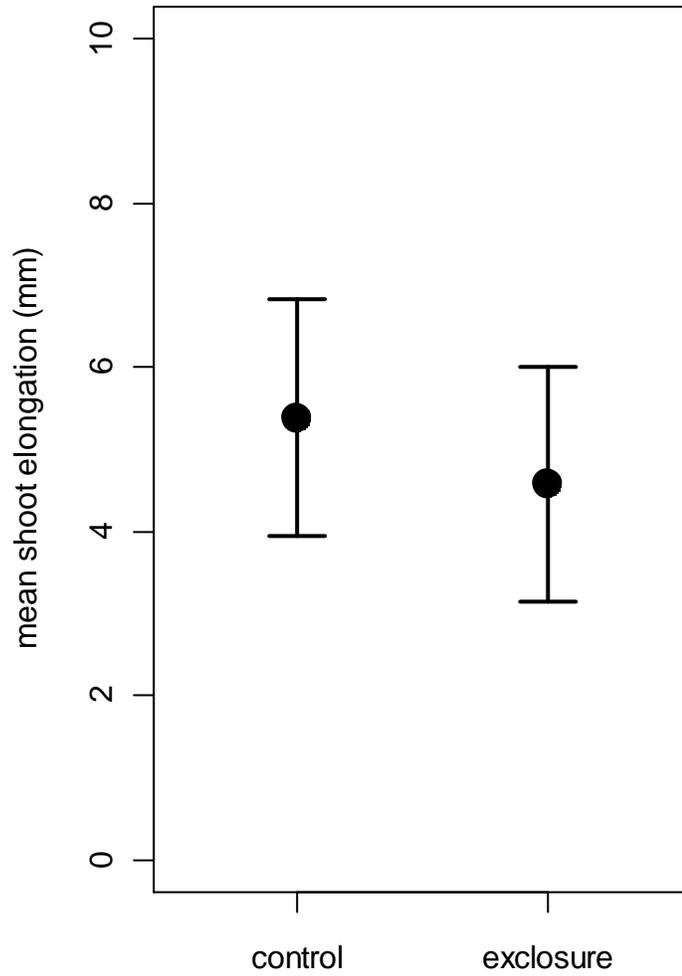


Figure 5. 2010 mean shoot growth (mean \pm 1 SE) for black cottonwood saplings to which birds and bats did (control) and did not (exclosure) have foraging access at Mono Lake, California, 2010. GLM interpolated means at mean 2009 shoot growth and averaged across pairs, back-transformed from natural log transformations.

DISCUSSION

Predator Exclusion Effects on Exposed-feeding Arthropods

The most fundamental prediction of this experiment was that bird and bat exclusion would lead to an increase in arthropod biomass and density on black cottonwood saplings. Contrary to this prediction, I found no evidence of arthropod suppression by birds and bats in any foraging functional group or for total arthropods. This result runs contrary to general conclusions provided by meta-analyses which have demonstrated widespread suppression of plant-dwelling arthropods by birds (Gunnarsson 2007, Van Bael et al. 2008) or birds, bats, and lizards (Mooney et al. 2010). Nonetheless, meta-analyses are only as valuable as the range of effects of the studies analyzed, and the results of this experiment fall well within the range of the studies examined. The question remains: what ecological characteristics of this system might explain the lack of an effect and what characteristics of the system I studied are similar to other experiments that also found no top-down suppression of arthropods? Below, I discuss five possible explanations.

One possible explanation predicted by theory (Holt and Polis 1997) and supported by experimentation with mostly invertebrate predators (see review by Vance-Chalcraft et al. 2007), is that intraguild predation (i.e., predation of predators) can weaken the overall observable effects of top predators on herbivore densities (Polis and Holt 1992). In their review, Vance-Chalcraft et al. (2007) found that in the absence of mostly invertebrate top predators (e.g., spiders), intermediate predators or parasitoids are released from predation and can subsequently suppress their herbivorous prey resulting in weaker effects of top

predator control on herbivores. For two reasons, however, I suspect that this explanation is not applicable in my system. First, neither predator and parasitoid biomass nor herbivorous prey biomass were changed by bird and bat exclusion (Table 4), suggesting no intraguild release. Second, ants (Formicidae) may be important intraguild arthropods in my study area because their mutualistic or predatory relationships with other arthropods can respectively strengthen or weaken effects of top predator removal (e.g., Sipura 2002, Mooney 2007), but I recorded similar ant biomass inside and outside exclosures (0.80 ± 1.31 and $0.82 \pm 2.97 \text{ mg}^{-100 \text{ leaves}}$, respectively). Though complex species-level interactions certainly could have been masked by family and functional groupings (Ohgushi et al. 2007), my results suggest that effects of bird and bat exclusion were not weakened by the compensatory effects of intraguild predation.

A second and better supported explanation for why I found no effect of bird and bat removal on herbivores is that the ratio of intermediate predator to herbivore densities (IP:H) on cottonwood saplings was low. When summed across control black cottonwood saplings for each survey, the IP:H in my study ranged from 1:19 to 1:190 (without ants as predators) and 1:9 to 1:30 (with ants as predators). Mooney et al. (2010) recently found that systems with naturally low IP:H demonstrated significantly weaker bird, bat and lizard predatory effects on arthropods than those with higher ratios; all values in my study fell within the low ratio ranges of the 113 experiments compiled by Mooney et al. (2010), in which IP:H ratios on control plants ranged from 1:167 to 4:1. The findings of Mooney et al. (2010) contradict those predicted by intraguild theory (e.g., Holt and Polis 1997) in which high IP:H ratios are expected to weaken top predator effects on herbivores. The

mechanisms underlying this pattern warrant further study, but Mooney et al. (2010) suggest that the ability of highly mobile vertebrate predators to opportunistically prey switch between prey groups of different abundance may cast them as unique intraguild predators not well-defined by existing theory. The ability to resolve these empirical and theoretical contradictions extends beyond the scope of my study, nonetheless my study corroborates the finding of Mooney et al. (2010) that low IP:H ratios corresponded with weaker predatory effects of birds, bats and lizards.

Bird foraging observations support a third and likely explanation for the lack of predation effects on cottonwood sapling dwelling arthropods. Data on bird foraging attack height revealed that while 40% of cottonwood attacks took place below 3 m, very few attacks (4%) took place on saplings at most 3 m in height (i.e., the maximum height of experimental saplings). It logically follows that fewer attacks on saplings would result in fewer arthropods consumed, thus minimizing the differences between arthropods on saplings to which birds did and did not have access. Cottonwood saplings may harbor different densities or types of arthropod prey compared to the lower branches and canopies of mature cottonwood trees, and bird foraging behavior can be arthropod density-dependent and selective for different types of arthropod prey. For example, Dickson and Whitham (1996) found that the percentage of cottonwood aphid petiole galls attacked by birds was significantly and positively related to the number of galls available per branch, and Kearsley and Whitham (1989) found that gall aphids were 70 times as common on mature *P. angustifolia* trees than on juvenile trees while leaf-consuming beetles (*Chrysomela confluens*) had densities 400 times as high on juvenile than on

mature trees. I did not sample arthropods from mature cottonwoods at my site for direct comparison, but informative comparisons can be made to findings by Bridgeland et al. (2010) who reported arthropod biomass (mg) on mature *P. angustifolia* x *P. fremontii* using methodologies similar to this study. The biomass of total arthropods, herbivores, leaf chewers and predator/parasitoids were all lower on control black cottonwoods saplings at Mono Lake than on control mature *P. angustifolia* x *P. fremontii* trees in experimental gardens of northern Utah, U.S.A. (valley and upland sites 2006-2007, Bridgeland et al. 2010), suggesting reduced prey options for birds on saplings versus mature trees. An exception was ant biomass, which was higher on Mono Lake saplings. The relatively high ant biomass in my study (27% of total biomass), and the complex roles that ants can play in food webs as herbivore predators or protectors and predaceous arthropod predators or competitors (Sipura 2000) suggests that ants may have regulated arthropod biomass on black cottonwoods saplings in my study area, despite the lack of bird and bat predation effects on their densities. Nonetheless, Bridgeland et al. (2010) found that birds reduced total arthropod biomass (mg) on mature cottonwoods by as much as 35% when compared to cottonwoods to which birds were denied access, but bird predation effects were contingent on year, site and arthropod community composition.

Fourth, bird and bat abundance or bird species richness may have been insufficient to dampen invertebrate biomass on cottonwood saplings at any height. This explanation, however, is unlikely in my study system for several reasons. First, timing of bird nest hatch, fledge and peak arthropod biomass were such that the six year average of peak nest hatch coincided with the beginning of arthropod biomass increase in 2010 and

peak arthropod biomass coincided with the weeks of and following the six year average peak nest fledge (Figure 1). Twenty-four percent of black cottonwood attacks were made by juvenile birds ($n = 92$ known age cottonwood attacks), whose attacks were first observed during the July 2, 2010 survey. Further, the number of mid-July echolocation calls of the foliage-gleaning long-eared myotis indicates that activity for this species was highest during peak arthropod biomass. Second, the mean number of cottonwood foraging birds^{-visit} summed across sapling pairs in June 2010 (104 ± 4) was higher than during previous research at the same study site (range $43 \pm 9 - 95 \pm 11$, 1999-2005 PRBO unpublished data). Third, I detected 24 bird species foraging on black cottonwood and at least two bat species as potential predators of arthropods on or near black cottonwoods, whereas Bridgeland et al. (2010), who found that birds reduced arthropod biomass (mg) by as much as 35% on mature cottonwoods, reported only 8 – 10 bird species at their sites. In tropical agroforestry systems, Van Bael et al. (2008) found that bird species richness correlated positively with percent reduction of arthropods of all sizes, while Perfecto et al. (2004) showed that experimentally placed invertebrates were reduced more on farms with higher bird densities, and that predation was likely attributable to a few “most effective insectivores”. In my study system, yellow warblers comprised the majority of cottonwood foraging attacks (45%), were the most detected species via point counts (Table 1), and maximum numbers of yellow warblers per sapling pair were within the upper range of estimates for yellow warbler numbers in other riparian reaches and meadows in region (Heath 2008). Though I did not examine the diet of yellow warblers in this system, stomach content analysis of yellow warblers in

California fruit orchards ($n = 98$) found Hymenoptera to compose 30% of the diet, about half of which were ants (Beal 1907). Other food items included caterpillars and a few adult moths (18%), beetles (16%), Hemiptera (mostly leaf hoppers, 19%) and flies (9%). Thus, the yellow warbler is the most likely bird species to be an effective predator, if there is one, in my study system. Nonetheless, neither numbers of total cottonwood foraging individuals nor numbers of yellow warblers were correlated with differences between control and enclosure sapling arthropod biomass.

Finally, I did not examine bird, arthropod, plant or their interactive responses to chemical plant defenses in my system, but it is possible that such plant-mediated effects influenced the experimental outcomes in this study. Plants belonging to the Salicaceae family (including willows and cottonwoods) synthesize secondary metabolites (Pearl and Darling 1971, Palo 1984, Tuskan et al. 2006, Mellway et al. 2009) which when induced can differentially influence the distribution, abundance, growth and behavior of arthropods (Howe and Jander 2008, Ohgushi et al. 2009), and the cascading effects of bird predation on arthropods and plants (Sipura 1999). For example, when comparing effects of bird predation on leaf chewing herbivore densities in two sympatric willow species (*S. phyllicifolia* and *S. myrsinifolia*) with different concentrations of herbivore-resistant secondary metabolites Sipura (1999) found no effect on the willow with 50-fold higher concentrations of phenolic glycosides and a significant bird predation effect on the willow with milder concentrations. Given the high structural and genetic diversity of disease and insect resistance genes in black cottonwoods (Tuskan et al. 2006) and the

influences of individual cottonwood genotypes on arthropod abundance and bird predation (Smith et al. 2011), this is an area of study that warrants further investigation.

Predator Exclusion Effects on Concealed Arthropods

I tended to find more leaves with leaf folds, ties, rolls and cases on control saplings than on exclosure saplings (Table 4), as did Sipura (1999) and Low and Connor (2003) on willows. It is not clear why results from three bird exclosure studies corroborated the weak negative effects of bird exclusion on concealment structures in Salicaceae but mechanistic studies would likely provide insight and are warranted given the prevalence of concealment structures in these systems and their important role in shaping community interactions (Marquis and Lill 2007, Lill and Marquis 2007). Shelter-building arthropods add another level of complexity to investigations of the cascading effects of bird predation because shelters can both provide escape from bird foraging attacks (Altegrim 1989) and search images for birds thereby incurring higher rates of attack (e.g., Dickson and Whitham 1996, Murakami 1999). Further, shelter-building arthropods can influence the distribution and abundance patterns of plant-dwelling arthropod communities because they engineer additional habitat for themselves and for secondary dwellers (inquilines, Marquis and Lill 2007, Lill and Marquis 2007). For example, Martinsen et al. (2000) found four times as many arthropod species and seven times as many individuals on *P. angustifolia* × *P. fremontii* shoots that contained a leaf roll than on shoots without leaf rolls. In my study, leaf folds, ties, rolls, galls and cases represented 16% of structure and exposed arthropod counts and nearly twice as many

arthropods were present within silk tied leaf folds as the number of folds investigated, suggesting that engineers and inquilines within concealment structures contributed greatly to overall arthropod biomass on black cottonwood saplings.

Trophic Cascades

Direct predation effects on herbivores are almost always stronger than the indirect cascading effects on plant damage or plant growth (Schmitz et al. 2000, Mooney et al. 2010). Given the apparent lack of arthropod response to bird and bat exclusion in this study, it is of little surprise that I found no compelling evidence of indirect bird predation effects on leaf damage or black cottonwood shoot extension. This result is contrary to the general findings of recent meta-analyses which have concluded that insectivorous birds (Mäntylä et al. 2011) or insectivorous birds, bats and lizards (Mooney et al. 2010) have indirect positive effects on plants via reduction of herbivory damage and plant mortality and in some cases increases in plant biomass. Clear general patterns derived from 81 to 113 separate experiments are still lacking, suggesting either an overall average of invariant top-down effects, or deficiencies in research to detect explanatory patterns: indirect effects of bird exclusion did not differ between trees and shrubs or mature trees and saplings, between agricultural and natural settings, or tropical, temperate and boreal regions, between bird and bat predators versus lizards or because of experimental duration, exclusion area or sample size (Mooney et al. 2010, Mäntylä 2011). Even when just considering studies investigating bird predation effects on five species in the Salicaceae family, results are mixed (Sipura 1999, Low and Connor 2003, Bridgeland et

al. 2010, this study). Bird and bat predation did not decrease leaf damage on two of the three willow species or on black cottonwoods, but when exposed to foraging birds, *P. angustifolia* × *P. fremontii* experienced a 13.9 – 17.7% increase in trunk growth compared to trees from which birds were excluded (Bridgeland et al. 2010) and *S. phyllicifolia* experienced a 71% increase in radial growth and a 33% increase in shoot length (Sipura 1999).

A unifying pattern among studies involving Salicaceae appears to be that bird- and bat-driven species-level trophic cascades were demonstrated for plants with higher leaf-chewing herbivore loads. Bridgeland et al. (2010) found a top predator effect on trunk growth only in the year and site in which herbivore loads were increased by an outbreak of leaf-chewing grasshoppers (*Melanoplus* spp.), and Sipura (1999) found significant increases in radial growth and shoot length on the willow species with six to nine times higher densities of leaf-chewing Lepidoptera and leaf beetle larvae densities than on the willow species for which no effect was found. Leaf-chewing herbivore densities on black cottonwoods in my study were comparatively low (Figure 3, Appendix A). The most prevalent leaf chewer in this study was the larval stage of *Nycteola cinereana* which averaged only 0.53 ± 2.78 larvae per sapling; these moths reached densities of up to 27 larvae per sapling, but large aggregations were observed on only a few saplings (only three control and two enclosure saplings harbored greater than four larvae during any survey). Sawfly larvae were the next most abundant leaf chewers, but only 50 exposed-feeding individuals were observed across all saplings and all surveys. I observed no grasshoppers (Orthoptera), and though the leaf-chewing striped willow leaf

beetle were noticeably abundant on *S. exigua* plants adjacent to black cottonwood saplings, one to four individuals were observed on only five out of 56 cottonwoods. This pattern runs contrary to the idea that bird predation may have minimal impact on herbivores during times of outbreak since a lower percentage of herbivores are consumed when their numbers are hyper-abundant (e.g., Morris et al. 1958, Holmes et al. 1979). This is thought to be especially true during the avian breeding season when territorial behaviors among conspecifics limit the number of avian predators per unit area (e.g., Loyn et al. 1983, Fayt et al. 2005). Nonetheless, territorial birds will change foraging patterns and diet composition in response to insect outbreak (e.g., Hogstad 2005) and bird populations do respond numerically to insect outbreak both immediately and over longer time scales (e.g., Koenig and Liebhold 2005, Koenig et al. 2011). It could be that though avian predators have minimal impacts on hyper-abundant herbivore populations, their complete removal from a system (i.e. via experimental exclosures) might still have significant cascading effects on herbivory or plant growth.

Finally, it is possible that the relative contributions of top-down effects on black cottonwood sapling growth are dependent on bottom-up forces such as water availability, as is generally suggested by Hunter and Price (1992). Cottonwoods are particularly prone to adjustments in leaf morphology or production and stomatal conductance in response to changing stream flow conditions (Smith et al. 1991) and annual changes in stream flow can determine rates of cottonwood growth. For example, Stromberg and Patten (1990) found that stream flow volume explained 66% of annual variation in black cottonwood tree-ring width at Mono Lake streams; a four to five increase in flow resulted in a

doubling of the annual ring width. Only two studies have explicitly examined the synergistic effects of water availability and bird and bat predation on herbivory and plant growth; they demonstrated that in conditions of higher water availability plants had higher primary productivity and arthropod abundance and experienced stronger cascading effects of top-down control than plants during drier conditions (Mazia et al. 2009, Bridgeland et al. 2010). During the year of my experiment, Mono Lake's tributary streams experienced among the highest peak daily stream flows that have been observed in over 30 years (Mono Lake Committee unpublished data); thus based on previous research I would have predicted weak top-down effects at minimum, but this was not the case.

CONCLUSION

I found no effect of bird and bat exclusion on arthropod biomass or density, leaf damage or sapling black cottonwood shoot extension during one year of study, suggesting that bird and bat predation may have little immediate effect on black cottonwood recovery in a restoration context. The combined results of my study and those of Bridgeland et al. (2010) suggest that for cottonwoods in particular, birds and bats are not very effective at facilitating cottonwood growth during conditions of low herbivore densities, but that insectivory may indirectly improve cottonwood growth during times of higher herbivore abundance when plants are most vulnerable to herbivory. These findings prompt the notion that insectivores might contribute to ecosystem resiliency during temporally and spatially variable herbivore outbreaks. Since this suggestion runs contrary to the idea that avian predators are most impactful on herbivores when herbivore densities are at endemic levels (e.g. Holmes et al. 1979), future research should explicitly investigate the cascading effects of bird and bat predation during arthropod outbreak. Testing this idea is challenging because short-term studies only capture marked temporal variation in top-down effects by chance, and investigations of temporal effects have to date been mostly limited to *post-hoc* comparisons of several short-term studies. Thus, the importance of long term studies (e.g., over the life-span of a plant) cannot be over-estimated. Studying variation in top-down effects might be especially valuable in the context of restoration since environmental conditions and biotic communities change relatively rapidly over time.

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PERSONAL COMMUNICATIONS

Szewczak, J. 2011. Personal communication. Humboldt State University, 1 Harpst St. Arcata, CA, 95503.

Appendix A. Number of arthropods^{-100 leaves} (mean \pm standard deviation, $n = 28$ saplings per treatment and survey combination) on black cottonwood saplings at Mono Lake, California, 2010.

Arthropod group	May 22 - June 7		June 15 - July 2		July 11 - July 23		August 3 - August 15	
	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure
Araneae	0.01 \pm 0.04	0.01 \pm 0.02	0.10 \pm 0.13	0.09 \pm 0.17	0.13 \pm 0.21	0.10 \pm 0.19	0.11 \pm 0.22	0.11 \pm 0.16
Acari	0.01 \pm 0.03	0.01 \pm 0.03	0.12 \pm 0.18	0.14 \pm 0.22	0.13 \pm 0.40	0.17 \pm 0.42	0.09 \pm 0.23	0.13 \pm 0.27
Ephemeroptera	0.001 \pm 0.003	0.001 \pm 0.004	0.05 \pm 0.10	0.03 \pm 0.09	0.14 \pm 0.28	0.07 \pm 0.16	0.08 \pm 0.17	0.04 \pm 0.08
Odonata	0	0	0	0	0.002 \pm 0.009	0	0.001 \pm 0.006	0
Plecoptera	0	0	0.005 \pm 0.028	0	0.006 \pm 0.032	0	0	0
Hemiptera	3.93 \pm 4.46	4.64 \pm 4.62	7.76 \pm 18.07	7.49 \pm 17.18	31.41 \pm 89.65	19.61 \pm 55.14	25.91 \pm 123.37	18.35 \pm 37.74
Heteroptera	0.65 \pm 1.95	0.23 \pm 0.44	4.26 \pm 17.32	0.85 \pm 2.56	18.96 \pm 70.34	3.43 \pm 7.57	6.26 \pm 29.90	1.14 \pm 2.10
Tingidae	0.59 \pm 1.93	0.14 \pm 0.41	4.19 \pm 17.22	0.78 \pm 2.53	18.94 \pm 70.34	3.38 \pm 7.58	6.23 \pm 29.90	1.11 \pm 2.10
Auchenorrhyncha	3.05 \pm 3.5	2.87 \pm 3.29	1.56 \pm 2.16	1.7 \pm 2.02	0.31 \pm 0.30	0.27 \pm 0.30	0.14 \pm 0.18	0.12 \pm 0.15
Sternorrhyncha	0.23 \pm 0.53	1.53 \pm 3.81	1.94 \pm 5.74	4.94 \pm 17.26	12.13 \pm 43.01	15.91 \pm 55.43	19.49 \pm 93.57	17.07 \pm 38.06
Aphididae	0.22 \pm 0.53	1.51 \pm 3.82	1.79 \pm 5.73	4.94 \pm 17.26	12.13 \pm 43.01	15.91 \pm 55.43	19.47 \pm 93.57	17.07 \pm 38.06
Thysanoptera	0.37 \pm 0.47	0.32 \pm 0.48	0.21 \pm 0.29	0.22 \pm 0.28	0.18 \pm 0.20	0.14 \pm 0.14	0.07 \pm 0.08	0.12 \pm 0.15

Appendix A. Number of arthropods^{-100 leaves} (mean \pm standard deviation, $n = 28$ saplings per treatment and survey combination) on black cottonwood saplings at Mono Lake, California, 2010 (continued).

Arthropod group	May 22 - June 7		June 15 - July 2		July 11 - July 23		August 3 - August 15	
	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure
Coleoptera	0.02 \pm 0.04	0.02 \pm 0.04	0.10 \pm 0.18	0.07 \pm 0.12	0.15 \pm 0.21	0.12 \pm 0.25	0.04 \pm 0.07	0.07 \pm 0.18
Neuroptera	0.001 \pm 0.006	0	0.002 \pm 0.009	0.004 \pm 0.013	0.016 \pm 0.041	0.007 \pm 0.017	0.005 \pm 0.020	0.002 \pm 0.010
Hymenoptera	0.26 \pm 0.43	0.68 \pm 1.67	0.24 \pm 0.29	0.37 \pm 0.55	0.73 \pm 1.74	0.53 \pm 0.81	1.76 \pm 6.63	1.22 \pm 2.10
Sawfly Larvae	0.004 \pm 0.015	0	0	0.01 \pm 0.04	0.03 \pm 0.10	0.03 \pm 0.06	0.03 \pm 0.05	0.01 \pm 0.04
Sawfly Adult	0	0.003 \pm 0.015	0.01 \pm 0.03	0	0.02 \pm 0.07	0.001 \pm 0.004	0	0.004 \pm 0.017
Formicidae	0.26 \pm 0.43	0.68 \pm 1.67	0.23 \pm 0.29	0.36 \pm 0.56	0.68 \pm 1.73	0.49 \pm 0.82	1.73 \pm 6.63	1.14 \pm 2.08
Trichoptera	0	0	0	0	0.003 \pm 0.018	0	0	0
Lepidoptera Larvae	0.01 \pm 0.05	0.01 \pm 0.02	0.01 \pm 0.03	0.03 \pm 0.08	0.07 \pm 0.19	0.25 \pm 0.81	0.03 \pm 0.04	0.03 \pm 0.04
Lepidoptera Adult	0.003 \pm 0.015	0	0.002 \pm 0.007	0.004 \pm 0.022	0.02 \pm 0.05	0.01 \pm 0.04	0.003 \pm 0.010	0.004 \pm 0.013
Mecoptera	0	0	0	0	0	0	0	0.001 \pm 0.005
Diptera	0.15 \pm 0.15	0.14 \pm 0.14	0.22 \pm 0.33	0.18 \pm 0.20	0.29 \pm 0.35	0.15 \pm 0.17	0.30 \pm 0.30	0.36 \pm 0.36

Appendix A. Number of arthropods^{-100 leaves} (mean \pm standard deviation, $n = 28$ saplings per treatment and survey combination) on black cottonwood saplings at Mono Lake, California, 2010 (continued).

Arthropod group	May 22 - June 7		June 15 - July 2		July 11 - July 23		August 3 - August 15	
	Control	Exclosure	Control	Exclosure	Control	Exclosure	Control	Exclosure
Order unknown	0	0	0.004 \pm 0.020	0.01 \pm 0.04	0	0	0	0.01 \pm 0.02
Herbivores	4.15 \pm 4.58	4.79 \pm 4.60	7.91 \pm 18.05	7.70 \pm 17.13	31.70 \pm 89.61	20.05 \pm 55.06	26.03 \pm 123.36	18.49 \pm 37.72
Leaf chewers	0.02 \pm 0.05	0.01 \pm 0.02	0.01 \pm 0.04	0.04 \pm 0.08	0.11 \pm 0.20	0.29 \pm 0.81	0.06 \pm 0.06	0.04 \pm 0.05
Predators and parasitoids	0.21 \pm 0.3	0.20 \pm 0.22	0.32 \pm 0.30	0.30 \pm 0.29	0.32 \pm 0.41	0.30 \pm 0.47	0.24 \pm 0.33	1.07 \pm 2.80
Leaf folds, rolls, ties, leaf cases	1.71 \pm 1.92	1.31 \pm 1.76	1.81 \pm 1.85	1.79 \pm 1.93	3.37 \pm 3.11	2.56 \pm 2.32	3.62 \pm 2.92	2.57 \pm 2.03
Petiole galls	0.20 \pm 0.34	0.70 \pm 2.39	0.26 \pm 0.38	0.44 \pm 1.01	0.38 \pm 0.79	0.56 \pm 1.42	0.78 \pm 2.16	0.91 \pm 1.62
Leaf galls	0.09 \pm 0.32	0.05 \pm 0.18	0.08 \pm 0.23	0.05 \pm 0.19	0.60 \pm 1.60	0.17 \pm 0.54	0.80 \pm 2.12	0.22 \pm 0.70

Appendix B. Repeated measures linear mixed effects model results examining the effects of the bird and bat exclusion treatment on total arthropod biomass ($\text{mg}^{-100 \text{ leaves}}$) and total arthropod density^{-100 leaves} on black cottonwood saplings during four survey periods at Mono Lake, California, 2010. Log-transformations performed on both response variables.

Response variable	Fixed effects	df	<i>F</i>	<i>P</i>
Total arthropod biomass	Pair	27, 27	2.92	0.004
	Survey	3, 162	32.89	<0.001
	Treatment	1, 27	0.79	0.38
	S×T	3, 162	1.83	0.14
Total arthropod density	Pair	27, 27	3.94	<0.001
	Survey	3, 162	3.39	0.02
	Treatment	1, 27	0.10	0.75
	S×T	3, 162	2.42	0.07

Appendix C. Results of paired non-parametric repeated measures tests examining the effects of the bird and bat exclusion treatment on arthropod functional group biomass ($\text{mg}^{-100 \text{ leaves}}$) on black cottonwood saplings during four survey periods at Mono Lake, California, 2010.

Response variable	Effect	ANOVA-type statistic	df	<i>P</i>
Herbivore biomass	Survey	28.77	2.9	<0.001
	Treatment	0.55	1.0	0.46
	S×T	1.80	2.8	0.15
Leaf chewer biomass	Survey	18.76	2.8	<0.001
	Treatment	0.82	1.0	0.36
	S×T	0.19	2.3	0.15
Predator and parasitoid biomass	Survey	8.03	2.8	<0.001
	Treatment	0.04	1.0	0.85
	S×T	1.92	2.7	0.13
Concealment structure density	Survey	28.83	1.8	<0.001
	Treatment	2.99	1.0	0.08
	S×T	0.78	2.0	0.46
Gall density	Survey	17.93	2.5	<0.001
	Treatment	0.17	1.0	0.68
	S×T	0.25	2.5	0.82

Appendix D. Analysis of deviance tables for generalized linear models (GLM) examining the effects of the bird and bat exclusion treatment on frequency of leaf chew damage (%), leaf area chewed (%) and sapling shoot growth (mm) on black cottonwood saplings at Mono Lake, California, 2010. Arcsine square root and natural log transformations were applied to leaf area chewed and shoot growth, respectively.

Response variable	Fixed effects	SS	df	<i>F</i>	<i>P</i>
Frequency of leaf chew damage ^a	Pair	168.65	27	1.77	0.07
	Treatment	1.93	1	0.55	0.47
	Residuals	95.16	27		
Leaf area chewed ^b	Pair	0.22	27	1.78	0.07
	Treatment	0.01	1	2.95	0.10
	Residuals	0.13	27		
Shoot growth ^b	Pair	6.04	27	1.95	0.05
	Ln(2009 growth)	2.71	1	23.60	< 0.001
	Treatment	0.36	1	3.17	0.09
	Residuals	2.98	26		

^aQuasibinomial GLM

^bGaussian GLM