

Interactions among elk, aspen, galling sawflies and insectivorous birds

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Using two years of observational and experimental data, we examined the hypothesis that browsing by elk on aspen indirectly affects the distribution of a leaf-galling sawfly, which in turn affects insect diversity and foraging patterns of insectivorous birds. We found that: i) in an analyses of 33 arthropod species, the presence of sawflies significantly increased arthropod richness and abundance by 2 X and 2.5 X, respectively. ii) browsing by elk reduced sawfly gall abundance such that 90% of the galls were found on unbrowsed aspen ramets. iii) insectivorous birds attacked 60–74% of the galls on unbrowsed shoots compared to 11% on browsed shoots. When leaf-galler abundance was experimentally held constant on browsed and unbrowsed shoots, predation by insectivorous birds did not differ significantly. This result suggests that browsing affects the patterns of avian predation by altering the distribution of a galling insect. These data argue that bottom-up, top-down, and lateral factors can act in concert to affect the distribution of a galler, structure arthropod communities and affect predation by insectivorous birds.

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Complex interactions among mammals, plants and arthropods are probably common, however, few studies have documented actual chains of interactions and their impacts on diverse organisms (Jones et al. 1998, Martinsen et al. 1998). Independently, bottom-up factors such as host plant quality and phenology and top-down impacts by predators affect insect population dynamics and community structure (Price and Clancy 1986, Greenberg 1987, Hunter 1987, 1992, Atlegrim 1992, Marquis and Whelan 1994, White and Whitham 2000). Most studies of bottom-up or top-down interactions demonstrate direct and indirect effects among plants, herbivores, predators, and their parasitoids (Roininen et al. 1996, Dyer and Letourneau 1999, Forkner and Hunter 2000, Ritchie 2000) but don't include the effects of other dominant herbivores, abiotic conditions (but see Forkner and Hunter 2000, Ritchie 2000), or other community members. For example, Forkner and Hunter (2000) showed how environmental conditions

that positively affected growth of oaks, also positively affected arthropod herbivore abundance and increased predation. Other factors, such as herbivory, that positively or negatively affect plant quality may also influence trophic level interactions.

Interactions between common and/or keystone species are likely to result in community-wide consequences. For example, Martinsen et al. (1998) showed how beavers affected the distribution of a common leaf-feeding beetle, which in turn affects other diverse taxa and trophic levels. Others have shown how dominant herbivores, and shelter building insects (i.e. leaf-gallers, folders, and tiers), positively affect other arthropods (Damman 1987, Cappuccino 1993, Martinsen et al. 2000). Lastly, studies have demonstrated how insectivorous birds can affect the abundance of many insect groups through predation (Greenberg 1987, Atlegrim 1992, Marquis and Whelan 1994). Here, we combine bottom-up and top-down trophic interactions and

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browsing by a dominant mammalian herbivore to document links among aspen (*Populus tremuloides*), elk (*Cervus canadensis*), and a leaf galling insect (sawfly, *Phyllocolpa bozemanii*, Cooley) and their combined effects on arthropod diversity and insectivorous birds.

We experimentally documented these links using 4 year old U.S. Forest Service elk exclosures, simulated elk browsing experiments and by adding artificial leaf folds to test the response of birds to increased gall abundance. Experiments examining the community effects of shelter building insects are rare (Martinsen et al. 2000), and few studies have attempted to combine all factors described above to demonstrate how bottom-up and top-down trophic level interactions and lateral effects act in concert.

Methods

Study sites

Studies were conducted in the Hochderfer Hills region of the Coconino National Forest northwest of Flagstaff, Arizona USA (Bailey and Whitham 2002). Here, many young aspen stands are regenerating due to several consecutive extreme fire years. In 1996, the U.S. Forest Service established two elk exclosures of ~75 hectares each after a wildfire burned nearly 6,640 hectares of forest. The exclosures were intended to eliminate browsing and facilitate the regeneration of aspen stands because browsing can reduce aspen biomass by up to 95% and prevent aspen regeneration (Bailey and Whitham 2002). Aspen has the largest distribution of any North American deciduous tree species and studies have shown that in montane ecosystems, aspen stands have high associated plant biodiversity and provide critical food and habitat to a variety of animals (Basey et al. 1990, Romme et al. 1995, Baker et al. 1997).

Elk impacts on sawflies

The leaf-edge galling sawfly, *Phyllocolpa bozemanii*, is a common insect with a widespread distribution on *Populus*, which induces a folded-gall on the margin of the leaf (Fritz and Price 1988). In 1999 and 2000 we randomly selected and visually censused 30 ramets within (no elk) and outside the exclosures (elk present) to experimentally examine how browsing of aspen affected the distribution of sawflies (n = 60). Aspen ramets were from 1.5 m to 2.5 m tall. We compared abundances of sawflies between the two exclosures and found no significant difference and therefore ramets representing multiple aspen clones (B. Young, unpubl.) were pooled for analysis. Furthermore, to examine how sawflies might respond to changes in plant quality

caused by browsing, we simulated natural levels of browsing by clipping 35% of the terminal shoots on 15 randomly selected aspen ramets prior to leafing out in 1999 and compared them to 15 unclipped ramets (n = 30; Hjältén et al. 1993, Bailey and Whitham 2002). We selected 35% as an experimental clipping level as it represented moderate levels of browsing naturally occurring in our system. Sawflies were quantified as being present or absent, data were analyzed using Chi-square.

Because many sawflies prefer vigorously growing tissue and browsing has been shown to reduce aspen vigor (Romme et al. 1995, Baker et al. 1997), we quantified differences in average leaf area between browsed and unbrowsed ramets (i.e., within and outside exclosures). Mean leaf area was measured using a CID-202 leaf area meter (CID Inc. Vancouver, Washington). We standardized measurements by quantifying the same-aged leaves of similar plastochron, using leaf position 5 from the terminal leaf on five shoots of 28 randomly selected browsed and unbrowsed ramets (Larson and Isebrands 1971). We analyzed leaf area using a students t-test.

Arthropod community consequences

We randomly selected 16 unbrowsed ramets inside the exclosures, counted the number of galls (from 0–4 galls), and visually censused the arthropod community on the ramet and within the gall for both richness and abundance (Dickson and Whitham 1996, Wimp and Whitham 2001, Bailey and Whitham 2002). All ramets were of the same age and were the result of suckering after the 1996 Hochderfer fire. Because a single abundant species such as aphids may drive abundance patterns, arthropod abundances were standardized to unit maxima (Wimp and Whitham 2001). By using unit maxima, the ramet with the greatest number of each species was given a value of one and all other ramets were assigned values proportional to that maximum (Faith et al. 1987). Because arthropod richness and abundance met assumptions of normality and equality of variance, we regressed arthropod richness and abundance by the number of galls on a ramet.

In addition to the above analyses of arthropod communities, we examined how the presence of galls affected the composition of the arthropod community using Non-metric Multidimensional Scaling (NMDS) techniques developed in the program DECODA (Minchin 1987a, b). NMDS arranges samples in ordination space based on the similarity between samples. In this case, samples were aspen ramets, and the similarity matrix was based on arthropod taxonomic richness and abundance. This arranges aspen ramets with similar species and abundances closer together in ordination space. Although originally developed for plant communities, it has also been used in analyses of arthropod communities (Dungray et al. 2000, Bailey and

Whitham 2002). This method of analysis allowed us to determine whether insect species composition differed between ramets with and without galls. Potential differences between groups were analyzed using an Analysis of Similarity (ANOSIM) test (Kantvilas and Minchin 1989, Oksanen and Minchin 1997).

Elk-avian interactions

To determine if browsing could potentially affect avian foraging on sawflies, we quantified gall predation rates on browsed and unbrowsed ramets both within and outside exclosures. Substantial damage to the leaf-gall by the presence of a peckmark or tear was considered successful bird predation (Dickson and Whitham 1996). We randomly surveyed browsed and unbrowsed ramets until we found 20 galls and examined them for evidence of bird predation.

Galls were found to be rare on browsed ramets (i.e. < 5%), which suggested that elk could affect avian foraging by altering prey density. Alternatively, birds might forage differently on browsed and unbrowsed ramets independent of gall abundance. To discriminate between these two alternative hypotheses, we experimentally tested whether differences in bird predation between browsing treatments was site or food resource related. We equalized the abundance of galls on browsed and unbrowsed ramets by simulating leaf galls (Martinsen et al. 2000). A single, small mealworm was rolled into a leaf and held in place using a paper clip. We created 50 simulated galls on 25 randomly selected browsed and unbrowsed ramets to simulate a natural food item for insectivorous birds. Because birds either “opened” a gall or not, data were analyzed using Chi-Square. A successful bird attack was recorded if the simulated gall was pecked or torn in the way observed in natural galls.

Results

Elk impacts on sawflies

The direct effects of browsing significantly reduced the average leaf area on browsed ramets ~4X (mean leaf area per ramet ± 1 SE, $9.95 \text{ cm}^2 \pm 2.88$ and $41.26 \text{ cm}^2 \pm 1.75$, respectively; $n = 28$ pairs, $t = 6.975$, $p < 0.0001$). Because many species, including the sawfly, *P. bozemanii*, are known to prefer large leaves and vigorously growing tissues (Price 1991), the impact of browsing on aspen vigor was predicted to negatively affect the distribution of this insect.

Consistent with our hypothesis, in 1999 and 2000 browsing negatively affected the distribution and abundance of sawflies (Fig. 1A). In 1999, we found that 91% of the galls were found on unbrowsed ramets (i.e. 50

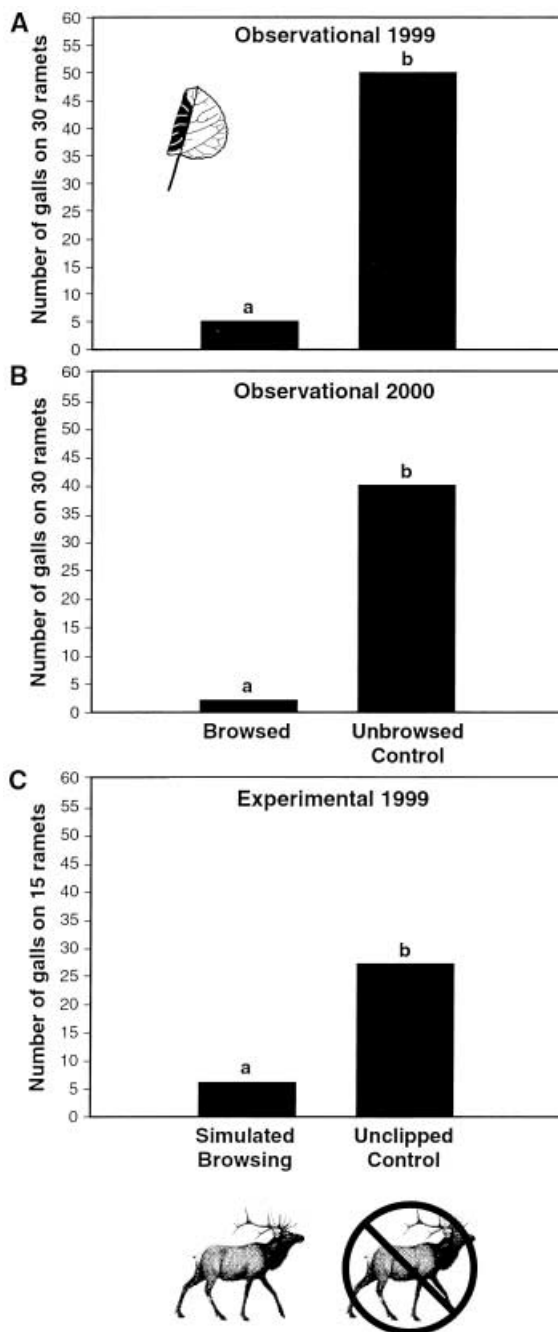


Fig. 1. Results of observational data in 1999 show that galls made by sawflies occur significantly more often on unbrowsed ramets than on ramets browsed by elk (Panel A. 1999- $\chi^2 = 24.83$, $p < 0.05$). This pattern was confirmed experimentally in 1999 with a clipping experiment that simulated natural levels of elk browsing (Panel B. $\chi^2 = 4.76$, $p < 0.05$). Observational data in 2000 again confirmed that galls occur significantly more often on unbrowsed ramets (Panel C. 2000- $\chi^2 = 20.0$, $p < 0.05$). Different letters indicate significant differences.

galls/30 ramets) compared to only 9% on browsed ramets (i.e. 5 galls/30 ramets; $df = 1$, $\chi^2 = 73.64$, $p < 0.0001$). Furthermore, in 2000, we observed the same pattern; 95% of the galls occurred on unbrowsed aspen ramets (i.e. 40 galls/30 ramets) compared with only 5% on browsed ramets (i.e. 2 galls/30 ramets; Fig. 1B, $df = 1$, $\chi^2 = 68.76$, $p < 0.0001$).

These patterns were confirmed with simulated browsing experiments in which 82% of the galls were found on unclipped ramets (i.e. 27 galls/15 ramets) relative to only 18% on clipped ramets (i.e. 6 galls/15 ramets; Fig. 1C, $df = 1$, $\chi^2 = 26.73$, $p < 0.0001$). Because these ramets were clipped before leaf flush and the sawfly oviposits after leaf flush, they suggest that browsing affects the oviposition behavior of the sawfly. Because shelter builders are known to affect other diverse community members, the next section examines how the altered distributions of sawfly galls caused by elk might affect the rest of the arthropod community.

Arthropod community consequences

Gall density on unbrowsed ramets was associated with greater arthropod species richness; ramets with two galls had 2X as many species as ramets without a leaf gall (Fig. 2A, $n = 16$, $F = 4.876$, $r^2 = 0.429$, $p < 0.026$). Similarly, mean arthropod abundance per aspen ramet was also significantly related to the number of galls present (Fig. 2B, $n = 16$, $F = 35.585$, $r^2 = 0.718$, $p < 0.0001$). Relative to ramets with no galls, ramets with two galls have ~4X as many arthropods.

Using NMDS ordination of individual species standardized to species maxima, we found that arthropod community composition differed significantly when galls were present on aspen ramets (Fig. 3, $n = 16$, $r = 0.8413$, $p < 0.00001$). These data suggest that localized shelters have community-wide effects. Combined with richness and abundance data, this suggests that trees with galls may be more lucrative for foraging insectivorous birds. For example, of the 33 species documented in this study, at least 90% of the abundance of 5 arthropod herbivore species and 6 arthropod predator species were found within galls (Table 1), suggesting that sawfly galls are a reliable food source.

From these data several patterns emerge. First, browsing by elk reduced average leaf area relative to leaves on unbrowsed ramets, and thereby negatively affected the distribution of sawflies. Because sawflies oviposit after leaf flush, the effect of elk on sawflies is indirect via their effects on plant quality that affects sawfly oviposition preferences. Second, sawflies positively affect arthropod species richness, abundance, and overall diversity. And third, because sawflies positively affect the arthropod community, the negative impacts of elk on sawflies can eliminate up to 33% of the arthropod community associated with sawflies (Table 1).

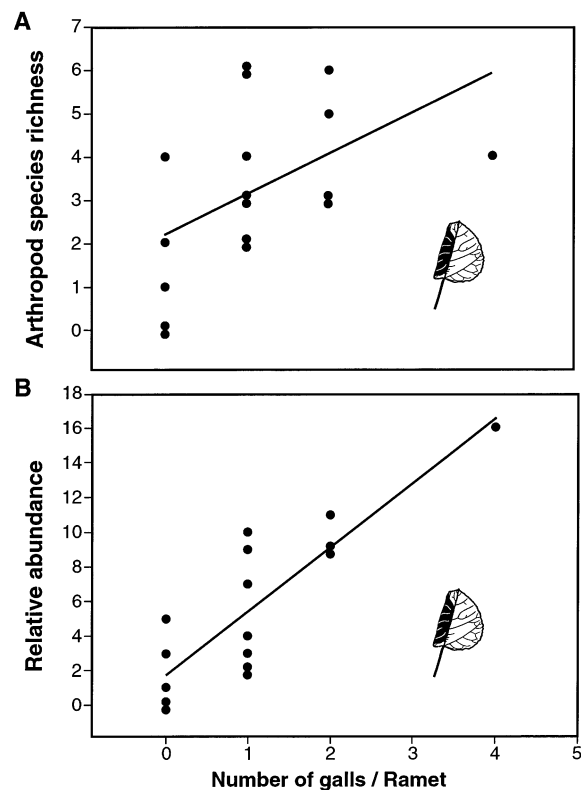


Fig. 2. Using linear regression, there is a positive relationship between galls and arthropods. As the number of galls increased on a ramet, arthropod species richness (Panel A, $F = 4.88$, $r^2 = 0.43$, $p < 0.026$; $y = 2.19x + 0.93$) and abundance (Panel B, $F = 35.59$, $r^2 = 0.72$, $p < 0.0001$; $y = 1.78x + 3.68$) significantly increased.

Elk-avian interactions

Bird predation was significantly greater on natural galls of unbrowsed ramets (Fig. 4A, $n = 40$, $df = 1$, $\chi^2 = 33.81$, $p < 0.05$) than on browsed ramets. Sixty percent of the galls on unbrowsed ramets were attacked, compared to only 10% on browsed ramets. There were two likely hypotheses to explain the foraging patterns of these insectivorous birds. First, birds foraged where sawfly densities were greatest, or independent of sawfly density birds foraged on unbrowsed ramets due to other innate site differences.

When we experimentally equalized abundances using artificial galls on browsed and unbrowsed ramets (i.e. by placing 50 simulated galls on each group) to simulate natural levels on unbrowsed ramets, there was no significant difference in bird predation (Fig. 4B, $n = 100$, $df = 1$, $\chi^2 = 1.45$). On unbrowsed ramets 74% of the galls were attacked and 64% of the galls on browsed ramets were attacked. We reject the hypothesis that innate differences among sites of browsed and unbrowsed ramets affected patterns of bird foraging and conclude that browsing impacts bird foraging on galls by altering the density of their prey.

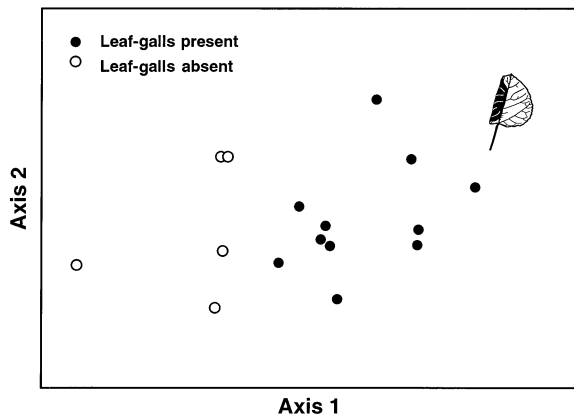


Fig. 3. Using NMDS ordination analyses (see text), we found that the composition of the arthropod community was significantly different on ramets with galls than on ramets without galls ($r = 0.8413$, $p < 0.0001$). Community composition was based on combined arthropod richness and abundance on aspen ramets with and without sawfly galls. ANOSIM compared within and between group differences.

Table 1. Arthropod groups found on observational and experimental trees.

Order	Family	Trophic level	Leaf-gall
Acarina	1	Predator	no
Acarina	2	Herbivore	no
Araneidae	1	Predator	yes
Araneidae	2	Predator	yes
Coleoptera	Coccinellidae 1	Predator	no
Coleoptera	Coccinellidae 2	Predator	yes
Coleoptera	Curculionidae 1	Herbivore	no
Coleoptera	Curculionidae 2	Herbivore	no
Diptera	Syrphidae	Predator	yes
Gastropoda		Herbivore	yes
Hemiptera	Miridae	Herbivore	no
Homoptera	Cicadellidae 1	Herbivore	no
Homoptera	Cicadellidae 2	Herbivore	no
Homoptera	Cicadellidae 3	Herbivore	no
Homoptera	Cercopidae 1	Herbivore	no
Homoptera	Aphidae 1	Herbivore	yes
<i>(Chaitophorous neglectus)</i>			
Homoptera	Aphidae 2	Herbivore	no
Homoptera	Aphidae 3	Herbivore	no
Homoptera	Diasphididae	Free Feeding	no
Hymenoptera	Formica 1	Predator	yes
Hymenoptera	Formica 2	Predator	no
Hymenoptera	Tenthredinidae	Herbivore	no
Lepidoptera	Geometridae 1	Herbivore	no
Lepidoptera	Gelechiidae 1	Herbivore	yes
Lepidoptera	Gracilariidae	Herbivore	no
Lepidoptera	Lasiocampidae	Herbivore	no
Lepidoptera		Herbivore	no
Lepidoptera		Herbivore	no
Lepidoptera		Herbivore	no
Lepidoptera		Herbivore	no
Lepidoptera	Sphingidae	Herbivore	no
Neuroptera	Chrysopidae	Predator	yes
Thysanoptera	Thripidae 1	Herbivore	yes
Thysanoptera	Thripidae 2	Herbivore	yes

Notes: List includes arthropod taxa found both on aspen ramets and within leaf-galls. Arthropod taxa were considered associated with a leaf-gall when greater than 90% of their abundance was found within the gall.

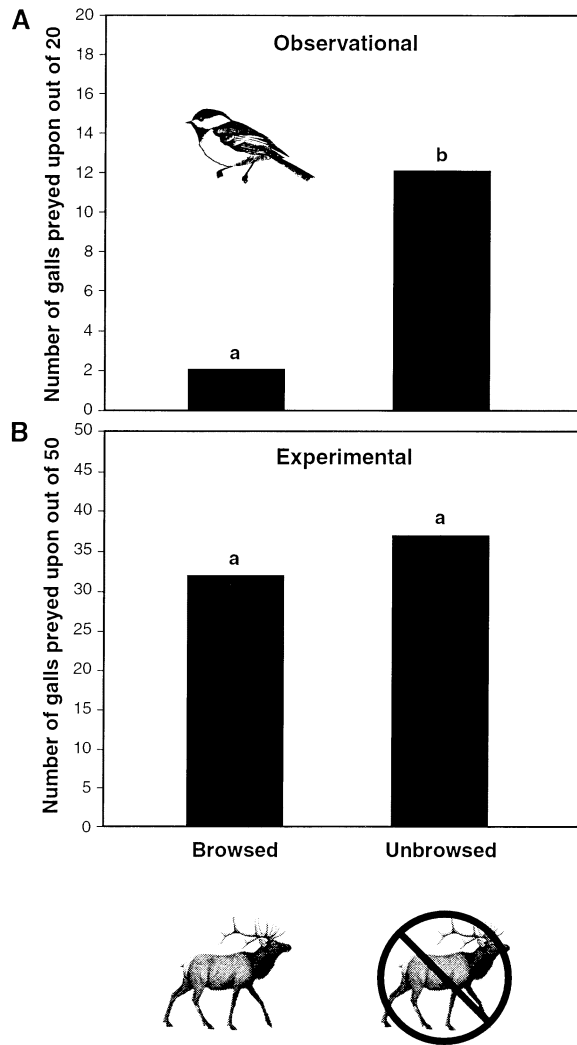


Fig. 4. Results of observational data in 2000 indicated that bird predation was significantly higher on galls on unbrowsed ramets than on browsed ramets (Panel A. $\chi^2 = 33.81$, $p < 0.05$). When gall abundance was experimentally held constant on browsed and unbrowsed ramets, no significant differences in bird predation were detected indicating that birds alter foraging in response to prey density rather than innate differences between browsed and unbrowsed ramets (Panel B. $\chi^2 = 1.45$). Different letters indicate significant differences.

From these experiments, two conclusions were made. First, insectivorous birds selectively foraged where sawfly densities were greatest. Second, browsing by elk can affect predation pressure and foraging patterns of insectivorous birds by altering the distribution of their sawfly prey.

Discussion

Positive effects of gall on the community

Our study suggests that small-scale (i.e. leaf-galls) structures can affect biodiversity at the ramet level and affect trophic level interactions. Several studies have also demonstrated the positive effects of small-scale shelter builders on arthropod diversity. For example, Waltz and Whitham (1997) and Martinsen et al. (2000) demonstrated that *Pemphigus betae*, a leaf-galler, and *Anacampsis niveopulvella*, a leafroller, increased overall arthropod biodiversity within the shelter due to habitat modification. Martinsen et al. (2000) also compared community effects of shelter building insects versus non-shelter building insects and suggested that positive community effects were the result of the shelter. Jones et al. (1997) argued that habitat modifying ecosystem engineers can have both positive and negative effects at “small scales,” but the effects become positive at “larger scales” due to increased landscape heterogeneity.

These data suggest three ways sawfly galls positively affect arthropod diversity and can extend to higher trophic levels. First, 33% of the arthropod community can be associated with sawfly galls. Second, the unique arthropods associated with a single gall disproportionately increased arthropod richness and abundance by 2–2.5X on unbrowsed ramets. Third, community composition of insects on unbrowsed ramets with galls was significantly different from the community of insects on unbrowsed ramets without galls. And, even at relatively low density of just 0–5 galls per ramet, the presence of sawfly galls affects the foraging patterns of insectivorous birds. In combination, these results argue that galling sawflies have high community importance relative to their low abundances (Power et al. 1996).

Interactions of elk and sawflies

Interactions among species that affect plant diversity, quality and quantity are likely to impact important herbivores (Martinsen et al. 1998), arthropod communities (Bailey and Whitham 2002), and trophic interactions. For example, Martinsen et al. (1998) showed that beaver browsing of cottonwoods positively affects the distribution and abundance of *Chrysomela confluenta*; a beetle that affects the distribution of many other herbivores, predators and parasites. Bailey and Whitham (2002) showed that arthropod communities associated with aspen changed depending upon the interaction of fire and elk herbivory. These studies indicated how responsive herbivores and arthropod communities can be to changes in host plants due to biotic and abiotic factors.

Linkages between vigorously growing host plants and sawflies are well documented in the literature (Price et al. 1998, Price and Carr 2000). Price and Carr (2000) showed that many species of common sawflies including both gallers and free feeders preferred to oviposit on long vigorous shoots. The sensitivity of sawflies to browsing of aspen (91% occur on unbrowsed ramets compared to only 9% on browsed ramets) could be explained by two hypotheses. First, there may be a preference by the sawfly for aspen that are not browsed. Second, on a per unit biomass, there is actually no difference in sawfly density.

Based on leaf biomass estimates from Bailey and Whitham (2002) and the sample effort in this study, we found an equal number of sawfly galls on 1476 g of unbrowsed leaf material compared to 5400 g of browsed leaf material, suggesting that browsing alters the distribution of sawflies by reducing the vigor of aspen ramets. Elk often browse the most vigorous growing terminal shoots of aspen ramets, which are often the preferred ovipositional site for many galling insects. The fact that sawflies oviposit on leaves after most browsing occurs, argues that browsing indirectly affects leaf quality and the subsequent oviposition behavior of sawflies. The experimental clipping of shoots to simulate browsing confirmed this effect on sawfly oviposition (Fig. 1C). Browsing also can negatively affect aspen re-generation (Romme et al. 1995), and decrease average leaf area and its attractiveness to sawflies. These factors are likely to negatively affect the distribution of this sawfly. In northern Arizona, where aspen regeneration is limited and elk herds are large, the positive effects of this sawfly on arthropod diversity and their potential effects on higher trophic levels could easily be affected.

Elk-avian interactions through sawflies

Because animals tend to accumulate in shelters (Martinsen et al. 2000), predators, such as insectivorous birds may identify them as an easy and reliable food resource. Using exclosures and synthetic galls (Fig. 4A, B) we showed that insectivorous birds attacked 60–74% of galls. Many studies have shown linkages between bird foraging and insect presence and abundance (Heinrich and Collins 1983, Greenberg 1987, Atlegrim 1992, Marquis and Whelan 1994, Dickson and Whitham 1996). For example, Dickson and Whitham (1996) showed a positive relationship between the foraging of black-capped chickadees, *Parus atricapillus*, and the density of its prey, the galling aphid, *P. betae*. Heinrich and Collins (1983) also showed that birds used leaf morphology (including leaf-folds) as foraging clues.

Overall, our study demonstrates that herbivory by elk influences trophic interactions depending upon as-

pen responses to browsing. For example, we have shown that browsing by elk reduces the vigor of aspen ramets, which negatively affects an important herbivore, its associated arthropod community, and the foraging patterns of insectivorous birds. Because even relatively simple systems are complex and structured by many factors, diversity is not likely to be controlled by a single trophic level or abiotic variable, but more likely by the interactions among trophic levels, indirect effects such as herbivory, and environmental variation. We also expect the positive effects of the gall produced by this sawfly to extend to larger scales, however the magnitude of those effects depends on factors such as quantity and quality of aspen habitat, and the indirect negative effects of browsing.

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