

THE DISRUPTION OF AN ANT–APHID MUTUALISM INCREASES THE EFFECTS OF BIRDS ON PINE HERBIVORES

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Abstract. Predators affect herbivores directly and indirectly, by consumptive and nonconsumptive effects, and the combined influence of multiple predators is shaped by interactions among predators. I documented the individual and combined effects of birds (chickadees, nuthatches, warblers) and ants (*Formica podzolica*) on arthropods residing in pine (*Pinus ponderosa*) canopies in a factorial field experiment. Birds and ants removed herbivores but simultaneously benefited them by removing predatory arthropods. Birds and ants had net negative and positive effects, respectively, on the abundance of herbivore prey, supporting the notion that vertebrate predators have stronger negative effects on herbivores than do arthropod predators. Aphids (ant-tended and untended species) constituted three-quarters of herbivore biomass. The effect of birds on ant-tended aphids was twice that on untended aphid species or tended aphid species without ants. This was not due to there being more ant-tended aphids for birds to prey on; tended and untended aphid species were in similar abundances in the absence of birds. Instead, the effects of birds were strengthened by attributes of the mutualism that rendered tended aphids susceptible to predation.

These dynamics led to nonadditive effects of birds and ants: birds only reduced tended aphid species and total herbivore abundances on trees with ants, while ants only increased tended aphid species and total herbivore abundances in the absence of birds. Consequently, top predators in this system only influenced total herbivore abundance when they disrupted an ant–aphid mutualism.

Key words: ant–aphid mutualism; canopy arthropod community; *Cinara*; emergent multiple-predator effect; *Essigella*; indirect effect; insect community ecology; intraguild predation; mutualism; *Pinus ponderosa*; *Schizolachnus*; trait-mediated indirect interaction.

INTRODUCTION

Community ecologists have long recognized the importance of predation for its potential to regulate herbivore populations (Holling 1959) and consequently provide indirect benefits to plants (Hairston et al. 1960). Early work on predation measured the magnitude of predator effects on prey and compared these findings to those from comparable studies on competition and other community level interactions (Gurevitch et al. 2000). More recent work has begun to investigate some of the less obvious, but no less important, details of how predation operates in ecological communities.

Investigations that focus on mechanism have revealed three features that fundamentally change our understanding of predator function. First, predators traditionally assumed to occupy the same trophic level are now recognized to frequently prey upon each other (Polis et al. 1989). In addition, some predators may also feed upon plant resources (Coll and Guershon 2002). Omnivory is now recognized to be nearly ubiquitous and

calls into question the usefulness of the trophic-level concept that underlies much theory in community ecology (Polis and Strong 1996). Second, predators affect prey not only through the act of consumption (density-mediated interactions; Abrams 1995), but also by changing the behaviors or other phenotypes of individual animals they do not consume (trait-mediated interactions; Petranka et al. 1987, Abrams 1995, Preisser et al. 2005). Just as predator consumption of herbivores can indirectly affect plants (density-mediated indirect interaction), so too can trait-mediated predator effects (trait-mediated indirect interactions); predator-induced changes to herbivore phenotype can alter the interactions between potential prey and plants and thus reduce plant damage (Schmitz et al. 2004). Third, multiple predator effects are often nonadditive (Sih et al. 1998), being either subadditive (antagonistic; Ferguson and Stiling 1996) or superadditive (synergistic; Losey and Denno 1998). Incorporating intraguild predation, trait-mediated effects, and nonadditive predator effects into food web models may allow us to better predict the influences of predators upon herbivores and plants.

Insectivorous birds and ants are two of the most studied groups of predators in terrestrial communities. Birds have frequently been credited with controlling herbivore populations and benefiting plants (Dickson et al. 1979, Holmes 1990), but the empirical evidence for

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PLATE 1. Two ants (*Formica podzolica*) passing on a ponderosa pine (*Pinus ponderosa*) trunk. The ant on the right is returning to the mound carrying an aphid of an untended species (*Essigella fusca*). Photo credit: K. Mooney

this claim is somewhat equivocal. Some studies have shown that birds reduce plant damage (e.g., Marquis and Whelan 1994, Sipura 2002), but others have not (e.g., Forkner and Hunter 2000, Murakami and Nakano 2000). Ants not only prey upon herbivores, but can also increase the abundance of mutualist hemipterans by protecting them from enemies (Way 1963). The net effect of ants on herbivore biomass therefore depends on the relative strengths of these two influences (Adlung 1966, Messina 1981, Rosengren and Sundstrom 1991, Davidson et al. 2003). As generalists, both birds and ants feed as intraguild predators in that they consume both herbivores and predatory arthropods. As a consequence of these complexities, a well-synthesized understanding of bird and ant effects on herbivore abundance and plant growth and fitness is still forthcoming.

Birds and ants co-occur in most terrestrial communities. The interactions between birds and ants are likely to be important determinants of their combined effects on herbivore populations, but there are few studies to speak to this prediction (but see, Campbell et al. 1983, Haemig 1994, 1996, 1997). Mutualisms between ants and hemipterans are contingent upon the ecological contexts in which they occur (Cushman and Whitham 1989, Cushman and Addicott 1991, Bronstein 1994, Sakata 1994), and generalist predators, including birds, may affect the interactions between mutualists. Because ant-aphid mutualisms depend on precise and compliant behaviors from both participants (Way 1963), one could predict that generalist insectivores, including birds, will affect these mutualists in a trait-mediated fashion by

altering ant and/or hemipteran behaviors. Ants can also aggressively repel foraging birds in some communities (Haemig 1994, 1996), and chemical defenses (e.g., formic acid) make some ants unpalatable (Hölldobler and Wilson 1990, Mackay and Mackay 2002). The broader consequences of such interactions between birds and ants for food web structure are unknown.

In the present study I identified the individual and combined effects of canopy-gleaning birds and the ant *Formica podzolica* Francour on the canopy arthropod community of ponderosa pine (*Pinus ponderosa* Laws. *scopulorum*) using factorial field experiments. *Formica podzolica* is a facultative mutualist with several aphids that contribute significantly to total herbivore abundance on pines. Other work in this community has shown that birds increase pine wood growth via their negative effects on ant-tended aphids (K. A. Mooney and Y. B. Linhart 2006). With the current experiments I addressed the following questions: What are the individual effects of birds and ants on the pine-arthropod community? Do bird and ant effects act independently, or are they contingent upon each other? Can ants repel foraging birds and thus protect mutualist aphids? Do birds affect the functioning of this mutualism? Finally, what are the consequences of bird effects on the ant-aphid mutualism for total herbivore abundance in pine canopies?

MATERIALS AND METHODS

I conducted this work at the U.S. Department of Agriculture Forest Service's Manitou Experimental Forest in Woodland Park, Colorado, USA (39°06'00''

N, 105°05'00" W), in mature stands of ponderosa pine at an elevation of 2400 m (Appendix A), where at least 22 bird species commonly forage on ponderosa pine (Appendix B). *Formica podzolica* (see Plate 1) is the most abundant ant at this study site, where it builds gravel mounds and forages in pine canopies. This ant is a predator of most arthropods, but engages in a mutualism with several species of aphid (Mooney and Tillberg 2005) in which it receives carbohydrate-rich aphid excreta ("honeydew") while protecting aphids ("tending") from their arthropod enemies (Way 1963). *Formica* spp. ants produce formic acid (Hölldobler and Wilson 1990, Mackay and Mackay 2002), which makes them unpalatable to most birds in temperate forest communities except ant-feeding specialists such as woodpeckers and flickers (Picidae).

Bird and ant exclusion study

I selected 16 pairs of similarly sized pine trees associated with *F. podzolica* mounds. Trees within pairs were 1.7–8.0 m apart (5.6 ± 1.1 m, mean \pm SE), and pairs of trees were all >200 m apart and distributed over 750 ha (Appendix A). Tree heights were 4.5–13.5 m (8.6 ± 0.5 m), and tree diameters were 14–32 cm (21.5 ± 8 cm). From 1 to 15 June 2000, I installed bird and ant exclusions on the experimental trees. I excluded ants from one member of each pair with sticky paste (Tanglefoot Company, Grand Rapids, Michigan, USA) and applied a similar amount of paste to half the trunk diameter of control trees (Appendix A). The sticky paste on control trees had little or no effect on ant foraging. Ant abundance on control tree trunks was high, and as a result few other arthropods traveled on the trunks of control trees. Consequently, the sticky paste eliminated ants, but it is unlikely that it had significant direct effects on other canopy arthropods. On each tree, I selected pairs of branches and assigned one as a control and one to a bird exclusion treatment of a 2.5-cm mesh nylon netting bag (Appendix A). Enclosures constructed of similar materials have been found to have minimal effects on light levels (Marquis and Whelan 1994).

During the first week of August and September I beat the experimental branches with a padded bat to dislodge arthropods into a 1.5×1.5 m fabric tub (0.5 m deep) for collection and preservation in 70% ethanol. This methodology, described elsewhere (Mooney and Tillberg 2005), captures most ($>97\%$) arthropods with the exception of adult flies (Diptera), bees, and wasps (Hymenoptera). I used arthropod lengths to calculate dry biomass from published algorithms (Rogers et al. 1976), cut and weighed pine branch fresh mass at the conclusion of the experiment, and analyzed these data as "mg arthropod/kg pine branch fresh mass." This metric of arthropod abundance is the equivalent of Root's (1996) "load." Expressing the effects of birds and ants on herbivore load provides the best indication for the likely indirect effects of birds and ants on pine growth and fitness.

I divided the pine canopy arthropod community into the following seven categories: (1) ant-tended aphid species (*Cinara schwarzii* Wilson and *C. arizonica* Wilson), (2) untended aphid species (*C. solitaria* [Gillette and Palmer], *C. glabra* [Gillette and Palmer], *Essigella fusca* [Gillette and Palmer], and *Schizolachnus piniradiatae* [Davidson]), (3) planthoppers and leafhoppers (Hemiptera, suborder Auchenorrhyncha, 36 species not tended by ants), (4) tissue-damaging herbivores (caterpillars [larval Lepidoptera, five species], thrips [Thysanoptera, one species], adult herbivorous beetles [Coleoptera excluding Coccinellidae, 102 species]) hereafter referred to as "chewing herbivores," (5) web-spinning spiders (Araneae, 14 species from five families), (6) hunting spiders (Araneae, 13 species from five families), and (7) specialist aphid predators (larval and adult Coccinellidae beetles, larval Neuroptera, and five species of Miridae [Hemiptera] from three genera [*Daerocoris* spp., *Pilophoris* spp., *Phytochoris* spp.]). Mites (Acari, three species), barklice (Psocoptera, nine species), and springtails (Collembola, one species) were not considered in these analyses. At the time of arthropod collection I documented the frequency of ant visits to control trees with five-minute counts of the number of ants ascending and descending tree trunks.

This experiment was a split-plot repeated-measures design: tree was the subject, ant treatment was an among-subject factor, and bird treatment and time were within-subject factors (Zar 1999). I tested for all main effects and interactions among birds, ants, and sampling month on the abundance of arthropods in each group using PROC GLM of SAS Version 8.2 (SAS Institute 2001). Birds and ants had large effects on arthropod abundance, and my experimental design did not prevent prey depletion, so a multiplicative null model was appropriate (Sih et al. 1998, Hamback and Beckerman 2003), requiring log-transformed data (Zar 1999).

Interactions between birds and an ant-aphid mutualism

I conducted several analyses and behavioral experiments to characterize the interactions between birds, mutualist ants, and aphids. Specifically, I sought to address the following questions: First, do birds affect the abundance of ants and tended aphid species via trait-mediated effects? Second, does the mutualism with ants have consequences for the top-down effects of birds on aphids, and if so how? And third, can *F. podzolica* repel foraging birds as has been shown for its congener *F. aquilonia* Yarrow (Haemig 1994, 1996), and in doing so perhaps protect mutualist aphids?

Trait-mediated effects of birds on ants and tended aphid species.—I conducted two behavioral studies investigating possible trait-mediated mechanisms for the direct effects of birds on ants and tended aphid species. The first experiment ("sticky-trap experiment") tested whether jumping from pine branches by ants and tended aphid species (documented predator-avoidance behaviors in other species of ants and aphids [e.g., Haemig 1997,

Losey and Denno 1998]) was increased by exposure to birds. In July 2001 I selected single branches on 10 pairs of neighboring trees and placed netting bags around the branch of one tree in each pair. One meter beneath each branch I suspended a horizontally oriented, 60 × 120 cm plywood sheet coated with sticky paste and covered with 5-cm wire mesh to prevent birds from becoming entangled. After 48 hours I counted the number of ants and aphids of tended species per sticky-trap. I conducted two 10-minute counts of ant traffic going to and from each branch. At the conclusion of the experiment I determined the number of tended aphids on each branch by the same arthropod collection methodology described above (see *Materials and Methods: Bird and ant exclusion study*). I tested for bird effects on the number of jumping ants with ant traffic as a covariate (ANCOVA). For tended aphid species, both ants and the number of aphids on each branch might influence the number of jumping aphids caught in sticky-traps. Consequently, I tested for the effects of birds on the number of trapped aphids using both aphid counts from branches and ant traffic as covariates (ANCOVA).

The second experiment (July 2002, “ant feeder experiment”) tested whether ants changed their foraging behavior in response to the risk of predation from foraging birds. I selected pairs of branches on 10 ant-foraged trees, removed arthropods, and girdled the branches to prevent aphid recolonization. On each branch I placed two ant feeders consisting of capped 50 cm³ tubes filled with a 30% sucrose solution and drilled with four 1-mm feeding holes (Appendix A). I excluded birds with a netting bag from one branch on each tree. Over the next two weeks I counted the ants within 10 cm of the feeders on eight occasions. Because I maintained a constant supply of ant food on these experimental branches, any effect of birds on ants was direct and could not have occurred via resource competition. Because single ant colonies foraged on each tree, any difference in ant abundance between control and bird exclusion branches was not due to bird reduction of ant colony size (i.e., a density-mediated interaction), but instead reflected changes in ant foraging behavior (i.e., a trait-mediated interaction). Using the number of ants per branch summed over all eight observations as the dependent variable, I tested for an effect of bird exclusion in an ANOVA with the two factors being bird exclusion and tree. These data could not be transformed to meet the assumptions of a normal distribution, and consequently this analysis was performed on rank-transformed data (Zar 1999).

Consequences of the ant–aphid mutualism for bird effects on aphids.—I conducted two analyses of the arthropod data from the bird and ant exclusion experiment (see *Materials and Methods: Bird and ant exclusion study*) to investigate whether being in a mutualism with ants had consequences for the magnitude of bird effects on aphids, and how such consequences might arise. First, I formally compared the effects of birds on tended

and untended species of aphids (two and four species, respectively) by adding aphid type (tended aphid species, untended aphid species) as an additional factor to the statistical model. Specifically, I tested for the main effects of and interactions among bird exclusion, ant exclusion, and aphid type on aphid abundance. In all other respects, these analyses were performed according to the statistical methods used in my original analyses of these data.

Second, I tested whether birds might alter the functioning of the ant–aphid mutualism independent of their effects on the abundance of ants and tended aphid species. I compared the slopes (ANCOVA) and coefficients of determination (R^2) (Fisher’s Z: Zar 1999) for the abundance of tended aphid species regressed on ant abundance between branches with and without birds. The slopes and R^2 are parameters indicating the strength of association between the two mutualists (Breton and Addicott 1992), and these analyses tested whether birds affected this mutualism as indicated by changes in these parameters. I performed this analysis on branch data averaged across months ($N = 32$). To meet assumptions of homoscedasticity, I log-transformed both variables (Zar 1999).

Effects of ants on birds.—This experiment measured the net effect of ants on birds via both interference and exploitation competition (Haemig 1994, 1996). Between 18 July (one month after excluding ants) and 31 August, I observed bird activity on 14 of the 16 pairs of ant exclusion and control trees (see photo in Appendix A) for one to three hours at a time, between 06:30 and 09:30. I first observed each pair for at least six hours, and then continued to observe pairs with lower amounts of observed bird activity to approximately equalize the observed activity among pairs. Observation time per pair averaged 10 ± 1.2 h and ranged from 6 to 21.3 h. I recorded the species and occupancy time of each bird landing on experimental trees and divided these observations into three behaviors (branch foraging, trunk foraging, perching) and three species groups (canopy insectivores [i.e., foliage and bark gleaners], seed-eaters and flycatchers, [i.e., birds not foraging on the tree per se], woodpeckers [i.e., larger birds limiting foraging to trunks]). I tested for effects of ant exclusion on minutes of bird activity per hour of tree observation for the behavioral and species groups with two-way ANOVAs, with tree pair as a block effect. To help meet the ANOVA assumption of normal distribution, I transformed data with square roots (the species groups “insectivores” and “all-birds” and the behavioral class “branch foraging”) or fourth roots (all other dependent variables).

RESULTS

Bird and ant exclusion study

In August and September I collected 13 530 and 6732 arthropods, respectively, which amounted to densities of 68 ± 9 mg arthropod/kg pine tissue (mean \pm SE) and 39

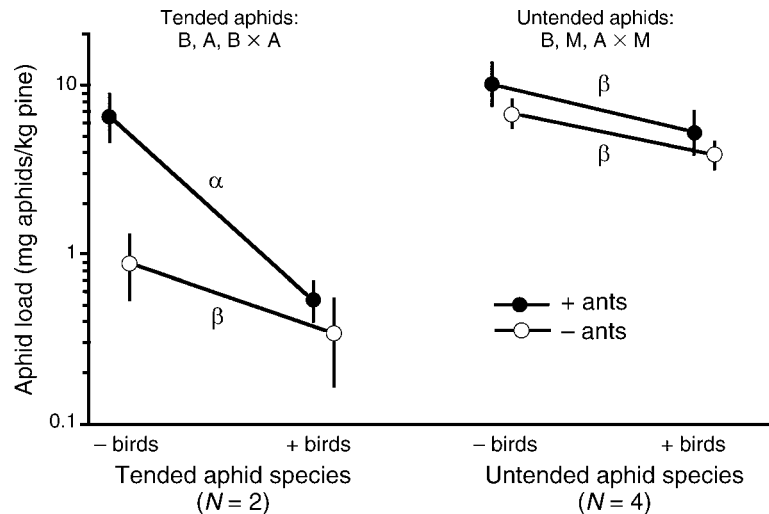


FIG. 1. Ant-tended aphid species ($N = 2$ aphid species) and untended aphid species ($N = 4$ aphid species) on control, bird exclusion, ant exclusion, and dual-exclusion branches. Aphid abundance (mean \pm SE) is shown across August and September 2000, with ants (solid circles) and without ants (open circles) for trees without and with birds. Letters above the two aphid types (tended and untended species) indicate all significant ($P < 0.05$) effects (B, birds; A, ants; M, month) and interactions for ANOVAs conducted separately within each aphid type. See Appendix C for details on statistics. Greek letters (α , β) near the four lines show results of ANOVA testing for interactive effects of birds, ants, and aphid type on aphid abundance. The slopes of lines (i.e., bird effects) not sharing a Greek letter differ significantly ($P < 0.05$). See *Results: Consequences of the ant-aphid mutualism for bird effects on aphids* for details on statistics. Note the y-axis log scale (for all figures).

± 4 mg arthropod/kg pine tissue, respectively. The percentages of total arthropod biomass represented by herbivores, ants, and predators were 51%, 38%, and 11%, respectively. The percentages of herbivore biomass as untended aphids, tended aphids, chewing herbivores, and hoppers were 48%, 24%, 24%, and 4%, respectively. Both bird and ant exclusions were effective. Netting bags remained sealed around all branches, and ants were not observed on exclusion trees. Ant counts averaged 5.7 ± 0.8 and 6.4 ± 1.0 ants/min in August and September, respectively. I observed 1.8 ± 0.5 min of bird activity per tree per hour of observation.

The effects of birds and ants were consistent between August and September in most cases (Appendix C, few interactions with month). Where interactions did occur, the differences between months were in effect magnitude, not direction. Consequently, Figs. 1 and 2 present arthropod abundances averaged across months. The presence of birds (vs. exclusion) had strong negative effects on many arthropod groups; birds significantly ($P < 0.05$) reduced the abundance of tended aphid species and untended aphid species by 60% and 45%, respectively (Fig. 1) and ants by 62%. There was a trend ($0.10 > P > 0.05$) toward a negative effect on specialist aphid predators (Fig. 2). The presence of ants (vs. exclusion), in contrast, had differing effects on herbivores and predators; ants increased the abundance of both tended and untended aphid species by 380% and 45%, respectively (Fig. 1), and reduced hunting spider abundance by 38%. There was a trend toward a negative effect of ants on specialist aphid predators (Fig. 2).

There were no effects of birds and ants on the abundance of either chewing herbivores or web-spinning spiders (Fig. 2). Birds and ants had opposing effects on total herbivore abundance; birds reduced herbivore abundance by 60% while ants increased it by 84% (Fig. 3).

The significant main effects of birds and ants on tended aphids (Fig. 1) and total herbivore abundance (Fig. 3) were complicated by the fact that these effects were highly contingent upon each another. Birds reduced the abundance of tended aphid species by 92% in the presence of ants ($F_{1,15} = 26.56$, $P < 0.0001$), but had no effect in their absence ($F_{1,15} = 2.57$, $P = 0.13$). This same interaction can be viewed from the perspective of ant effects; ants increased the abundance of tended aphid species by 640% in the absence of birds ($F_{1,15} = 11.60$, $P = 0.0039$), but had no detectable effect in their presence ($F_{1,15} = 0.91$, $P = 0.36$). These nonadditive effects of birds and ants on tended aphid species were mirrored in total herbivore abundance (Fig. 3); birds reduced herbivore abundance by 70% in the presence of ants ($F_{1,15} = 298.38$, $P < 0.0001$), but had no detectable effect in their absence ($F_{1,15} = 3.38$, $P = 0.09$). Viewed from the perspective of ant effects, ants increased herbivore abundance by 230% in the absence of birds ($F_{1,15} = 9.12$, $P = 0.0086$), but had no detectable effect in their presence ($F_{1,15} = 0.21$, $P = 0.65$).

Interactions between birds and an ant-aphid mutualism

Trait-mediated effects of birds on ants and tended aphid species.—Birds had no effect on the rates at which ants jumped from pine branches. There was no relationship

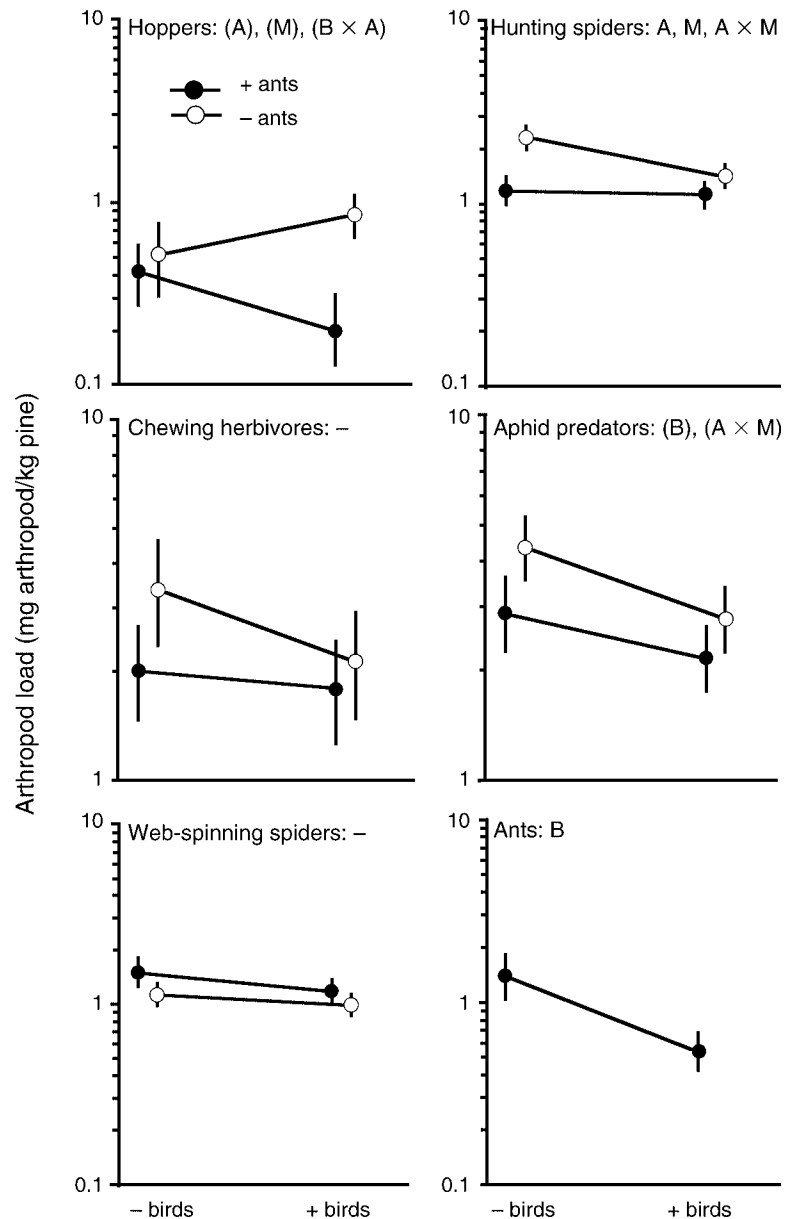


FIG. 2. Pine canopy arthropod community (except for aphids, shown in Fig. 1) on control, bird exclusion, ant exclusion, and dual-exclusion branches. Herbivore abundance (mean \pm SE) is shown across August and September 2000, with ants (solid circles) and without ants (open circles) for trees without (left) and with (right) birds. Letters in each panel indicate significant ($P < 0.05$) effects (B, birds; A, ants; M, month) and all interactions. Main effects and interactions are indicated by letters without parentheses when they are significant and within parentheses when they are between 0.05 and 0.1. Only significant interactions are shown, or marginally significant ones when they are in parentheses. Dashes (-) following "chewing herbivores" and "web-spinning spiders" indicate no significant effects or interactions. See Appendix C for details on statistics.

between the ant traffic counts and the number of caught ants ($F_{1,7} = 1.26$, $P = 0.30$), so I removed this covariate from the model. In this reduced model, the number of ants caught from control branches (16 ± 6 ants/branch; mean \pm SE) and bird exclusion branches (15 ± 5 ants/branch) did not differ significantly ($F_{1,9} = 1.04$, $P = 0.35$). In contrast, jumping by tended aphid species was significantly higher on branches with birds than on bird

exclusion branches. Ant abundance did not influence aphid jumping ($F_{1,5} = 4.16$, $P = 0.10$) so I removed it as a covariate from the model. In this reduced model, the number of aphids caught was significantly influenced by aphid abundance on the branch ($F_{1,5} = 5.95$, $P = 0.0448$), i.e., branches with high aphid abundance also had more individuals jumping. The slope of this relationship was the same both for branches with and without birds ($F_{1,5}$

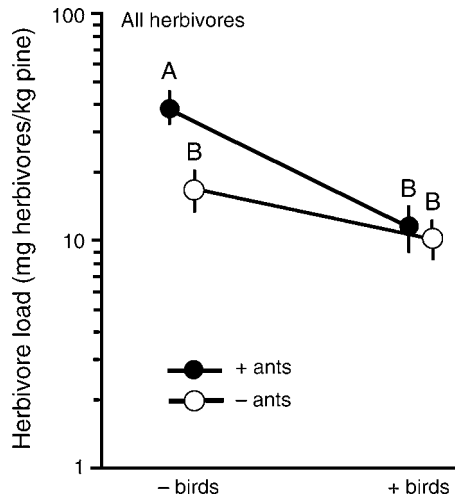


FIG. 3. Interaction graph for the effects of birds and ants on total herbivore abundance in pine canopies. Herbivore abundance (mean \pm SE) is shown across August and September 2000, with ants (solid circles) and without ants (open circles) for trees without (left) and with (right) birds. The interaction between bird and ant effects is significant (Appendix C). Means that do not share letters differ significantly ($P < 0.05$).

$= 0.72$, $P = 0.43$). Controlling for the number of aphids on each branch, the number of aphids per sticky-trap differed significantly by branch type ($F_{1,7} = 7.96$, $P = 0.0257$); traps beneath control branches had seven times more aphids than those beneath bird exclusion branches (adjusted means 7 ± 1 aphids/trap and 48 ± 2 aphids/branch, respectively). Jumping aphids (24 ± 4 aphids/trap) represented 15% of aphid abundance on branches (164 ± 81 aphids/branch).

The ant feeder experiment demonstrated that ants adjusted their foraging patterns in response to the presence of birds. Birds reduced ant abundance by 22%; there was a mean of 9.0 ± 1.1 ants at feeders on exclusion branches and 7.0 ± 1.0 ants on control branches ($F_{1,9} = 6.43$, $P = 0.0319$).

Consequences of the ant-aphid mutualism for bird effects on aphids.—The mutualism with ants significantly increased the effect of birds on aphid abundance, as demonstrated by the significant three-way bird \times ant \times aphid interaction ($F_{1,60} = 5.47$, $P = 0.0227$) shown in Fig. 1. Birds reduced the abundance of ant-tended aphids by 92%, but birds reduced aphids without ants (of both tended and untended species) by only 47%. This three-way interaction can be attributed to the effects of birds, i.e., the four line slopes in Fig. 1, differing significantly based on both the presence of ants and whether or not aphids were of tended or untended species. I formally compared these four slopes in pairwise comparisons with separate two-way ANOVAs. First, birds had greater negative effects on tended aphid species in the presence than in the absence of ants (i.e., a two-way interaction between bird and ant effects on tended aphid species; Appendix C). Second, on trees with ants, birds had

greater negative effects on tended than on untended aphid species (i.e., two-way interaction between bird effects and aphid type on trees with ants; $F_{1,15} = 8.29$, $P = 0.0115$). Finally, on trees without ants, the effect of birds did not differ between tended and untended aphid species (i.e., no two-way interaction between bird effects and aphid type on trees without ants; $F_{1,15} = 0.23$, $P = 0.64$).

The fact that birds had twice the effect on tended as compared to untended aphids was not simply a consequence of density-dependent predation, i.e., there being more ant-tended aphids for birds to prey on; in the absence of birds, both tended and untended aphid species were in similar abundance (Fig. 1). Instead, some aspect of aphid association with mutualist ants strengthened the effect of birds. This enhanced bird effect may have been due to birds influencing mutualism function (Fig. 4); bird exclusion affected the slopes ($F_{1,28} = 5.67$, $P = 0.0243$) but not the coefficients of determination ($Z = 1.14$, $P = 0.16$) for aphid abundance regressed on ant abundance. This back-transformed slope was decreased by 80% in the presence of birds (1.5 mg aphid/mg ant) as compared to bird exclusion branches (7.4 mg aphid/mg ant). This effect of birds on aphid : ant ratio constitutes a trait-mediated effect, as it occurred independently of bird effects on ant and aphid density.

Effects of ants on birds.—There were no indications that ants affected bird foraging. I observed experimental trees for 175 h during which time there were 5.4 bird tree-hours of visitation by 22 species (Appendix B). Nuthatches, chickadees, and warblers accounted for 95% of canopy insectivore visitation. Differences between ant exclusion and control trees among foraging

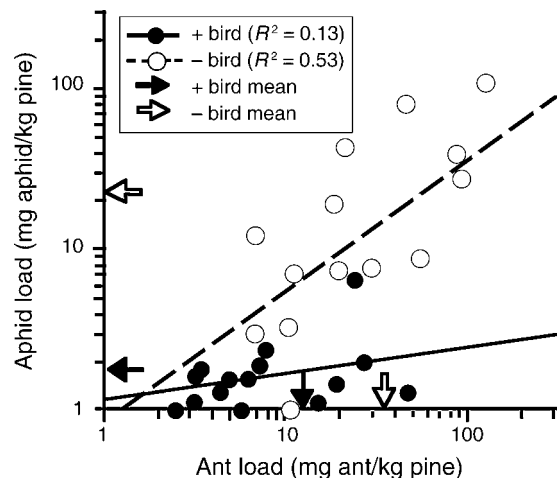


FIG. 4. Relationship between aphid and ant abundance on branches with birds (solid circles, solid line) and without birds (open circles, dashed line). These data are branch means (across August and September 2000) from trees with ants. The slopes of these two lines differ significantly, but not the coefficients of determination (see Results). Arrows show mean densities for ants and aphids on branches with birds (solid arrows) and without birds (open arrows).

groups and behavioral classes were small and not statistically significant (Appendix B).

DISCUSSION

Birds and ants had strong effects on both predatory and herbivorous arthropods in pine canopies. In several instances, bird and ant effects were nonadditive, where the effect of one was contingent upon the presence or absence of the other. Furthermore, at least some of these bird and ant effects were nonconsumptive, trait-mediated interactions. These results bolster the emerging view that a complete understanding of predator function requires the incorporation of intraguild predation, trait-mediated effects, and nonadditive predator effects into food web models. In the following paragraphs, I discuss my results with respect to these three dynamics.

Intraguild predation

Birds and ants were both intraguild predators in this pine canopy community. Birds reduced the abundance of sap-feeding herbivores (tended aphid species, untended aphid species) while simultaneously reducing the abundance of predatory arthropods (ants, a trend for specialist aphid predators) that presumably preyed upon those same herbivores. These results suggest that some of the direct negative effects of birds on herbivores were counterbalanced by the benefits of removing predatory arthropods. In contrast, ants provided a net benefit to untended aphids, despite the fact that elsewhere it has been shown that ants preyed upon them (Mooney and Tillberg 2005). Consequently, the benefit of ants as consumers of predatory arthropods (hunting spiders, a trend for specialist aphid predators) apparently outweighed the ants' negative effects as consumers of untended aphids (Fritz 1983). This variation in the net effects of birds and ants as intraguild predators is consistent with a meta-analysis suggesting that vertebrate predators have stronger net negative effects on herbivores than do invertebrate predators (Schmitz et al. 2000). For example, Spiller and Schoener (1994) found that lizards, but not spiders, affected amounts of plant damage by herbivores on Bahamian islands.

Trait-mediated interactions

Birds affected the local abundance of both ants and tended aphid species via effects on their behavior. These two groups constituted over half of all arthropods, so these effects were important at the community level. Birds caused ants to change their foraging patterns (ant feeder experiment), thus reducing the local abundance of ants by 20%. How ants "learned" to preferentially forage on bird exclusion branches is unclear. Occasional encounters between branch-foraging birds and ants may have left chemical cues (e.g., alarm pheromones) that caused subsequent ants to either avoid or shorten their occupancy of bird-exposed branches (Wilson and Regnier 1971). This apparently nonadaptive response of ants to branch-foraging birds that do not consume

Formica ants (Grundel and Dahlsten 1991, Pravosudov and Pravosudova 1996, McMartin et al. 2002) may be a consequence of behaviors evolved in response to ant-feeding woodpeckers that forage on pine trunks. Birds did not cause an increase in ant jumping from pine branches (sticky-trap experiment), despite the fact that such predator avoidance behaviors have been documented for other Formica ants (Haemig 1997). In contrast to ants, tended aphid species increased their rate of jumping from branches by sevenfold in response to birds. In two days, the number of jumping aphids equaled 15% of the aphid population (sticky-trap experiment). Avian diet studies report Formica ants (which are unpalatable: Hölldobler and Wilson 1990, Mackay and Mackay 2002), and aphids to be rare in the diets of chickadees, nuthatches, and warblers (Grundel and Dahlsten 1991, Pravosudov and Pravosudova 1996, McMartin et al. 2002). Consequently, most or all of the direct effect of birds on *F. podzolica* and tended aphid species may have been due to the effects of birds on ant and aphid behavior, and not to bird consumption of these arthropods.

Additivity of bird and ant effects

Birds had significantly stronger effects on aphids associated with mutualist ants as compared to untended aphids; bird reduction of ant-tended aphid abundance was twice that of untended aphid species or tended aphid species in the absence of ants (Fig. 1). The fact that the ant-aphid mutualism strengthened the effects of birds can be seen in complementary comparisons of aphids with and without ants at the intra- and interspecific level. First, the effects of birds on species of aphids that engaged in mutualisms with ants (*Cinara schwarzii* and *C. arizonica*) varied as a function of the presence or absence of ants (Fig. 1, compare slopes in left half). Second, the effects of birds differed between tended aphid species (*C. schwarzii* and *C. arizonica*) and untended aphid species (*C. solitaria*, *C. glabra*, *Essigella fusca*, and *Schizolachnus piniradiatae*) on trees with ants (Fig. 1, compare slopes connecting solid circles). This stronger effect of birds was not the consequence of there being more ant-tended aphids for birds to remove (i.e., density-dependent predation) as the abundances of tended and untended aphid species were similar in the absence of birds (Fig. 1).

Consequently, some aspects of the aphid association with ants increased the influence of birds on those aphids. There are several nonmutually exclusive explanations. First, birds could have affected tended aphids not only directly, but also indirectly by effects transmitted through mutualist ants. Birds reduced ant abundance by 22% by inducing changes in their foraging behavior (ant feeder experiment). In addition, birds caused the remaining ants to reduce the quality of their services to mutualist aphids as indicated by an 80% reduction in the aphid:ant ratio (Fig. 4) (Breton and Addicott 1992). The principal benefit of ants to

mutualist aphids is protection from enemies (Way 1963, Way and Khoo 1992) (but see Flatt and Weisser 2000). Accordingly, the indirect effect of birds on tended aphids via ants was not the result of reduced ant attendance *per se*, but rather the result of a subsequent increase in aphid predation by carnivorous arthropods. Tended aphid species may have been especially vulnerable to arthropod predators as a function of evolved traits (morphological and behavioral) that are adaptive in the context of a mutualism with ants, but that render aphids vulnerable to arthropod predators in the absence of ants (Bristow 1991).

Second, ant-tended aphids may have been especially visible to insectivorous birds. Tending ants are larger, more active, and less cryptic in coloration than aphids. In addition, tended aphids aggregate more than untended aphids (Way 1963), possibly further increasing their visibility. Once attracted to groups of tended aphids, birds could have reduced their abundance directly, by feeding on aphids and inducing jumping behaviors, and indirectly, by effects on ant abundance and aphid-tending behaviors.

Third, the *F. podzolica*-aphid mutualism may have been especially vulnerable to birds because this ant could not repel foraging birds (Appendix B). This is in contrast to *F. aquilonia* Yarrow, which repelled insectivorous birds (*Parus* spp. and others) in spruce forests (Haemig 1996). This discrepancy between my findings and those of Haemig may be attributable to variation between ants. *F. podzolica* and other members of the *fusca* species group are smaller and less aggressive than species in the closely related *rufa* species group that includes Haemig's *F. aquilonia* (Mackay and Mackay 2002). Bait experiments at Manitowish showed *F. podzolica* to be subordinate to *F. planipilis* Creighton that is also in the *rufa* group (K. A. Mooney, unpublished data). *Formica podzolica* cannot grasp and pinch human skin, while the larger *F. planipilis* is capable of doing so. Such variation in ant size and aggression had consequences for the aphids tended by these ants; while searching for tended aphid colonies, I found *C. schwarzi* colonies tended by *F. planipilis* that were an order of magnitude larger (>500 aphids per colony, $N = 10$) than colonies tended by *F. podzolica* (mean \pm SE = 34 ± 5 aphids per colony, $N = 120$) (K. A. Mooney, unpublished data). Consequently, the strong negative effects of birds on the *F. podzolica*-aphid mutualism may have been due to the inability of *F. podzolica* to repel birds.

In summary, insectivorous birds had stronger effects on ant-tended than untended aphids. Ant-aphid assemblages may have been relatively more visible to birds as compared to untended aphids that were present in the same abundance. Once located by foraging birds, *F. podzolica* exhibited predator avoidance behaviors that left aphids vulnerable to arthropod enemies. The behavioral responses of *F. podzolica* to birds were likely greater than those of its larger and more aggressive congeners. The *F. podzolica*-aphid mutualism was thus

vulnerable to disruption by birds, and the effects of birds on aphids differed in strength based on the presence or absence of the mutualism.

Bird and ant effects on total herbivore abundance

The interactive effects of birds and ants on tended aphid species led to an analogous interaction for total herbivore abundance (Fig. 3). On trees without ants, birds did not have a detectable effect on herbivore abundance. On trees with ants, the ant-aphid mutualism enhanced the effect of birds on tended aphid species and consequently on total herbivore abundance. The presence (or absence) of the ant-aphid mutualism thus determined the top-down effect of birds on herbivores. Likewise, whether or not ants increased herbivore abundance depended on the presence (or absence) of birds.

It has been unclear whether hemipteran-tending ants provide a net cost to plants by facilitating mutualists, or a benefit by feeding upon nonmutualist herbivores (Adlung 1966, Messina 1981, Rosengren and Sundstrom 1991, Davidson et al. 2003). Mutualisms are sensitive to the contexts in which they occur (Cushman and Whitham 1989, Cushman and Addicott 1991, Bronstein 1994, Sakata 1994), and so it is expected that ecological conditions, including predation pressure, are relevant to the net effects of ant-aphid mutualisms on plants. I show here that predatory birds decreased the aphid:ant ratio by 80% (Fig. 4). From the plant's perspective, the costs and benefits of the ant-aphid mutualism were thus strongly influenced by birds, with plant costs (the number of aphids) being reduced relative to plant benefits (the number of ants).

The effects of birds and ants on herbivore abundance (herbivore load, *sensu* Root 1996) have implications for pine growth and fitness. Forest ecologists have often asserted that birds and ants have positive effects on tree growth by removing foliage-chewing herbivores (Adlung 1966, Dickson et al. 1979, Holmes 1990, Rosengren and Sundstrom 1991). Aphids dominated the pine herbivore community, while foliage-chewing herbivores comprised less than a quarter of total herbivore abundance. Furthermore, neither birds nor ants affected foliage chewers. Consequently, these assumptions about the roles of birds and ants in forests should be revisited.

Implications

The interaction between bird and ant effects on pine herbivore biomass has implications for the spatial patterning of food web structure (Mooney and Tillberg 2005). Given the often patchy distribution of ants within a forest, the effect of birds on herbivores likely varies between forest stands, or neighboring trees, based on the presence of ants. Conversely, variation in bird communities may determine whether ants increase herbivore abundance. Such dynamics may generate similar variation in the indirect effects of birds and ants on pine growth and fitness.

The effect of birds on herbivores was stronger when birds were able to disrupt an ant–aphid mutualism. This occurred, at least in part, because bird-induced changes in ant behavior indirectly reduced aphid abundance. While the importance of trait-mediated indirect interactions has recently been recognized (Werner and Peacor 2003, Preisser et al. 2005), there is as yet no predictive framework for when and where such dynamics are likely to occur. Ant–hemipteran mutualisms may provide key elements in food webs that, because of their behavioral sensitivity, leverage the top-down effects of predators on herbivores and plants.

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APPENDIX A

Photographs depicting the field site and experimental methodologies (*Ecological Archives* E087-107-A1).

APPENDIX B

A description of the ponderosa pine bird community and analysis of ant effects on bird foraging (*Ecological Archives* E087-107-A2).

APPENDIX C

Statistical tables for analysis of bird and ant effects on pine arthropods (*Ecological Archives* E087-107-A3).