

The Influence of Ants on the Foraging Behavior of Birds in an Agroforest¹

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ABSTRACT

Ants limit bird foraging success via interference or exploitative competition. We compared bird foraging (number and duration of visits, bird species visiting) on ant (*Azteca instabilis*)-infested and ant-free tropical trees (*Inga micheliana* and *Alchornea latifolia*). Ants did not affect the number of bird visits or the number of species visiting. Ant presence shortened visit duration (overall and for insectivores) only on *A. latifolia* where ant activity was higher. Ants may thus hinder bird foraging on some tropical trees potentially shaping how predators affect arthropod communities; yet ant effects depend on bird foraging guild and ant activity.

RESUMEN

Las hormigas limitan el forrajeo exitoso por aves ya sea por interferencia o competencia explotativa. Comparamos la actividad de aves (número y duración de visitas y especies de aves visitadoras) en dos especies de árboles tropicales (*Inga micheliana* y *Alchornea latifolia*) con y sin la hormiga *Azteca instabilis*. Las hormigas no afectaron el número de visitas o el número de especies de aves visitadoras a estos árboles tropicales, con la excepción de *A. latifolia* donde la duración de visitas se acortó (en general y para las especies insectívoras) debido a la alta presencia de hormigas. Concluimos que la presencia de las hormigas disminuyen la actividad forrajera por aves en algunos árboles tropicales, potencialmente influyendo en los efectos de depredadores en comunidades de artrópodos. Sin embargo los efectos de las hormigas dependen del forrajeo de las aves.

Key words: *Alchornea latifolia*; *Azteca instabilis*; birds; Chiapas; coffee agroecosystem; exploitative competition; *Inga micheliana*; México; multiple predator effects.

BIRDS AND ANTS ARE TWO PREDATORS THAT OFTEN OCCUR TOGETHER and their effects on prey assemblages differ significantly (Philpott *et al.* 2004). Yet it is unclear how interactions between ants and birds may change their overall effects on arthropod prey or plants because ants are both bird prey and bird competitors. Birds consume ants (Poulon & Lefebvre 1996, Strong & Sherry 2000) and tend to reduce ant densities (Philpott *et al.* 2004). On the other hand, two studies of ground-nesting ants in northern Europe have demonstrated that bird activity (number of visits and total time of visits) may decrease on trees or in territories with ants (Haemig 1992, Aho *et al.* 1997). Reduced bird activity in trees may be a direct result of ant aggression (Haemig 1996). Decreases in bird activity, particularly for insectivores, may also result from resource competition when ants lower food availability for birds (Haemig 1992, 1994). In addition, decreased food availability within ant territories may negatively affect reproductive success of particular bird species (Aho *et al.* 1999). Aho *et al.* (1999) demonstrated that Eurasian treecreeper (*Certhia familiaris*) fledglings in red wood ant (*Formica rufa* group) territories had lower mass and lower survival than those outside ant territories, most likely due to reduced food supply. Thus exploitative and interference competition between ants and birds exists in temperate areas with ground-nesting ants. The prevalence of competitive interactions between tree-nesting ants and birds in tropical ecosystem types is not known.

Tropical forests and agroforests contain arboreal ants that may strongly affect birds in tree canopies. The dominant arboreal ant species are numerically abundant, competitively superior to other

ants, and are often aggressive (Leston 1973). Dominant ant species are also predaceous, polydomous, and often display mosaic spatial distribution patterns whereby different species occupy mutually exclusive trees (Leston 1973, Room 1975, Majer 1978). Different species of dominant arboreal ants may have different diets and/or different effects on canopy arthropods (Koptur 1984, Davidson *et al.* 2003, Philpott *et al.* 2004) and thus may also differ in their effects on birds. Because ants can be either prey or competitors of birds, this makes it difficult to separate the effects of these two predator guilds on other arthropods. If ants negatively affect bird foraging, high ant activity may compensate for reduced predation pressure from birds. Similarly, excluding ants may result in increased bird foraging, thereby masking any effects of ants as predators. In this study we test the proposition that ants negatively affect bird foraging activity in trees in a tropical agroforest. We predict that in trees occupied by ants: (1) birds make fewer visits, (2) bird visits are of shorter duration, and (3) fewer bird species visit.

We conducted our research at Finca Irlanda (15°11' N, 92°20' W; 900 m elevation; 4500 mm rain/yr), an organic, shaded coffee farm in the Soconusco region of SW Chiapas, Mexico. The shade canopy at Finca Irlanda is diverse (>60 species), but is dominated by *Inga micheliana* Harms (Fabaceae: Mimosoideae) and *Alchornea latifolia* Swartz (Euphorbiaceae) (Perfecto & Vandermeer 2002). Approximately 60 species of birds and 60 species of ants forage on *Inga* spp. and *A. latifolia* trees at this site (Dietsch 2003, Philpott 2004). The most abundant ant is *Azteca instabilis* F. Smith (Hymenoptera: Formicidae), an aggressive ant that often nests in shade trees in large colonies (Philpott 2004). We investigated the effect of ant presence on bird foraging behavior in two dominant species of canopy trees (*I. micheliana* and *A. latifolia*) observing bird

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TABLE 1. Number and length of bird visits to two canopy trees (*Inga micheliana* and *Alchornea latifolia*) in a coffee agroforest either with *Azteca instabilis* (with ants) or without (no ants). Shown are mean number (\pm SE) of individual bird visits over 30 min and mean length of visit (min) (\pm SE) overall and for four bird guilds. Paired trees with and without ants were compared with ANOVA using a Bonferroni correction for each bird guild ($\alpha = 0.0125$).

	<i>Inga micheliana</i>					<i>Alchornea latifolia</i>				
	With ants	No ants	F	df	P	With ants	No ants	F	df	P
Number of visits										
Total	0.58 \pm 0.18	0.79 \pm 0.23	0.523	1,46	0.473	4.10 \pm 0.56	3.74 \pm 0.49	0.195	1,98	0.660
Granivores	0.04 \pm 0.04	0 \pm 0	1	1,46	0.323	0.04 \pm 0.03	0.02 \pm 0.02	0.338	1,98	0.562
Insectivores	0.25 \pm 0.14	0.38 \pm 0.15	0.39	1,46	0.535	3.26 \pm 0.45	3.14 \pm 0.44	0.036	1,98	0.849
Nectivores	0.25 \pm 0.12	0.29 \pm 0.11	0.062	1,46	0.804	0.30 \pm 0.12	0.18 \pm 0.08	0.707	1,98	0.402
Omnivores	0.04 \pm 0.04	0.13 \pm 0.09	0.687	1,46	0.412	0.32 \pm 0.11	0.26 \pm 0.10	0.162	1,98	0.688
Length of visits (min)										
Total	0.68 \pm 0.09	0.87 \pm 0.23	0.525	1,17	0.478	1.21 \pm 0.12	1.69 \pm 0.18	4.721	1,82	0.033
Granivores	0.50 \pm 0	NA	NA	NA	NA	0.75 \pm 0.25	0.50 \pm 0	0.333	1,1	0.667
Insectivores	0.58 \pm 0.08	0.58 \pm 0.08	0.000	1,8	1	1.25 \pm 0.12	1.83 \pm 0.20	5.733	1,78	0.019
Nectivores	0.81 \pm 0.19	1.08 \pm 0.58	0.132	1,8	0.725	1.22 \pm 0.45	1.18 \pm 0.30	0.004	1,12	0.953
Omnivores	0.50 \pm 0	1.50 \pm 0.50	1.333	1,1	0.454	0.97 \pm 0.20	0.88 \pm 0.28	0.073	1,16	0.791

visits to trees with and without colonies of *A. instabilis*. We selected five trees of each species with *A. instabilis* and five without. On separate days, we conducted observations of birds in each tree for 30 min recording the species of each bird visitor and the duration (min.) of each visit. Each *I. micheliana* tree was observed for 5 d and each *A. latifolia* tree was observed for 10 d; thus, there were twice as many observations on *A. latifolia* than *I. micheliana*. Tree order was rotated daily. Trees from one species, with and without ants, were paired and observed simultaneously (two observers) in most cases. When this was not possible, we alternated between observing trees with and without ants first.

To assess ant activity on a tree, we tapped tree trunks (6 m height) five times with a pole, placed the pole against the trunk and timed (sec.) how long it took *A. instabilis* to attack the pole. Tapping was replicated five times per tree at the same spot with *ca* 2 min. between each replicate. *Azteca instabilis* usually make nests in tree trunks or at the base of large branches and the nests are often polydomous (*i.e.*, composed of one main nest and several satellite nests; Philpott 2004). The distance from nests to where trees were tapped varied with each tree but in all cases a nest was located ≤ 2.5 m from the tap location. Both trees with and without ants were tapped, and those without ants were observed for a maximum of 30 sec. following tapping to assure that no *A. instabilis* were present on the trees. All tapping was done between 1300 and 1430 h under similar climatic conditions.

We recorded number and duration of visits for all bird species later separated into four bird guilds (granivores, insectivores, nectivores, and omnivores) (Howell & Webb 1995). For all birds combined we compared mean numbers of visits and mean visit duration on trees with and without ants using ANOVA ($\alpha = 0.05$). We used individual ANOVAs to compare visit number and duration for each bird guild, using a Bonferroni correction ($\alpha = 0.0125$) to correct for multiple tests and to reduce the likelihood of type I errors.

We also recorded the identity and number of each bird species visiting trees with and without ants. Species accumulation curves (for observed species richness or for richness estimators) for bird observations on *I. micheliana* did not reach asymptotes, thus to compare bird species richness we generated rarefaction curves using Coleman estimates in EstimateS (Colwell & Coddington 1994). We plotted rarefaction curves (with 95% confidence intervals) standardized for the average number of individuals captured per sample and visually compared richness on trees with and without *A. instabilis* (Gotelli & Colwell 2001).

Background ant attack rates were high on trees with *A. instabilis* nests. On *I. micheliana*, *A. instabilis* attacked after 6.23 ± 1.83 sec (mean \pm 1SE) and on *A. latifolia*, ants attacked poles after 1.84 ± 0.24 sec, significantly faster than on *I. micheliana* (Tukey's test, $P = 0.006$). No ant attacks were observed on trees without *A. instabilis*.

The number of individual bird visits per 30-min observation (overall or for any guild) to either *I. micheliana* or *A. latifolia* was not affected by the presence of *A. instabilis* (Table 1). Furthermore, the duration of visits to *I. micheliana* was not affected by *A. instabilis* (Table 1). However, bird visits to *A. latifolia* with *A. instabilis* were significantly shorter than visits to trees without *A. instabilis* for all birds and tended to be shorter for the insectivorous guild. There were no differences in visit duration for granivores, omnivores, or nectivores (Table 1).

Overall, the number of bird species visiting *A. latifolia* or *I. micheliana* trees was not affected by *A. instabilis* presence (Fig. 1). The total number of bird species visiting *I. micheliana* was slightly higher on plants without ants (11 *vs.* 8 species) but for a comparable sampling effort in terms of individuals seen (13), bird richness was similar on trees with (9) and without (8) ants. The same number of bird species overall visited *A. latifolia* with and without ants (26 species each) and bird richness did not differ for a comparable

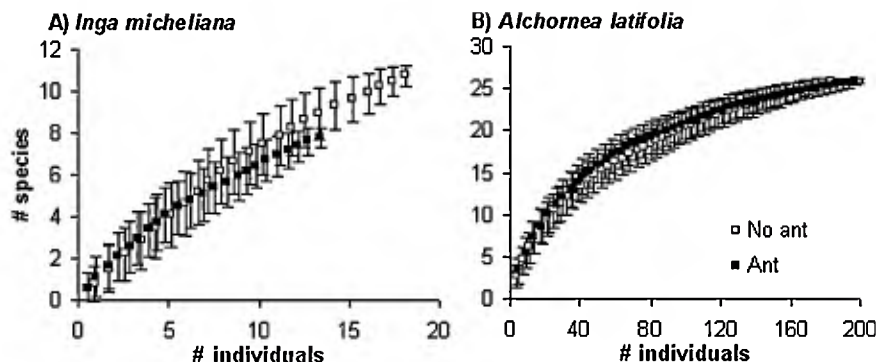


FIGURE 1. Rarefaction curves for bird species richness on (A) *Inga micheliana* and (B) *Alchornea latifolia* trees with and without *Azteca instabilis* ants in a coffee agroforest in Chiapas, Mexico. Coleman (rarefaction) curves were generated with EstimateS (Colwell & Coddington 1994) and x axes are standardized by the average number of individuals per sample. Error bars show standard deviation for Coleman estimates.

number of individuals captured (180) on trees with and without ants (25 species each).

Ants compete with birds both via exploitative and interference competition. If ants primarily affect birds via interference competition we would expect that birds will make fewer visits to trees with ants, bird visits would be shorter on trees with ants, and all bird foraging guilds should be equally affected as ants are unlikely to direct aggression more toward particular bird guilds. If ants primarily affect birds via exploitative competition there is no reason to expect ant presence to affect numbers of bird visits to trees because birds unlikely have complete information about prey distributions on a given tree. In other words, lower arthropod abundance on trees with ants would not influence visit frequency—birds will visit trees at random and thus one tree is as likely to be visited as another. Regarding duration of visits, there are two possibilities. First, we may expect visit duration of insectivorous birds in ant-infested trees, where ants compete for arthropod food with birds, to be longer than in noninfested trees because birds will spend more time searching for food. In addition, we would expect only insectivores, and not other bird guilds to be affected by ant presence. On the other hand, if birds forage to maximize the rate at which they capture arthropods, visit duration on trees with fewer arthropods (*e.g.*, those with ants) may be expected to decrease. Again, only insectivores would pay shorter visits.

Studies to date show that birds are affected both by exploitative and interference competition resulting in fewer and shorter visits (Haemig 1992, 1994, 1996; Aho *et al.* 1997, 1999). It is most likely, based on our experimental evidence, that *A. instabilis* ants affect bird foraging via exploitative competition, but this effect may depend on ant activity. Here, we saw no effect of *A. instabilis* presence on the number of visits to either tree species for any bird guild, suggesting that birds were not affected by interference or aggression by ants. Duration of bird visits, although not affected by *A. instabilis* presence on *I. micheliana* trees, was significantly reduced on *A. latifolia* trees. Furthermore, only activity of insectivores, and no other bird guilds, tended to be lower with *A. instabilis* presence. This result provides some evidence that bird visits may be shorter on trees with ants because of lower availability of shared resources

and not because of direct interference or aggression. Our results corroborate previous studies demonstrating that foliage-gleaning insectivores, but not seed-eaters or birds feeding on flying insects, made shorter visits and spent less time foraging on trees with ants due to reduced food supplies (Haemig 1992, 1994; Aho *et al.* 1997). Furthermore, ant attacks on poles were also significantly quicker on *A. latifolia* trees than on *I. micheliana* trees, and *A. instabilis* nests tended to be larger on *A. latifolia* trees (S. Philpott, pers. obs.). Thus there may be some threshold ant activity level above which arthropod densities and thus bird foraging are affected by ants. In fact, Aho *et al.* (1997) documented that where ant densities were reduced (but not eliminated) arthropod numbers increased rapidly thereby resulting in increased duration of treecreeper visits.

Because *A. instabilis* reduced the duration of bird visits to at least one species of canopy tree examined here, the possibility exists that the effects of *A. instabilis* ants and birds of prey may be compensatory. In other words, increased bird foraging and predatory activity on ant-free trees may compensate for decreased predation pressure accompanying ant removal. Although *A. instabilis* may feed on nectar and homopteran honeydew (Davidson *et al.* 2003), they also act as predators within coffee agroecosystems (Philpott 2004). Philpott *et al.* (2004) found that the removal of *A. instabilis* from *I. micheliana* trees did not result in changes in arthropod densities. Yet if the number or duration of bird visits increases on trees from which ants are removed (Haemig 1992, 1994; Aho *et al.* 1997), the overall negative effects of birds on arthropod communities may increase the masking of the effects that ants have on arthropods. Here, we found that *A. instabilis* did not affect bird activity on *I. micheliana* trees; thus it is unlikely that bird predation compensated for ant removal, masking the predatory effects of *A. instabilis* on this canopy tree. However, *A. instabilis* did significantly reduce the length of bird visits and tended to reduce the duration of insectivore visits (but not for other guilds) to *A. latifolia* trees indicating the possibility that ants are limiting bird foraging via exploitative competition and that the effects of birds and ants on some canopy trees may combine in a nonlinear fashion.

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