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GEOGRAPHIC VARIATION IN SPECIES COMPOSITION OF MIXED SPECIES FLOCKS IN LOWLAND HUMID FORESTS IN BRAZIL

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ABSTRACT

The composition and structure of flocks were studied at three Amazonian Brazilian sites and one site in Espírito Santo in the Atlantic Forest of Brazil. All sites have the antshrike, Thamnomanes caesius, *which has been implicated as the key species in the creation and maintenance of understory flocks. At the Amazonain sites, the understory flocks with* T. caesius *are similar in composition among sites and very distinct from the canopy flocks. Canopy flocks are similar in composition across sites in Amazonia, but only at one site did a sentinel species,* Lanio versicolor *in Rondônia, play a significant role.*

Flocks in Espírito Santo differed substantially from Amazonian flocks. Flocks with T. caesius *were not strongly differentiated from canopy flocks. Flocks were less stable and* T. caesius *appeared to play a less obvious role as a sentinel. The differences between flocks in Amazonia and Espírito Santo, as well as the absence of sentinel species in canopy flocks at two Amazonian sites suggests that the unusual stability of Amazonian flocks is not due primarily to the response of the flocks to the presence of sentinel species.*

Mixed species bird flocks are a prominent feature of the avifauna nearly worldwide. They have been extensively studied in temperate regions (see Morse 1970), while tropical flocks have received somewhat less attention (Powell 1985). There have been two major studies of mixed species flocks in the lowland humid tropical forests of South America. These studies examined mixed species flocks in Amazonia: at Manu National Park in southeastern Peru (Munn and Terborgh 1979, Munn 1985, Munn 1984); and near Manaus, Brazil (Powell 1985, Powell 1989). Both studies concluded that understory flocks center around antshrikes of the genus *Thamnomanes*, especially *T. caesius* and its allospecies *T. schistogynus*.

Flock members receive protection from avian predators through the sentinel behavior of *Thamnomanes*, while in turn, flushing insects that the antshrikes eat. *Thamnomanes caesius* besides giving prominent and persistent alarm calls, also has calls that act to maintain flock cohesion, and assemble flocks at the beginning of the day or when the flock has become dispersed during the day (Powell 1985). Munn (1985) has extended this scenario to the stable flocks of canopy insectivorous birds that occur in the same forests, with *Lanio versicolor* (an insectivorous

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tanager) in the sentinel role. A similar situation seems to occur in Africa with various especies of *Dicrurus* feeding on insects flushed by other flock members, and acting as a sentinel (Swynnerton 1915, Willis pers. comm.). However, Grieg-Smith (1978) found no evidence of insect-flushing in mixed species flocks containing *Dicrurus adsimilis* in Ghana.

The genus *Thamnomanes* (see Schulenberg 1983) contains two superspecies *ardesiacus* (including *saturninus*) and *caesius* (including *schistogynus)*. Within each pair, the taxa are similar morphologically, behaviorally, and to a large extent vocally, but replace one another geographically. Throughout Amazonia, most sites contain representatives of both superspecies, and the two often occur together in the same flocks.

Thamnomanes caesius, in addition to being widespread in Amazonia, occurs in the lowland forest of eastern Brazil south to Rio de Janeiro in mixed-species flocks, but the flocks of this region have not been discussed in the literature. Here, I compare the composition of both understory and canopy flocks from three Amazonian forest sites and a lowland forest site in eastern Brazil. I consider the implications of some differences in flock composition and structure for the interpretation of the evolution and function of flocks.

STUDY SITES

Colonia Apiaú, Roraima (2° 39' N 61º 12'W)

I worked at this small settlement on the east bank of Igarapé Serrinha from 30 September to 10 October 1987. It is about 50 kilometers west of the town Mucajaí at an elevation of approximately 150m. The habitat is mostly terra firme forest with a narrow band of seasonally flooded forest along the stream. Much of the terra firme forest within a kilometer of the road has been logged selectively. Logging roads crisscross the area and the forest has been opened up substantially. Farther from the road and along the stream the forest appeared essentially undisturbed. The terra firme forest canopy is about 35m high and numerous emergents reach about 50m. Where undisturbed, the understory is relatively open. Characteristic trees of this site include: *Tetragastris* sp. (Burseraceae), *Manilkara* sp. (Sapotaceae), *Caryocar* sp. (Caryocaraceae) and various palms (Nunes et al. 1988). Along the igarapé, the canopy is lower (about 25m), and emergents are few. The understory is dominated by *Heliconia*, although large areas are open. Vine tangles are common.

Cachoeira Nazaré, Rondônia (9° 44'S 61º 53'W)

I collected data at this site on flock composition from 10 Octobeer to 21 November 1986 and from 1 to 14 March 1988, although flock composition was recorded systematically only in 1988. This locality is the proposed site of a dam on the Rio Ji-paraná approximately 125km north of the city of Ji-paraná. For my study, I used the facilities and trail system constructed by the Consorcio Nacional de Engenheiros Consultores for preliminary geological and topographical survey of the site.

This site is predominantly terra firme forest on a nearly flat terrain. Forest along the river is of two types: (1) seasonally flooded forest, about 100m wide with tall trees and a very open understory; and (2) river bluff forest containing many Cecropia and balsa trees *(Ochroma pyramidale)* with relatively short trees (canopy about 30m), few emergents and relatively dense understory. The riverine forest grades into typical terra firme forest about 300 to 500m from the river. The terra firme forest has a closed canopy about 40m tall with emergents commonly reaching 60m. The understory is relatively open. Flocks were extremely rare within the riverine forest, and for comparison with other sites I use only terra firme forest flocks.

Reserva Ducke, Amazonas (3° 08'S 60º 02'W)

This reserve of 10,000 hectares about 26 km NE of Manaus, is run by the Instituto Nacional de Pesquisas da Amazônia (INPA). I spent 36 days at this side, 17 May to 24 June 1988, observing flocks along the trails of the northwestern quadrant of the reserve (see Willis 1977). The habitat within the reserve is almost exclusively terra firme forest on moderately hilly terrain, with ridges about 20m high. Near the highway at the northewestern corner, are small clearings and facilities for workers, along with a series of plantations of native trees for silvicultural experiments. The canopy is closed and generally ranges from 35 to 40 meters in height, with emergents reaching about 50m. The understory is denser than is typical in Amazonian forests and is dominated by small palms of several genera, especially *Astrocaryum*. Along the streams, the forest is a little lower, with palms such as *Mauritia* and *Oenocarpus* important canopy elements.

Reserva Florestal Rio Doce, Espírito Santo (19° 30'S 40°00'W)

This private reserve of about 22,000 hectares is run by Companhia Vale do Rio Doce for silvicultural research on native trees. Most of the reserve is forested, for except scattered plantations of native trees within the forest, the far western edge where research facilities and housing are located, and native grassland in the southeastern corner of the reserve. An extensive system of dirt roads along with a few forest trails provide access to the forest. Most of the roads have continuous canopy over them.

I spent 28 days at this site between 29 July and 27 August 1988. The reserve is almost perfectly flat and is at 50m elevation. It is one of the largest remaining blocks of forest in lowland eastern Brazil and is contiguous with the similarly-sized Sooretama Biological Reserve. Together, the two encompass about 25 percent of the remaining lowland Atlantic forest north of Rio de Janeiro.

The forest canopy is broken, but averages about 30 meters with emergents up to about 50m. As a result of a long, severe annual dry season, the forest is partially deciduous; about 40 percent of the trees completely lose theirs leaves during June through August (M. Harritt pers. comm.). With the relatively open canopy and partially deciduous forest, much light reaches the forest floor and the understory is dense and viny, making walking away from trails and roads difficult. Although the forest is considered primary (R. de Jesus pers. comm.), there is evidence of selective cutting.

METHODS

At all sites, I encountered flocks as I walked through the forest. When I heard a flock anywhere close to the trails I pursued the flock and followed it, except at Rio Doce where dense understory made movement away from trails considerably more difficult. There I followed flocks only when I encountered them along the edge of roads or trails. While following flocks, I noted all bird species observed and the number of individuals of each species. I followed flocks for up to two hours, although most were followed for thirty to forty-five minutes. Although I recorded flock composition for all flocks encountered, those followed for less than fifteen minutes were not included in analyses of flock composition, as I did not consider species lists to be complete.

I defined mixed species flocks as associations of individuals of two or more species in proximity, moving in the same direction for at least five minutes with no external resource concentration. Two common tropical forest aggregations that are excluded under this definition are the gathering of birds around antswarms, and frugivorous birds gathering in fruiting trees. Several species of birds around antswarms often will move with the swarm for long periods of time; however, these aggregations are strinctly tied to the presence of the ants. Without ants, the birds disperse widely through the forest.

The importance of *Thamnomanes* to flocks in Amazonia is clear (Munn and Terborgh 1979, Powell 1985), so I divided flocks into those containing *Thamnomanes* antshrikes and those without *Thamnomanes*. At the Amazonian sites, this effectively divides the flocks into understory and canopy flocks (Munn 1985). In Espírito Santo, this distinction is not so clear (see discussion).

I do not use Moynihan's (1962) classification system for flocking species (nuclear vs. attendant, active vs. passive), as that system is too dependent on subjective interpretation of the motivational states of flock members. Instead, I define classes by the tendency of species to be in flocks and to associate with flocks containing *Thamnomanes* or those without *Thamnomanes*. This classification scheme is based on that of Munn and Terborgh (1979). I refer to species that are always in a particular flock type as core species (here used for species observed over 90% of the time in flocks). Regular flock members that are often observed away from flocks are referred to as "flocks joiners". "Flock-switchers" are species that occur regularly in both canopy and understory flocks. "Casual flockers" refers to species that are regularly encountered away from flocks, but only rarely and for brief periods follow flocks.

To examine the similarity in flock composition, I used reciprocal averaging (Hill 1973) to ordinate canopy and understory flocks from the sites in species space; to perform these calculations, I wrote a program (Stotz 1990, Appendix B) in SAS IML (SAS 1985). The percentage occurrence of species in canopy and understory flocks were used as variables. For this analysis, in order to minimize the effects of biogeographic differences, I treated allospecies and obvious congeneric replacements as the same species. I excluded *Thamnomanes caesius*, *T. saturninus* and *T. ardesiacus* from the analysis, since their presence or absence was used to define flock type originally.

RESULTS

Mean flock species richness varied about twofold from 9.77 species for non-*Thamnomanes* flocks in Espírito Santo to 19.67 species for *Thamnomanes* flocks at Reserva Ducke. The number of individuals in flocks also varied across a twofold range, from an average of 16.02 to 31.1 individuals per flock (Table 1). Flocks at all sites averaged between 1.3 and 1.85 individuals per species. Most species are represented in these flocks by one mated pair (Munn 1984).

Species occurring in flocks with *Thamnomanes* and without *Thamnomanes*, along with the percentage of flocks in which they occurred are given in the appendix. The *Thamnomanes* flocks are dominated by members of the families Dendrocolaptidae, Furnariidae, and Formicariidae, all insectivorous suboscines of the suborder Furnarioidea. At all four sites, over fifty percent of the species in an average flock come from these three families. By contrast, the two groups that dominate canopy flocks, Tyrannidae and Thraupinae, are members of different suborders. In both families, but especially among the tanagers, a number of the flocking species are omnivorous.

The occurrence of canopy species in flocks with *Thamnomanes* is variable among sites (Table 2). Most occurrences resulted from full canopy flocks above, but traveling with, full understory flocks. Such flocks may spend several hours together before the canopy component and understory component separate. The large size of *Thamnomanes* flocks at Reserva Ducke (Table 1) compared to the other sites mainly results from a considerably larger than average canopy component (Table 2). This reflects a greater tendency for joint canopy-understory flocks. At Reserva Ducke, seventeen of thirty *Thamnomanes* flocks contained more than five canopy species, suggesting joint flocks. At the other sites, no more than three had such large canopy components.

Table 1. Number of species and individuals in mixed-species flocks by locality and type

		Rondônia	Reserva Ducke	Roraima	Espírito Santo
with *Thamnomanes*					
N? of flocks		46	30	22	17
species/flock	$\bar{x}$	12.33	19.67	10.27	12.76
	s.d.	3.69	7.28	2.94	3.01
individuals/flock	$\bar{x}$	19.36	31.10	16.14	19.11
	s.d.	5.54	12.02	5.04	4.15
total species		73	72	49	36
without *Thamnomanes*					
N? of flocks		14	33	22	219
species/flock	$\bar{x}$	15.15	15.27	15.86	9.77
	s.d.	3.00	4.64	4.27	3.84
individuals/flock	$\bar{x}$	20.23	25.64	29.23	16.02
	s.d.	7.34	10.51	9.87	6.87
total species		58	76	54	91

Table 2. Average number of species by flock-use class in *Thamnomanes* flocks at all study sites

	Reserva Ducke	Rondônia	Roraima	Espírito Santo
Understory core	7.80	7.91	6.05	5.24
Understory joiner	2.17	.78	.82	2.59
Canopy core	5.63	1.83	1.27	1.35
Canopy joiner	.87	.20	.55	.29
Flock switcher	2.87	1.28	1.23	2.90
Casual flocker	.36	.31	.40	.35

The non-*Thamnomanes* flocks are nearly identical in size (Table 1) and are similar in composition (Table 3) at the three Amazonian sites. By contrast, such flocks are about forty percent smaller at Espírito Santo (Table 1). This smaller size is due primarily to a considerably smaller representation of strictly canopy species, only five compared to eleven or more at Amazonian sites (Table 3). Tanagers (Thraupinae) and vireos (Vireonidae) are particularly poorly represented in the Espírito Santo non-*Thamnomanes* flocks.

Ordination of flocks using reciprocal averaging based on species composition produces three significant axes (Table 4). The first axis separates understory flocks from canopy flocks. On this axis, the understory and canopy flocks do not overlap, and the understory flocks from the four sites form a relatively tight cluster (Figure 1). The substantial canopy element in the *Thamnomanes* flocks at Reserva Ducke causes that point to fall nearest the cluster of canopy flocks. Similarly, the Espírito Santo canopy flock is an outlier from the other canopy flocks, as expected, since it has a relatively large understory component and a small canopy component (Table 3). The second axis contrasts Espírito Santo flocks with the Amazonian flocks (Figure 1). The third axis is complicated: the extremes are occupied by Rondônia canopy flocks and, at the other end, by flocks from Reserva Ducke and Roraima (Figure 2). It appears to be reflecting primarily within-Amazonia patterns of biogeography. The canopy flocks in Rondônia have distinctive set of species (Appendix) associated with them, including *Ancistrops, Philydor erythropterus, Pygiptila stellaris, Odontorchilus cinereus,* and *Lanio versicolor.* Reserva Ducke and Roraima are located within the Guianan center of endemism, the most distinctive biogeographic subunit in Amazonia (Haffer 1974, Cracraft 1985).

Table 3. Average number of species by flock-use class in *non-Thamnomanes* flocks at all study sites

	Reserva Ducke	Rondônia	Roraima	Espírito Santo
Understory core	.48	.43	.18	.92
Understory joiner	.58	.57	.05	.83
Canopy core	8.24	8.72	9.23	3.38
Canopy joiner	2.88	2.43	4.78	1.67
Flock switcher	2.55	2.72	1.50	2.69
Casual flocker	.42	.29	.14	.29

Table 4. Reciprocal averaging eigenvectors and variance statistics for analysis of flocks

Axis	1	2	3
Locality/flock type			
Ducke Canopy	.136	-.013	-.071
Rondônia Canopy	.111	-.082	.254
Roraima Canopy	.204	-.005	-.108
Espírito Santo Canopy	.023	.305	.034
Ducke Understory	-.071	-.067	-.063
Rondônia Understory	-.177	.120	.040
Roraima Understory	-.160	-.081	-.090
Espírito Santo Understory	-.148	.190	.036
eigenvalue	.496	.363	.230
% variance	38.1	28.0	17.7
cumulative % variance		66.1	83.8

Although Munn (1985) suggested *Lanio versicolor* plays the same role in canopy flocks that *Thamnomanes* plays for understory flocks, at my study sites *L. versicolor* is a regular member of such flocks only in Rondônia, where it occurred in 86 percent of the canopy flocks. At Reserva Ducke, the allospecies *Lanio fulvus* occurred in only nine percent of the non-*Thamnomanes* flocks, and in Roraima, *Lanio* was absent from the study site, although typical canopy flocks were present. Although I had no individually marked birds, flocks containing the same set of insectivorous species could be relocated across consecutive days in the same areas of the forest.

The basic structure and composition of *Thamnomanes* flocks was consistent across all the Amazonian sites. The Espírito Santo *Thamnomanes* flocks show a similar composition to Amazonian understory flocks, although with some substantial differences from the typical pattern. Most obviously, *Thamnomanes caesius* itself behaves differently than in the Amazon, giving many fewer alarm calls and in general being much quieter. The rallying calls, given by this species in Amazonia (Powell 1985, pers. obs.), were also not heard from *T. caesius* in Espírito Santo. In addition, most species associated with *Thamnomanes* are not exclusively in those flocks, in contrast to Amazonia where a set of species are nearly exclusively found in flocks containing *Thamnomanes*. *Thamnomanes* flocks were relatively rare in Espírito Santo, with large areas of the reserve filled with flocks lacking *Thamnomanes*. In these areas flock species that are regularly associated with *Thamnomanes* normally occurred in typical non-*Thamnomanes* flocks. However, there also existed some flocks with a composition much like a typical Espírito Santo *Thamnomanes* flock, but lacking the *Thamnomanes caesius*. Finally, it appears that species join and leave *Thamnomanes* flocks to a much greater degree than they do in Amazonia, where many of the individuals spend their entire time foraging with *Thamnomanes* flocks.

The picture of *Thamnomanes* flocks presented thus far ignores an anomaly at Reserva Ducke. At this site existed at least five different flocks that ranged in size from two to five species, containing *Thamnomanes ardesiacus*, but no *Thamnomanes caesius*. These flocks were stable, as three of them were observed on two or more days and seemed to occupy exclusive territories. Once, I observed a territorial dispute between a typical *Thamnomanes* flock and one of these incomplete flocks containing three species. These atypical flocks were not included in the previous summary, as they appear to represent a distinct pattern, which I discuss below.

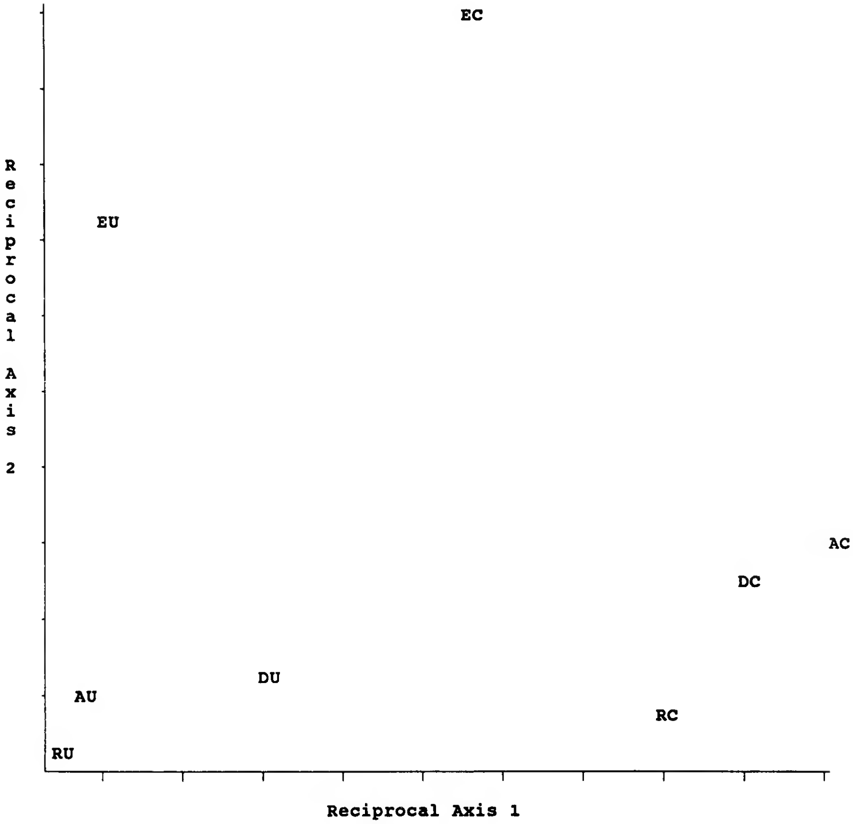

Figure 1, ordination of flocks by type and locality, reciprocal axis 1 vs. 2. Two letter designation gives locality and flock types. The codes for locality are: A = Roraima, D = Reserva Ducke, E = Espírito Santo, and R = Rondônia. For flock type: C = canopy flocks (non-*Thamnomanes*, U = understory flocks *Thamnomanes*.

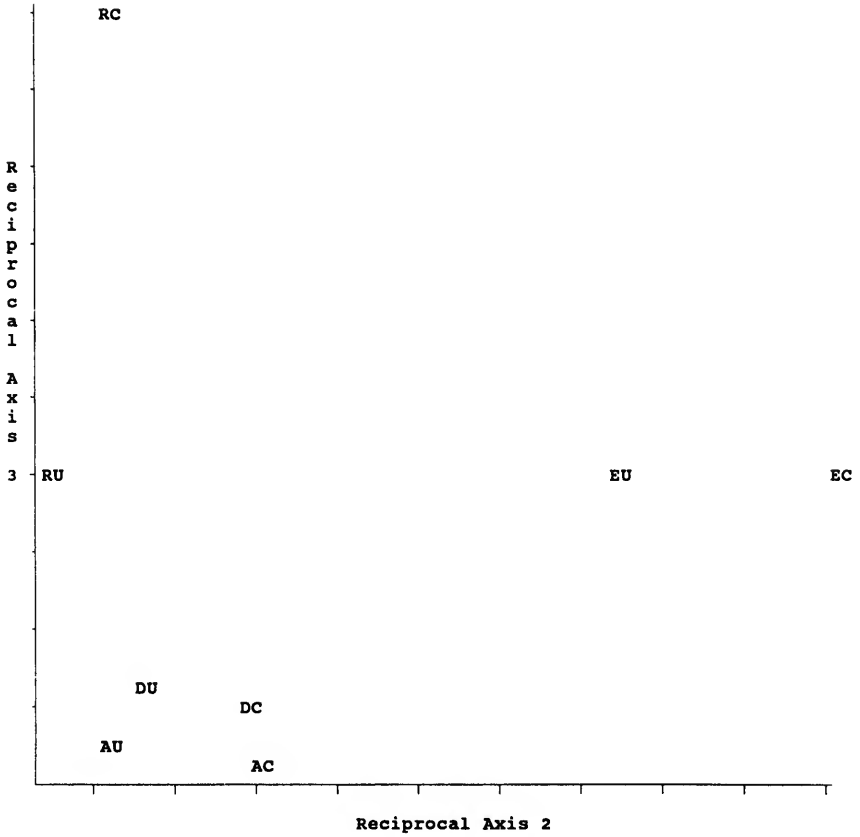

Figure 2, ordination of flocks by type and locality, reciprocal axis 2 vs. 3. Two letter designation gives locality and flock types. The codes for locality are: A = Roraima, D = Reserva Ducke, E = Espírito Santo, and R = Rondônia. For flock type: C = canopy flocks (non-*Thamnomanes*, U = understory flocks (*Thamnomanes*).

DISCUSSION

Depauperate flocks such as those I found formed around *Thamnomanes ardesiacus* at Reserva Ducke have not been previously reported in Amazonia. However, I have observed flocks of similar composition in small forest fragments. In three isolated forest fragments of ten hectares at the study site of the Biological Dynamics of Forest Fragments project, north of Manaus, understory flocks disappeared over about a five year period following forest fragmentation into these small forest patches. In the course of the loss of understory flock species, these flocks went through a period where their structure resembled that of the depauperate flocks at Reserva Ducke. Forest fragmentation does not appear responsible for the depauperate flocks at Reserva Ducke, however. Although this ten thousand hectare reserve is effectively isolated from surrounding forest, this has occurred only within the last five years, presumably too short a period for such a response in so large a reserve. In addition, birds far more sensitive to fragmentation, such as antswarm followers (Willis 1979, Lovejoy et al. 1984), remain at Ducke in large numbers. Finally, there are many typical understory flocks within the reserve that show no signs of decay.

It seems likely that the depauperate flocks in Reserva Ducke must be responding to local variation in the environment. Munn (1985) found something similar in canopy flocks; although understory flocks occurred throughout his study area, canopy flocks avoided large areas where the canopy height was below about 25 meters. At Ducke, one of the depauperate understory flocks was in an area from which the understory had been cleared about 20 years ago (Willis, pers. comm.). The rest of these flocks were found along the tops of the higher ridges where soils are sandier. However, no obvious differences in the forest structure were visible.

Otherwise, understory flocks led by *Thamnomanes* maintain a similar structure and composition across Amazonia. The adaptive scenario developed by Munn (1984) that *Thamnomanes* acts as a sentinel, providing other flocks members with protection from avian predators, while foraging on insects flushed by the other birds, may hold throughout Amazonia. However, the rate of predation by avian predators is apparently low in tropical forests (Munn and Terborgh 1979, Powell 1985, compare rates to Morse 1978). In canopy flocks, variation in composition is similar in magnitude to that in understory flocks (see Figure 1) and the flocks appear stable across at least a period of days; however, *Lanio*, identified by Munn as the sentinel species in canopy flocks, is absent from Roraima and is rare at Reserva Ducke. This suggests that a similar scenario proposed by Munn (1985) to account for canopy flocks does not apply throughout Amazonia. Only in Rondônia was *Lanio* abundant enough in canopy flocks to occupy the sentinel role.

The greater tendency of canopy flocks to occur with understory flocks at Reserva Ducke could be due to the rarity of the presumed canopy sentinel species, *Lanio fulvus*. Canopy flocks may stay with understory flocks in order to benefit from the sentinel behavior of *Thamnomanes*. However, *L. fulvus* was more common in canopy flocks that joined understory flocks than in pure canopy flocks, occurring in thirty percent of the *Thamnomanes* flocks and only nine percent of the non-*Thamnomanes* flocks (Appendix). In addition, at Roraima, where *Lanio fulvus* did not occur, canopy species joined with understory flocks at a lower rate than at either of the other Amazonian sites.

None of the additional canopy flock members at Reserva Ducke or Roraima seem to meet the proposed requirements for a sentinel species: foraging regularly through aerial hawking, and giving loud, persistent alarm calls (Munn 1985). Despite this, canopy flocks at Reserva Ducke and Roraima appear structurally similar to those in Rondônia, although both are dominated by tanagers and flycatchers to a greater degree. It is possible that flocks similar in structure and composition could form through dissimilar mechanisms. However, the similar structure and composition of canopy flocks even without the presence of sentinel species indicates that the stability of canopy flocks is not dependent upon the presence of a sentinel species.

In Espírito Santo, well-defined canopy and understory flocks do not exist. The canopy flocks do not have a large distinctive core of species as in Amazonia, and they are joined by a mumber of understory species (Table 3). *Thamnomanes* flocks exist, but are relatively rare and most birds are not full-time flock members. Neither does *Thamnomanes caesius* seem to act as a sentinel. In Amazonia, as one approaches a *Thamnomanes* flocks, *Thamnomanes caesius* almost invariably gives alarm calls. In fact, I located the vast majority of *Thamnomanes* flocks by the alarm calls of *Thamnomanes caesius*. By contrast, in Espírito Santo, I regularly followed flocks containing *T. caesius* for several minutes before I heard any calls. For the seven flocks for which I have data the time from the first encounter of the flock to the first alarm call of *Thamnomanes caesius* averaged over 3.5 minutes. No flock was located via the alarms of *Thamnomanes*.

Despite the strong Amazonian element to the avifauna in Espírito Santo, flocks at this site seem more similar to those in Central America and farther south in montane São Paulo. The flocks are smaller than Amazonian flocks (Table 1), they do not appear to have a core of species that defend identical territories like Amazonian flocks (Munn and Terborgh 1979), and many species appear to join and leave flocks. Flocks seen at the same location on different days are commonly very different in composition, unlike in either canopy or understory flocks throughout Amazonia.

Amazonian canopy flocks show similar composition, size and stability whether a sentinel species (*Lanio* sp.) is part of them or not. They contrast, as noted above, with the canopy flocks of Espírito Santo rather strongly. This suggests that such stability is really a consequence of being in the Amazon rather than a response by the members to a sentinel species.

Although it appears probable that, throughout Amazonia, understory flocks are intimately tied to *Thamnomanes* antshrikes, it seems likely that much of the stability and integration of these flocks is not a response to *Thamnomanes*. Rather, *Thamnomanes* probably has co-opted pre-existing relatively stable flocks. Early in the evolution of these flocks, *Thamnomanes* likely used the other members as beaters without being an integrated part of the flock, much as *Dicrurus* apparently does in Africa (Swynnerton 1915, Willis pers. comm.). Later, the birds in understory flocks may have responded to *Thamnomanes* producing, for example, the highly inflated home range size of the core species of the Amazonian flocks (Powell 1989).

In Espírito Santo, it appears that *Thamnomanes caesius* has not been able to co-opt the flocks there, perhaps because they are less stable. It could be argued, instead, that the *Thamnomanes* flocks there have decayed from the Amazonian structure, rather than having never developed the high stability and integration. However, it seems more likely that these flocks have always had effectively their present structure. First, they resemble the standard pattern for Neotropical flocks outside of the Amazon basin (see Moynihan 1962 and Jones 1977 for Central America, Machado 1990 for southern Brazil). Second, the *Thamnomanes* flocks of Espírito Santo contain a substantial element, including *Lepidocolaptes fuscus*, *Philydor atricapillus*, *Leptopogon amaurocephalus*, and *Habia rubica*, that are members of qualitatively similar flocks in eastern Brazil south at least to the lower montane areas of eastern São Paulo (pers. obs.). These flocks lack *Thamnomanes* and the Amazonian element of the Espírito Santo flocks, and have probably always lacked them. Finally, the structure of all flocks at Espírito Santo is similar and species overlap completely among those flocks with and without *Thamnomanes*. It seems an unlikely result if one flock type is in the process of decay.

Because I did not individually mark birds in Espírito Santo, these preliminary impressions of reduced long-term stability are tentative. To determine the structure of the flocks in Espírito Santo, it will be necessary to follow marked birds across a longer period. This shows great potential for giving insight into the functional relationships of species in the Amazonian *Thamnomanes* flocks, since *Thamnomanes* is present, but does not seem to play the pivotal role that it does in Amazonia.

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Appendix. Composition of flocks at study sites by flock type (percentage of flocks in which species observed)

	Reserva Ducke		Rondônia		Roraima		Espírito Santo	
	T	N	T	N	T	N	T	N
No. of flocks	30	33	46	14	22	22	17	219
Piaya melanogaster	23	21		21		9		
P. cayana			2	14	14	18	6	11
Heliothryx aurita		6						
Trogon rufus	3	3						
T. viridis		9			5			1
T. violaceus	10	6						
T. collaris								2
T. melanurus	7	3						
Galbula cyanicollis			4					
G. ruficauda							6	16
G. galbula					5			
G. dea	17	48		7				
Malacoptila rufa				2				
M. striata								1
Monasa atra	3	6						
M. morphoeus				7				1
Capito niger	10	27			5	41		
C. dayi			4	21				
Picumnus exilis					14	9		
P. aurifrons			16	21				
Piculus flavigula	67	45	11	21	36	14	24	24
P. chrysochloros		3	4					1
Celeus elegans				7				
C. grammicus				7				
C. undatus	10							
C. torquatus								1
C. flavus								1
C. flavescens								1
Veniliornis cassini	20	9			41	9		
V. affinis			42	29			53	38
Phloeoceastes rubricollis	3							
Dendrocincla fuliginosa	20	3	4		5		24	8
Glyphorynchus spirurus	33	6	20		45			7
Sittasomus griseicapillus	43	45	2	29		5		1
Deconychura stictolaema	43	3	11					
D. longicauda	17	3						
Xiphocolaptes albicollis								1
X. promeropirhynchus			2					
Hylexetastes perrotii	13	3	2					
Dendrexetastes rufigula	3	3						
Dendrocolaptes certhia	10	6						
D. concolor			7					
D. platyrostris							6	1
Xiphorhynchus elegans			87	7				
X. pardalotus	100	27			55			
X. obsoletus			2		18			
X. guttatus			18	21			65	16
Lepidocolaptes fuscus							76	23
L. squamatus								1

	Reserva Ducke		Rondônia		Roraima		Espírito Santo	
	T	N	T	N	T	N	T	N
L. albolineatus	39	55	7	57	32			
Campylorhamphus trochilirostris		3						
C. procurvoides			4					
Hyloctistes subulatus			4					
Ancistrops strigulosus			11	43				
Philydor erythrocercus	100	6	87	7				
P. ruficaudatus			2	14				
P. erythropterus			9	43				
P. pyrrhodes	7				5			
P. atricapillus							71	10
Automolus infuscatus	17		27		32			
A. leucophthalmus							47	11
A. ochrolaemus	7	3	7					
Cichlocolaptes leucophrys								1
Xenops minutus	36	3	2	14	36		29	7
X. rutilans							24	30
X. milleri	43	12	4	36				
Cymbilaimus lineatus	7	3	2		5			
Thamnophilus palliatus								1
T. murinus					5			
T. schistaceus			7					
T. punctatus							6	11
T. amazonicus			2					
Thamnomanes caesius		100	100		86		100	
T. ardesiacus		100			77			
T. saturninus			64					
Myrmotherula brachyura		6	9	29	5	23		
M. ambigua					14	59		
M. sclateri			53	86				
M. hauxwelli			4					
M. guttata					5			
M. menetriesii	93	3	100		77			
M. axillaris	53		11		32		100	46
M. iheringi			9					
M. longipennis	57		73		50			
M. urosticta							71	7
M. gutturalis	47							
M. leucophthalma			82					
M. haematonota					45			
M. ornata			4					
Microrhopias quixensis			47					
Pygiptila stellaris			40	36				
Drymophila squamata							12	2
Herpsilochmus rufomarginatus					9	27	53	47
H. dorsimaculatus	73	76				23		
Terenura spodioptila	53	36			9	73		
T. humeralis			7	29				
Cercomacra cinerascens			7					
Hypocnemis cantator					5			
Conopophaga melanops							6	
Phyllomyias fasciatus								1
Zimmerius gracilipes	13	18		57		64		

	Reserva Ducke		Rondônia		Roraima		Espírito Santo	
	T	N	T	N	T	N	T	N
Camptostoma obsoletum								7
Myopagis gaimardii	27	42	18	64	32	82		
M. caniceps	3	39						16
Elaenia flavogaster								1
Hemitriccus minor	3		2					
Myiornis auricularis							41	48
Ornithion inerme					5	18	6	4
Tolmomyias sulphurescens			11					
T. assimilis	63	55	33	79	36	68		
T. poliocephalus	3	33				18	47	77
T. flaviventris								7
Mionectes macconnelli	53	18						
M. oleagineus			2	7	9		6	10
Myiobius barbatus	13		13		5		18	5
Contopus cinereus								1
Conopias trivirgata								2
Coryphotriccus albovittatus	13	36				64		
Attila spadiceus	20	3			5			2
A. rufus								2
Myiarchus tuberculifer							12	7
M. ferox								1
Sirystes sibilator		6				27		18
Laniocera hypopyrra							6	
Rhytipterna simplex	27	3		7			24	19
Rhynchocyclus olivaceus			4				59	11
Leptopogon amaurocephalus			2				35	15
Pachyramphus surinamus		21						
P. castaneus				14				
P. polychopterus						5		1
P. marginatus	40	45		29	5	36	53	52
P. viridis								2
P. minor	20	27		7		18		
P. validus								5
Tityra semifasciata				7				
T. cayana	7	30				9		1
T. inquisitor								10
Piprites chloris	47	48	16	43		14		1
Corapipo gutturalis	3							
Tyranneutes stolzmanni			2					
Pipra erythrocephala					5			
P. pipra								1
P. nattereri			4					
Lipaugus vociferans		15				5		
Carpornis melanocephalus								1
Xipholena punicea		3						
Oxyruncus cristatus								1
Odontorchilus cinereus			13	72				
Thryothorus genibarbis			2					1
Polioptila guianensis				14		18		
Ramphocaenus melanurus	3				14		47	6
Cyclarhis gujanensis		6		7		14		
Vireolanius leucotis	40	48	4	21		14		

	Reserva Ducke		Rondônia		Roraima		Espírito Santo	
	T	N	T	N	T	N	T	N
Vireo olivaceus		24	2	21	5	32	12	25
Hylophilus semicinereus			2					
H. muscicapinus	73	94	17	71	45	82		
H. ochraceiceps	36		7		45			
Caryothraustes canadensis	7	30				41		6
C. humeralis			2	14				
Pitylus grossus			2					
Saltator maximus								16
Sporophila schistacea			2					
Arremon taciturnis								2
Coereba flaveola	3							4
Conirostrum speciosum								1
Cyanerpes nitidus				9				
C. caeruleus	3	6		7	5	50		
Chlorophanes spiza	3	18			9	68		
Dacnis cayana	3	27		14		36		19
D. lineata	3	18				27		
Euphonia chysopasta		9		21		36		
E. minuta	3	3		7	14			
E. cayennensis	10	27						
E. rufiventris			7	43				
E. pectoralis								1
Tangara punctata	10	36			5	41		
T. nigrocincta						27		
T. gyrola			2	21				
T. mexicana		3		7		14		15
T. chilensis		30		14		50		
T. seledon								6
T. velia		12		29		41		2
Hemithraupis flavicollis	7	36		14	9	59	6	49
H. guira						50		
Nemosia pileata								1
Lanio fulvus	30	9						
L. versicolor			13	86				
Habia rubica			20				53	10
Tachyphonus cristatus	57	67	4	64	9	55	47	68
T. luctuosus			4		27	9		
T. surinamus	13	12			9			
Thraupis palmarum		6		7				1
T. episcopus		3						
T. sayaca								3
Lamprospiza melanoleuca	7	39		14				
Dendroica striata						5		
Parula pitiayumi							35	67
Granatellus pelzelni			2		5	5		
Cacicus cela		12						
C. haemorrhous	7	3						5
Icterus chrysocephalus						9		

T = flocks containing *Thamnomanes*; N = flocks lacking *Thamnomanes*

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