

COMPARATIVE FORAGING BEHAVIOR BETWEEN SOLITARY AND FLOCKING INSECTIVORES IN A NEOTROPICAL FOREST: DOES VULNERABILITY MATTER?

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Resumen. – **Comportamiento comparativo de alimentación entre insectívoros solitarios y en bandadas en una selva Neotropical: es una cuestión de vulnerabilidad?** – Las bandadas mixtas de especies de aves insectívoras son una característica común en las selvas tropicales. Dos hipótesis han sido propuestas para explicar este comportamiento social: mejorar la obtención del alimento y la defensa antipredatoria. Este trabajo señala el comportamiento alimenticio y la selección del hábitat de especies en bandadas vs especies solitarias, para evaluar si su vulnerabilidad respectiva a los predadores podría estar relacionada con su facilidad a formar bandadas. Cuando las aves se están alimentando, su mayor vulnerabilidad es su visibilidad, su grado de vigilancia y la protección u ocultamiento provisto por la vegetación que las rodea. Seleccioné los 37 insectívoros más comunes y representativos de una selva lluviosa Neotropical y los dividí en tres grupos iguales según su grado de formar bandadas. Durante 944 ataques > 1 min, medí la detectabilidad y vigilancia de aves individuales. Comparadas con las aves que se alimentan solitarias o participan ocasionalmente en bandadas, las especies obligadas a bandadas fueron más detectables, menos vigilantes y más fácil de ser susceptibles a ataques por predadores. Ellas usaron técnicas más activas de forrajeo que fueron menos compatibles con la vigilancia sostenida y más conspicuas. Ellas también usaron sustratos menos protegidos y de un nivel riesgoso medio. De tales sitios de forrajeo, ninguno apareció suficientemente abierto para permitir un radio seguro de detección y escape, ni bastante denso que provea inaccesibilidad, ocultamiento o refugio. Los resultados sugieren que la aparente vulnerabilidad a la predación de al menos miembros obligados de bandadas puede ser determinante, más que una mera consecuencia o su comportamiento de bandada. Las bandadas pueden dar la protección antipredador necesaria para ellas para usar sin peligro su riesgoso comportamiento de forrajeo y hábitat. En resumen, los forrajeadores solitarios pueden tener sitios de forrajeo y comportamiento seguro, comparados con las especies obligadas a bandadas, las cuales deben forrajear en bandadas para retener el síndrome de comportamiento de riesgo, mientras los eventuales podrían tener comportamientos intermedios o adaptables y de esta manera variables, pero no beneficios esenciales para unirse en bandadas.

Abstract. – Mixed-species flocks of insectivorous birds are a common feature of tropical forests. Two hypotheses have been proposed to explain this social behavior: feeding enhancement and antipredator defense. This paper points out the comparative foraging behavior and habitat selection of flocking vs solitary species, to assess whether their respective vulnerability to predators could be related to their flocking propensity. When birds are foraging, their major components of vulnerability are their conspicuousness, their degree of vigilance and the protection or concealment provided by the surrounding vegetation. I selected the 37 most common and representative insectivores of a primary Neotropical rain forest understory and divided them into three equal groups according to their flocking propensity. During 944 continuous > 1-min feeding bouts, I measured the detectability and vigilance of individual birds. Compared to solitary foragers or occasional flock participants, obligate flock members were more detectable, less vigi-

lant, and more likely to be susceptible to attacks by stalking predators. They used more active foraging techniques that were both less compatible with sustained vigilance and made them more conspicuous. They also used less protective substrates and the more risky mid-level of open understory. Such foraging sites looked neither open enough to allow a safe radius of detection and escape, nor dense enough to provide inaccessibility, concealment, or refuge. The results suggested that the apparent vulnerability to predation of at least obligate flock members may be a determinant, more than a mere consequence, of their flocking behavior. Flocking may afford the antipredator protection necessary for them to use safely enough their risky foraging behaviors and habitats. In short, solitary foragers would have relatively safe foraging sites and behaviors, compared to obligate flock species which should forage in flocks to retain their risky behavioral syndrome, while facultative attendants may have intermediate or adaptable behaviors and thus derive variable, but not essential benefits from joining flocks. *Accepted 22 July 2002.*

Key words: Neotropics, rain forest, foraging, mixed-species flocking, predation risk, vigilance, vulnerability.

INTRODUCTION

Feeding in flocks is a widespread behavior among animals, especially birds (Barnard 1983, Morse 1985, Faaborg 1988). How foraging birds may increase their fitness by joining flocks in spite of increased costs due to higher detectability and competition has stirred intense debates (Pulliam 1973, Powell 1974, Bertram 1978, Hutto 1987, Terborgh 1990).

Two major hypotheses have been proposed. The first one claims that flocking may enhance predator avoidance from an earlier detection and warning of predators through cumulative vigilance of several individuals. Additional benefits may be derived from a higher potential for mobbing predators, from a confusion and dilution effect during attacks or from a patchy distribution reducing encounter rates with predators (Willis 1973, Curio 1976, Morse 1977, Elgar 1989). The second hypothesis postulates that birds in flocks may derive feeding benefits from reduced scanning rates and more time spent searching for food (Lazarus 1972, Powell 1985, Popp 1988), from cryptic prey displaced by neighbors, if not kleptoparasitism (Brosset 1969, Erard 1987), and from facilitation of food finding through information transfer, such as following successful individ-

uals, learning foraging techniques, substrates or patch quality and minimizing duplication effects (Krebs 1973, Krebs & Davies 1987, Ekman & Hake 1988, Sasvari 1992, Master *et al.* 1993, Giraldeau *et al.* 1994).

There are many types of flocking behaviors that may have different origins, determinants and functions. Most studies have considered monospecific groups in open habitats (e.g., Caraco 1979, Popp 1988, Cresswell 1994) or winter flocks of tits in temperate forests (e.g., Morse 1970, 1977, Ekman 1979, 1987, Smith & Buskirk 1988, Rollfinke & Yahner 1991, Suhonen 1993). In tropical forests, beside monospecific social groups, multispecific associations of foraging birds range from large canopy flocks to opportunistic aggregations of frugivores and specialized army ant followers at ground level (Moynihan 1962, Buskirk 1976, Willis & Oniki 1978, Thiollay & Jullien 1998). I shall concentrate here on the permanent mixed species flocks of insectivores in mid-understory levels of tropical forests (Buskirk *et al.* 1972, Wiley 1980, Munn 1985, Munn & Terborgh 1979, Graves & Gotelli 1993, Stotz 1993, Poulsen 1996, Jullien & Thiollay 1998). Previous authors, personal experience and a local study (Thiollay & Jullien 1998) have all shown that understory Neotropical forest insectivorous species can be divided into species that 1) either rarely if

ever join mixed flocks, or 2) occasionally and even consistently do so, but still also forage on their own, or 3) are obligate members of such flocks, almost never foraging alone. Is there any common trait whose variation among the three groups would explain this behavioral difference? The feeding behavior of obligate flock members will be compared with that of species only occasionally joining such flocks and with solitary foragers. The aim of this study is not to test directly the antipredator value of flocking behavior but to emphasize the behavioral characteristics of species foraging in flocks compared to those of solitary species using similar resources in the same habitat. The working hypothesis was that species or individuals whose foraging behavior and/or habitat structure made them most vulnerable to predators should forage in flocks, whereas species least vulnerable or individuals in low-risk situations could avoid the costs of flocking and adopt solitary foraging habits.

The risk of predation, or vulnerability to predators, may arise from three interrelated factors: 1) Conspicuousness of foraging behavior: in the gloomy rainforest understory, movements make birds often more conspicuous than do size or color pattern; 2) Degree of vigilance: interspecific differences may come from the relative ability to be vigilant when actually foraging; if scanning and searching for prey are incompatible, a bird becomes vulnerable when it forages and vigilance periods are at the expense of foraging time; 3) Safety of habitat structure: a bird is presumably less vulnerable either in a dense vegetation that provides concealment and refuge, or in an open forest because of an increased detection distance. Such relationships between foraging behavior, exposure of foraging sites, habitat structure or degree of vigilance and flocking tendency have already been stressed mostly in temperate passerines (Barnard & Stephens 1983, Ekman 1987,

Keys & Dugatkin 1990, Lima & Dill 1990, Suhonen 1993, Cimprich & Grubb 1994, Farnshaw 1995). If flocking was primarily an antipredator defence, it should increase in cases of higher conspicuousness, lower vigilance, and/or lack of concealment. As a working hypothesis, I tested the influence of habitat selection and behavioral characteristics of different species on their flocking propensity in a tropical rain forest where foraging in mixed flocks was prominent.

METHODS

Study area

All data were obtained in the Nouragues Natural Reserve, 100 km south of Cayenne, French Guiana (04°05'N-52°41'W). The area was uniformly covered with primary lowland (50–200 m a.s.l.) tropical rain forest. The study area was described in Thiollay (1989), the bird community in Thiollay (1994), the different categories of feeding associations in Thiollay & Jullien (1998), the social and foraging behaviors of mixed flocks in Jullien & Thiollay (1998) and the diurnal raptor community, including the most significant predators of adult birds at least by day, in Thiollay (1989). An undulating relief and numerous small streams (mean annual rainfall: 3500 mm) diversified the forest types. The dominant 40–50 m high mature forest with an open understory, on well drained slopes and plateaus, often gave way to naturally disturbed stands with lower, more irregular and denser undergrowth (Table 1). Tree fall gaps and palm swamps were not sampled because they were rarely used by local flocks.

Species selection

I selected, among the local forest bird community, as many as possible common, small to medium-sized, primary forest understory insectivores (37 species), representative of the main foraging techniques, substrates and

TABLE 1. Main habitat and foraging behavior of solitary foragers (overall occurrence in mixed flocks in the study area = 0–11%, Thiollay & Jullien 1998).

Group F ₀	Sample ^a	Habitat ^b	Foraging ^c	Speed ^d
White-tailed Trogon (<i>Trogon viridis</i>)	86(14)	A 3	Strike-foliage	Still 1 (0.1)
Blue-crowned Motmot (<i>Momotus momota</i>)	113(14)	A 2	Strike-litter	Still 1 (0.3)
Yellow-billed Jacamar (<i>Galbula albirostris</i>)	139(14)	A 2	Sally-air	Still 1 (0.2)
White-chested Puffbird (<i>Malacoptila fusca</i>)	63 (10)	A 2	Sally-air	Still 1 (< 0.1)
Mouse-colored Antshrike (<i>Thamnophilus murinus</i>)	57 (21)	B 3	Glean-foliage	Active 1 (6.7)
Warbling Antbird (<i>Hypocnemis cantator</i>)	91 (53)	B 1	Glean-foliage	Active 2 (7.0)
Spot-winged Antbird (<i>Pernostola leucostigma</i>)	18 (11)	B 1	Glean-litter	Active 1 (3.3)
Spot-backed Antbird (<i>Hylophylax naevia</i>)	33 (19)	B 1	Glean-litter	Active 1 (1.9)
Scale-backed Antbird (<i>Hylophylax poecilonota</i>)	68 (20)	A 1	Strike-litter	Still 2 (0.7)
Golden-crowned Spadebill (<i>Platyrrinchus coronatus</i>)	25 (10)	A 2	Strike-foliage	Still 2 (0.3)
Ruddy-tailed Flycatcher (<i>Terenotriccus erythrurus</i>)	32 (15)	B 3	Sally-air	Still 2 (0.7)
Collared Gnatwren (<i>Microbates collaris</i>)	20 (12)	B 1	Glean-litter	Active 3 (14.4)

^aContinuous foraging periods measured: cumulative length in min (number of bouts involved).

^bForest type and openness: A = high mature forest with open understory and closed canopy; B = moderately disturbed and denser stands + small gaps; C = low dense stands with vine tangles and broken canopy. Height of foraging birds: 1 = < 2 m; 2 = 2–10 m; 3 = (4)10–25 m

^cMain prey capture techniques (see text). Substrates: Foliage = leaves and branchlets; tangles = vine tangles and dense branches or lianas; epiphytes = from mosses to bromeliads and/or clumps of dead leaves; litter includes ground cover and low vegetation; air: flying insects; bark = on branches or trunks and any dead wood from twigs to logs.

^dStill: 1 = slow (= 1 move/min); 2 = quick (2–6 moves/min); Active: 1 = slow (4–10 moves/min); 2 = moderate speed (12–18 moves/min); 3 = fast (= 20 moves/min). In parentheses = hops/flights ratio. See methods for additional definitions.

microhabitat uses, and for which I obtained >10 suitable foraging records. These species were divided into 3 sets according to their flocking propensity, i.e., the proportion of all foraging individuals of each species observed in mixed flocks in a previous large sample of randomly encountered birds (data in Thiollay & Jullien 1998): group F₀ = 12 species rarely if ever joining flocks; group F₁ = 13 occasional, if not regular participants in mixed flocks, but also often feeding alone; group F₂ = 12 obligate understory flock members foraging almost only in association with mixed flocks (see Tables 1–3). A flock was defined as a lasting aggregation of > 5 individuals of > 2 species, and only the permanent mixed-species flocks of insectivores in the forest understory were considered (Jullien & Thiollay 1998).

The taxa sampled included the most regular insectivores seen at mid-level of this primary forest understory. All terrestrial species, woodpeckers, and canopy birds were excluded. Other candidates were too rare or elusive. Only in 2 species, a woodcreeper and an antwren, was the sample suitable to compare birds foraging alone and in flocks.

Sampling technique

I searched for birds by walking slowly through the forest over an area of several hundred hectares during 2 years. Different areas were surveyed on successive days, between sunrise and sunset during the main breeding seasons (February–April and September–November 1993–1994, Tostain *et al.* 1992). Because searches were at random, over

TABLE 2. Foraging behavior of occasional flocks participants (occurrence in mixed flocks: 22–55%).

Group F ₁	Sample ^a	Habitat ^b	Foraging ^c	Speed ^d
Black Nunbird (<i>Monasa atru</i>)	68 (13)	A 3	Strike-foliage	Still 1 (0.1)
Ruddy Foliage-gleaner (<i>Automolus rubiginosus</i>)	21 (10)	C 1	Search-litter	Active 2 (18.8)
Wedge-billed Woodcreeper (<i>Glyphorhynchus spirurus</i>)	42 (30)	A 3	Search-bark	Active 3 (14.5)
Fasciated Antshrike (<i>Cymbilaimus lineatus</i>)	33 (18)	C 2	Glean-tangles	Active 1 (15.7)
Amazonian Antshrike (<i>Thamnophilus amazonicus</i>)	30 (14)	C 2	Glean-tangles	Active 2 (11.0)
Rufous-bellied Antwren (<i>Myrmotberula guttata</i>)	49 (30)	A 1	Glean-litter	Active 2 (5.7)
Dot-winged Antwren (<i>Microrhopias quixensis</i>)	19 (12)	C 2	Glean-tangles	Active 3 (13.3)
Gray Antbird (<i>Cercomacra cinerascens</i>)	31 (17)	B 3	Glean-tangles	Active 2 (16.9)
McConnell's Flycatcher (<i>Mionectes macconnelli</i>)	35 (15)	A 1	Sally-air	Still 2 (0.7)
Olivaceous Flatbill (<i>Rhynchocyclus olivaceus</i>)	17 (10)	A 3	Strike-foliage	Still 2 (0.3)
Coraya Wren (<i>Thryothorus coraya</i>)	23 (15)	C 2	Glean-tangles	Active 3 (33.6)
Long-billed Gnatwren (<i>Ramphocaenus melanurus</i>)	22 (11)	B 3	Glean-tangles	Active 3 (43.7)
Fulvous-crested Tanager (<i>Tachyphonus surinamus</i>)	25 (13)	B 3	Glean-foliage	Active 1 (2.1)

^{a-d}see Table 1.

the whole area, crossing all forest types and recording any bird encountered, I assumed that existing habitat types, flock sizes and behaviors were adequately represented in the overall sample of foraging bouts. If conspicuous birds were more readily detected, then this applied to all three categories.

Only actively foraging birds, that did not appear to be aware of, or distracted from foraging by my presence, were selected and then used as focal individuals (Altmann 1974) followed as long as possible. Records of foraging events, using 10 x 42 binoculars, tape recorder, and digital stopwatch, began = 5 s after the individual was detected. Observations lasted = 60 s, and ceased when the bird departed, or became not fully visible, or stopped foraging (e.g., resting, preening, calling, interacted with other birds or manipulated a prey item for > 10 s). Scanning and = 10 s handling prey were included in foraging periods. No bird was recorded around abundant food sources (e.g., army ants, insect swarms), or in large canopy gaps, or in unusual situations, or when moving exceptionally fast or slowly. Every contact of a same species was both in widely spaced areas

(> 200 m apart) and on different days. This minimized the risk to record twice the same individual, and I assumed that samples were reasonably independent.

Eventually, a subset of 944 foraging periods (1921 min), all fitting the above restrictive conditions, was used to analyze the behavior of 37 species. Sample periods lasted 200–1800 s for large sit-and-wait predators and 60–240 s for other taxa. Habitat variables, position of the bird, flock size, visibility and foraging behavior were recorded once at the beginning of each individual sampling period, while movements, scans, prey attacks, substrate used and prey size were counted over all the observation period. Only birds in adult plumage were recorded, pooling males and females. All durations were in seconds.

Habitat and foraging behavior

For each observation period, I recorded 10 variables including habitat type, height of bird, capture technique and substrate, duration (s), number and length of moves, number of attacks, prey size and handling time. Three forest types were defined (see Table 1, and Thiollay 1994), as well as three levels of

TABLE 3. Foraging behavior of obligate flock members (occurrence in mixed flocks: 92-100%).

Group F ₂	Sample ^a	Habitat ^b	Foraging ^c	Speed ^d
Rufous-rumped Foliage-gleaner (<i>Philydor erythro-</i> <i>cercus</i>)	98 (71)	A 3	Search-epiphytes	Active 2 (12.7)
Olive-backed Foliage-gleaner (<i>Automolus infusca-</i> <i>tus</i>)	42 (27)	A 3	Search-epiphytes	Active 2 (11.3)
Plain Xenops (<i>Xenops minutus</i>)	28 (18)	A 3	Search-twigs	Active 3 (9.1)
Chestnut-rumped Woodcreeper (<i>Xiphorhynchus</i> <i>pardalotus</i>)	46 (33)	A 3	Search-bark	Active 3 (23.7)
Curve-billed Scythebill (<i>Campyloramphus procur-</i> <i>voides</i>)	22 (13)	A 3	Search-bark	Active 3 (14.5)
Dusky-throated Antshrike (<i>Thamnomanes ardesia-</i> <i>cus</i>)	68 (43)	A 3	Strike-foliage	Still 2 (0.8)
Cinereous Antshrike (<i>Thamnomanes caesius</i>)	119(74)	A 3	Strike-foliage	Still 2 (0.6)
Brown-bellied Antshrike (<i>Myrmotherula gutturalis</i>)	66 (45)	A 3	Search-dead leaves	Active 2 (7.9)
White-flanked Antwren (<i>Myrmotherula axillaris</i>)	53 (41)	A 3	Glean-foliage	Active 3 (9.9)
Long-winged Antwren (<i>Myrmotherula longipennis</i>)	101(79)	A 3	Glean-foliage	Active 3 (8.9)
Gray Antwren (<i>Myrmotherula menetriesii</i>)	85 (59)	A 3	Glean-foliage	Active 3 (12.3)
Sulphur-rumped Flycatcher (<i>Myiobius barbatus</i>)	33 (20)	A 3	Glean-foliage	Active 2 (3.3)

^{a-d}see Table 1.

foraging height which separated species foraging always low (< 2 m), at mid-level (2–10 m) or usually higher (4–25 m). Two basic foraging behaviors were defined according to prey capture maneuvers and substrates (Table 1): still-hunting, i.e., sit-and-wait from a perch (strike, sally), and active-hunting, i.e., continuous foraging with rapid movements and short stops (glean, search). Gleaning implied moving constantly in vegetation and picking up arthropods on foliage, bark or litter; it also included hanging, snatching, sweeping foliage or chasing disturbed insects. Searching included closely inspecting, probing, pecking or tearing wood, bark, epiphytes or dead leaves. Striking implied perch to substrate pounce or hover-glean; it also included kleptoparasitism. Sallying involved aerial hawking insects from a perch. Foraging moves, involving perch changes, were divided into hops (< 1 m), short flights (1–5 m) and long flights (> 5 m). Their mean duration was estimated to be 0.3, 0.6 and 1.5 s respectively. Still- and

active-hunting were divided into low and high speed classes according to the number of moves per min (Table 1). Prey attacks included both unsuccessful attempts and captures, divided into short (glean, snatch, peck) and long attacks (strike, sally, probe, chase, hover), using an average duration of 1 and 2 s respectively, including quick small insect swallowing. Only prey handling lasting 1–10 s were timed. Longer periods were excluded from measured foraging bouts. Prey sizes were classified as small and large, i.e., shorter and longer than bill length, a simple measurement better correlated with the bird's handling ability than the absolute prey length.

Conspicuousness and vigilance

Six summary variables, likely to affect the conspicuousness and the vigilance of a foraging bird, were computed for each individual sample.

Visibility. An index of visibility (VIS) assessed

the focal bird's detectability for a potential predator according to habitat density, vegetation structure and substrate type. Along six perpendicular axes (four in a plane parallel to the ground, one above and one below the bird), I scored the average distance between the bird and the first obstacle (vegetation item) likely to obscure it (0 = < 1 m; 1 = 1–5 m; 2 = > 5 m). All six scores summed, the index ranged from 0 (fully hidden birds) to 12 (completely exposed individuals). This was an indicator of concealment or accessibility: a branch or foliage may hide a bird or impair the possibility for a predator to attack it from this side, while a trunk or the ground prevent detection and access on one side. So the bird becomes vulnerable only from open sides, or it may be visible (e.g., through vine tangles), but difficult to reach, while still able to see approaching predators.

Velocity (VEL) or foraging speed. Was the number of moves (hops + flights) per minute. The detectability of a bird is expected to increase with the frequency of its movements, but, at the same time, its effective vigilance may be reduced since flying precludes attentiveness.

Foraging success (SUC) or attack rate. Was the number of prey capture attempts per minute, in addition to other moves. Prey attacks are noteworthy in the perspective of both the feeding enhancement hypothesis of flocking, and its antipredator advantages because prey attacks and manipulations may focus the bird's attention and reduce its vigilance even more than other foraging movements.

Percentage of time spent moving (MOVE). Hops + flights only were summed after being multiplied by their respective fixed duration.

Percentage of time spent searching for prey (SEARCH). This included prey attacks and

handling, any substrate inspection or manipulation (e.g., probing, tearing, pecking) and periods during which the bill was consistently close to, or directed toward a substrate that was also blocking view in that direction. Such restrictive criteria probably underestimated actual searching time. In those species where searching was easier to identify and measure than scanning, it was used as the basis for the proportion of time spent, together with MOVE, and SCAN was then estimated as the complement to 100%.

Percentage of time spent scanning or watching, supposedly for predators (SCAN). For birds foraging actively, it was sometimes possible to count the number of actual scans, when the bird stopped, the bill pointed upward or away from the nearest substrate. Such stops were divided into short (fixed average = 0.6 s) and long scans (> 1 s, then accurately timed). However, it was usually impossible to differentiate between true vigilance (scanning for predators) and looking for prey, foraging sites, next perches or surveillance of flockmates. Therefore, unless intentional scans could be clearly identified and timed, scanning included all stops or sit-and-wait activities that could allow some antipredator vigilance, even if it was not their main purpose. As a result, whereas SEARCH values may be conservative, actual SCAN often tended to be overestimated. In short, VIS was a variable that referred only to conspicuousness, SEARCH decreased and SCAN increased the vigilance rate, whereas VEL, SUC and MOVE all affected both conspicuousness and vigilance.

Data analysis

The descriptive habitat and foraging parameters characterized the foraging environment and behavior of species that were originally placed in groups on the basis of their flocking propensity alone. On the other hand, the six

summary variables (VIS to SCAN) were intended to look for differences in the assumed vulnerability to predators of the species in each group, using the implied degree of conspicuousness and the likely loss of vigilance as indicators of vulnerability.

I used species as independent statistical units although this assumption may not be true because some species within a group (especially F_2) were phylogenetically related (even congeners) and they tended to forage under quite similar conditions. Therefore their behavior may not be independent from a statistical point of view and this may produce a pseudo-replication effect. However, I have not statistically controlled for this phylogenetic effect because the main bird families were represented in all three groups (Thamnophilidae, Tyrannidae) or present in two of them (Dendrocolaptidae, Furnariidae) and the relative importance of different families within the subset of species studied was not different from that found in the whole insectivorous, arboreal, understory bird community of the study area (Thiollay 1994).

Variables used were an index (VIS), frequencies (VEL, SUC) or proportions (percent of total time spent: MOVE, SEARCH, SCAN) to weight foraging bouts of different lengths equally. However, by that very fact, VEL, MOVE, SEARCH and SCAN were intercorrelated. I did not attempt to reduce the number of variables, e.g., to principal component scores, because the main goal was to investigate the relative importance of these factors individually. MOVE, SEARCH and SCAN were used as dependent variables in univariate factorial ANOVAs, with VIS or VEL as factors. In parametric tests, VEL and VIS were log transformed, SUC was $\log(x + 1)$ transformed because of zero scores and MOVE, SEARCH and SCAN were arc-sine square root transformed. Normality and homoscedasticity of transformed data were

confirmed through Kolmogorov-Smirnov goodness-of-fit and Bartlett tests respectively (Sokal & Rohlf 1981). When successive univariate tests were conducted, I used a Bonferroni adjustment of the P value and a significance level of $P < 0.01$. Generalized linear models were used with individual observations as random effects, flocking categories as fixed effects (no pseudo-replications) and Tukey's test for post-hoc testing to explore factors affecting vulnerability, as well as Spearman's correlation coefficients on untransformed data. Logistic regressions of non-intercorrelated factors with flocking category as the dependent variable were used to assess the determinants of flocking propensity. All tests were two-tailed, all means were ± 1 SD, and minimum levels of significance were set at $P < 0.05$.

RESULTS

Habitat use. Six of the 12 solitary foragers were found in the most open of the three forest understory types (high mature, Table 1), while the 6 other species were chiefly recorded in stands of intermediate density.

The 13 species of occasional flock participants (Table 2) were distributed in all forest types and heights, but they included the only species (5) in our sample which were associated with the densest forest (C). In contrast, all the obligate flock members (Table 3) typically occurred at mid or upper level (class 3) of open understory, although they also used occasionally denser forest types. So, the proportion of species using the most open forest understory (A) and its highest level (3) increased with flocking propensity (8, 23 and 100% from group F_0 to F_2).

Even stronger differences appeared among groups in foraging substrates. Air and litter were used only by solitary foragers or occasional flock members (Tables 1 and 2), whereas almost all epiphyte, bark or twig

searchers and most foliage gleaners were found among obligate flock members (Table 3).

Foraging speed. The most active foragers (speed 2 and 3, Table 1) were few in group F_0 (2/12 species), numerous in F_1 (8/13) and included all the F_2 species (Table 3), except the Dusky-throated (*Thamnomanes ardesiacus*) and Cinereous (*T. caesius*) Antshrikes. The latter, only perch-hunting foragers among obligate flock members, were in fact kleptoparasites, mostly foraging on prey disturbed or caught by other species. They had also to move very often to follow their flock mates. Conversely, still hunting, which involved infrequent perch changes ($< 6/\text{min}$ on average), was found only among F_0 , and to a lesser extent, F_1 species (Tables 1 and 2).

Foraging behavior. Hunting techniques paralleled the above trends. Catching prey by strikes (on trees or litter) or aerial sallies was common in F_0 species (7/12), rare in F_1 (3/13) and restricted to the atypical *Thamnomanes* in F_2 . Conversely, the proportion of species using the most active techniques (gleaning and searching) was twice higher among the 12 obligate flocking species ($n = 10$) than among solitary foragers ($n = 5$).

The hops/flights ratio, that was related to both foraging method, density of vegetation and the kind of substrate, was highly variable between species in all three groups and no trend emerged. The percentage of relatively large prey in the set of observed captures was similar also between the three groups ($25.5\text{--}25.9 \pm 16.2\text{--}22.7\%$)

Detectability and flocking propensity. The larger (100–250 g) and only brightly colored taxa in our species set (*Trogon*, *Momotus*, *Galbula*) were solitary foragers, and they appeared very quiet and inconspicuous in their natural setting. The distribution of species among six

classes of \log_2 body masses (2 = 8–16 g, to 6 = 128–256 g, Thiollay 1994) did not differ among the three groups (Kruskal-Wallis ANOVA, $df = 2$, $H = 0.254$, $P = 0.880$).

It was difficult to estimate the relative importance of the frequency of movements (VEL) vs the visibility index (VIS) on the actual detectability (or conspicuousness) of a bird to a visually searching predator. VEL, that was directly related to the foraging behavior, was much lower ($F_{1,942} = 286.6$, $P < 0.001$) for sit-and-wait foragers (strickers = 2.9 ± 2.3 and sallyers = 2.5 ± 2.4 movements/min) than for active foragers (searchers = 21.9 ± 11.8 , gleaners = 17.5 ± 9.2). From the way VIS was measured, it was dependent upon habitat and substrate types. It decreased significantly ($F = 91.3$, $P < 0.001$) from mature open understory (6.9 ± 1.3) to low dense forest (1.9 ± 0.5), but not with increasing height above ground, where VIS ranged from 4.9 ± 1.6 to 6.0 ± 1.6 ($P = 0.435$). Of course, significant differences ($P < 0.001$) occurred among substrates used, where mean VIS indices ranged from 2.1 ± 1.0 in dense tangles to 7.5 ± 2.1 on the open perches of flycatchers. As a result, the mean species velocity increased sharply from solitary to obligate flock foragers (VEL = 7.0 ± 6.7 to 17.5 ± 11.0 moves/min, $F_{2,941} = 114.1$, $P = 0.001$). The mean index of visibility (VIS) varied widely among solitary and opportunistic foragers, but it was consistently high among obligate flock members (6.7 ± 1.6) and significantly higher than among occasional on non flocking taxa ($F_{2,941} = 120.2$, $P < 0.001$).

Vigilance ability and flocking behavior. When they are foraging, birds may be able to look at the same time for predators (vigilance) provided they are neither moving, nor manipulating or closely investigating a substrate. Thus, the proportion of time spent moving (MOVE) and searching (SEARCH) is expected to be

inversely correlated with vigilance. Scanning (SCAN), a straightforward measure of vigilance, was indeed negatively correlated with SEARCH, VEL and MOVE (Pearson's coefficient $r_s = -0.72$ to -0.99 , $P < 0.01$). Therefore frequent foraging movements or substrate searching may considerably lower the rate of vigilance.

All foraging behaviors pooled, mean SEARCH time increased significantly ($F_{2,941} = 345.5$, $P < 0.001$) from solitary foragers ($4.1 \pm 3.9\%$) to occasional (24.9 ± 26.4) and obligate flock members (62.0 ± 34.8), as did MOVE (from 5.0 ± 3.6 to 11.1 ± 5.7 , $F = 88.4$, $P < 0.001$), whereas SCAN decreased ($F = 332.0$, $P < 0.001$) respectively from 90.8 ± 7.7 to 65.5 ± 31.0 and $26.7 \pm 38.2\%$. Results would have been even more striking if species that have odd behaviors (*Thamnomanes* and *Myio-bius* in species group F_2 , see Appendix 1) had been excluded. This result is a consequence of the much higher proportion of both fast active gleaners and substrate searchers in flocking than solitary foraging birds. Among gleaners alone, search time increased and scanning decreased from solitary foragers to flock members.

Foraging success and flocking behavior. According to the feeding enhancement hypothesis of flocking, an increased foraging success (number of prey capture per min of active foraging time, SUC), and/or a decrease in the variance of feeding rate should be the main benefits and determinants of flocking. This rate, however, was difficult to interpret and compare between species because of its expected relationships with prey type, size, energy content and availability as well as predator body size and requirements.

Foraging success was inversely correlated with body size ($r = -0.123$, $t = -4.325$, $P < 0.001$). Gleaners had a significantly higher mean SUC (0.67 ± 0.57) than any other type of foragers (0.41 ± 0.38 to 0.54 ± 0.52 , t-tests,

$P < 0.005$), whereas there was no significant differences between the success rates of species pouncing, flycatching or searching ($P = 0.058$ to 0.329). Species foraging on foliage (0.70 ± 0.58) and bark (0.62 ± 0.60) had a higher SUC than those using any other substrates (0.39 to 0.49) and significantly so (t-tests, $P = 0.0002$ and 0.0132 respectively). Overall, the mean foraging success increased from solitary foragers (0.44 ± 0.47) to flock members (0.67 ± 0.55 , $F_{2,941} = 15.7$, $P < 0.001$) in parallel with the increasing proportion of small foliage gleaners and bark searchers.

Intraspecific differences between solitary and flock foraging. Only two species provided enough observation samples in contrasting situations, i.e., when they were foraging either associated with a multispecies flock or solitarily. The Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) occurred in most flocks but also regularly foraged independently, whereas the White-flanked Antwren (*Myrmotherula axillaris*) was an almost obligate flock member, rarely foraging in isolated pairs.

Within each species separately, the mean value of each variable was compared between flock and solitary foraging bouts (ANOVAs, Fig. 1). The woodcreeper exhibited no significant difference of its conspicuousness (VIS), foraging speed (VEL) and success rate (SUC) when foraging alone compared to foraging in flocks. Only its scan rate (SCAN) was significantly lower in flocks (-44%). For this species, joining opportunistically encountered flocks, social foraging apparently did not result in a decisive improvement of its foraging conditions. Conversely, the Antwren seemed to benefit more strongly from its association with flocks where it foraged faster (VEL = $+41\%$), in significantly more exposed sites (VIS = $+66\%$), and where it was less vigilant (SCAN = -21%) than when foraging alone (Fig. 1).

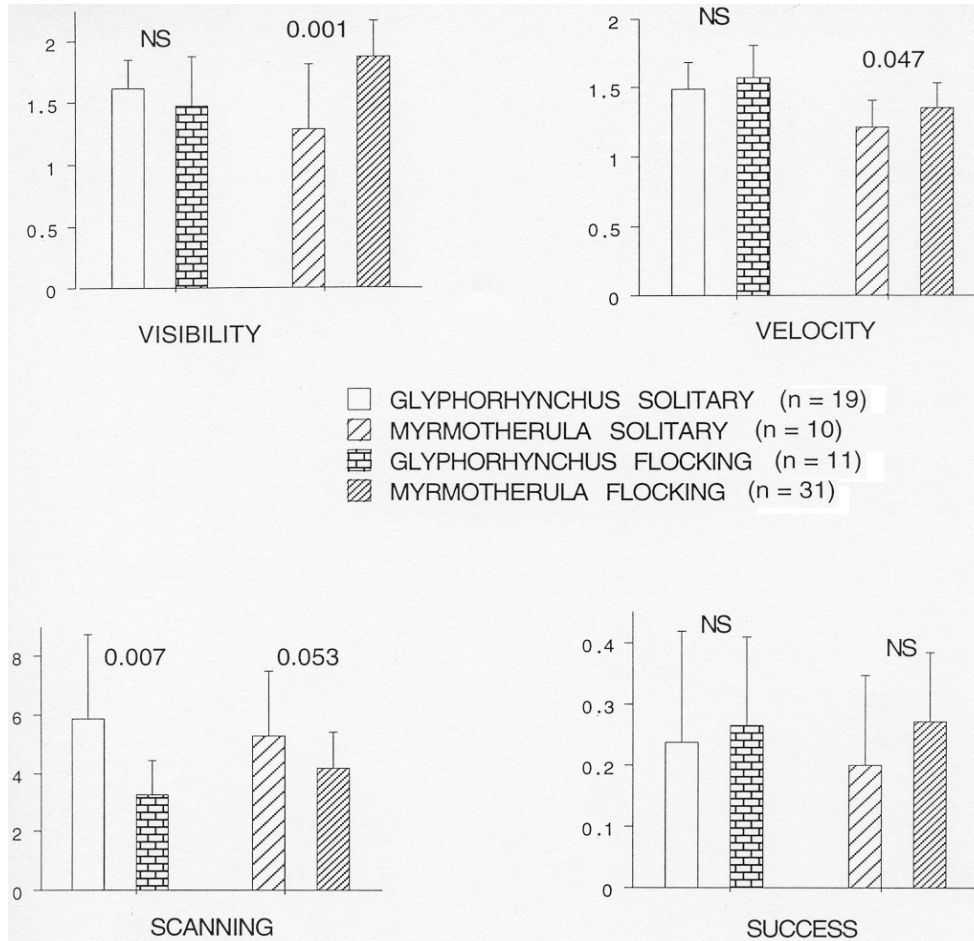


FIG 1. Intraspecific differences of the visibility index, foraging velocity, success rate, and scanning frequency of the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and the White-flanked Antwren (*Myrmotherula axillaris*) foraging either solitarily or in mixed flocks. Mean values \pm 1 SD. VEL, VIS and SUC are log-transformed. P values of the differences between solitary and flock foraging (ANOVAs) are given. NS = $P > 0.05$.

General correlates of flocking propensity. Using flocking category as the independent variable in a generalized linear model and pooling all species within groups, each of the six factors measured differed significantly between obligate, facultative and non flock members (ANOVA, $P < 0.001$). Foraging success (SUC), however, had a lower F ratio than VIS or VEL (15 vs 113–164), and MOVE had a

lower F value than SEARCH or SCAN (88 vs 336–351). All interactions between any of the VIS, VEL, SUC, SEARCH and SCAN factors were also highly significant ($F = 70$ –112, $df = 6$ –10, $P < 0.001$, Wilks Lambda = 0.42–0.67).

In a multiple logistic regression of VIS, VEL and SUC on flocking category, the overall coefficient of determination (R^2) was

0.280, but only VIS and VEL were significant ($c^2 = 250\text{--}340$, $P < 0.001$) and not SUC ($c^2 = 0.104$). Separately, MOVE, SEARCH and SCAN were also highly significant ($c^2 = 199\text{--}518$), but R^2 was lower for MOVE (0.106) than for SEARCH and SCAN (0.263–0.276).

In summary, the syndrome of at least obligate flocking is the conjunction of a more active foraging behavior than non flocking species (frequency of movements and/or substrate searching), in more exposed situations (density of the surrounding vegetation) and a lower vigilance (scanning rate).

DISCUSSION

There are many forms of flocking even in tropical forests alone (Thiollay & Jullien 1998), each of them with possibly different causes and consequences. Our results and interpretations here only refer to mixed-species flocks of insectivores in the understory of lowland Neotropical forests, one of the most permanent and highly evolved type of flocking.

For the flocking behavior to evolve, benefits must outweigh costs. This study could not, and no other study has yet measured and combined all the possible benefits and costs of flocking. Some benefits (e.g., feeding enhancement) may be more immediate and easily measurable than others (e.g., antipredator protection), though the former are not necessarily more determinant than the latter. Benefits also can be either root causes or mere consequences of feeding associations. The sit-and-wait or slow foraging behavior, or the semi-terrestrial habits, or the use of dense vegetation, or a small territory size, typical of non-flocking species, may be either simply not compatible with the speed and range of foraging flocks, or they may be sufficient antipredator defenses to make flocking unnecessary or unprofitable (incurred costs).

Costs and benefits of flocking. Potential benefits in terms of feeding success were not the topic of this study. Any bird feeding in group may be expected to look at flock mates and thus may get information, may improve its foraging technique and feeding rates, or merely may be stimulated by movements of other birds. In Madagascar rain forest, for instance, several species increased their feeding rates and modified their foraging techniques in heterospecific flocks through mutualism and commensalism (Hino 1998). However, that at least some birds may improve their fitness by following more experienced foragers may be a mere opportunistic consequence of such associations and not the primary determinant of flocking.

Interspecific differences are difficult to interpret. Obligate flock members should derive the most critical benefit from their association with other birds. A less decisive advantage is expected in facultative flocking. Only two such species could be compared in contrasting situations. The Wedge-billed Woodcreeper was on average neither in more exposed sites, nor moving faster, nor more successful when foraging in flocks. It probably did not derive from this association a benefit decisive enough to consistently outweigh the costs incurred. Conversely, the White-flanked Antwren, a nearly obligate flock member, showed an obvious advantage in joining flocks where it used more exposed sites, moved faster, had a higher success and lower vigilance. The two antshrikes were a particular case: they obtained a large part of their food from insects flushed by flock mates or from kleptoparasitism. This may be a strong incentive for them to join flocks. Because of their slower foraging speed, high vigilance and loud calls, they could act as efficient sentinels and they were mainly responsible for the cohesion of the flocks (Jullien & Thiollay 1998), from which they may also get protection (the “many eyes” and “safety in

number” hypotheses). Other flock members suffered (moderately) from their parasitism, but this may have been far outweighed by the protection gained from these sentinels.

Obligate flock species, in our study area, had a higher survival rate than solitary and even facultative flock members (Jullien & Clobert 2000). During > 1000 h spent watching mixed flocks (Jullien & Thiollay 1998, and unpubl.), in this forest with a rich predator community (Thiollay 1989), raptor attacks were very rare (7 observed) and actual captures even rarer (2 records). So, there was no evidence that an increased detectability of flocks resulted in increased predation rate.

Within flocks, suggestions of serious intra on interspecific competition were almost absent (only brief and occasional cases of aggressive interference). Most flocks included a single pair of each species (Jullien & Thiollay 1998), and birds followed independent paths, using their specific foraging behaviors, substrates and prey types. Even the average risk of kleptoparasitism by antshrikes was low. Therefore, the real cost of flocking was likely to be minimal, unless some scramble competition occurred.

Vulnerability and vigilance. Foraging behavior may be related to antipredator defense in two ways: 1) the degree of conspicuousness of a foraging bird, and 2) the level of vigilance it can maintain while looking for prey. Additionally, habitat structure may influence both foraging behavior, conspicuousness and vigilance requirements. Morphology, especially body size, may also affect conspicuousness and even foraging behavior.

The conspicuousness, or detectability, has two components: active (frequency of movements, i.e., velocity) and passive (density of vegetation, i.e., visibility). A bird may be either concealed by vegetation and substrate and inaccessible to a predator (e.g., in vine tangles) or it may be in the open at a safe dis-

tance from any hide from where a predator could launch a surprise attack.. Therefore, both very open (high detection radius) or very dense (protective) vegetation may confer the lowest predation risk. The semi-open understory of primary forest is intermediate, and thus expected to be the most risky habitat. It may provide some protection if nearby refuges are available, but foraging birds remain visible and stalking predators are often concealed by trunks and dim light.

Frequent movements or substrate probing preclude, or at least reduce, vigilance, unless the bird stops to scan (loss of foraging time). On the contrary, perch hunting allows some antipredator vigilance while looking for prey. So, when velocity or searching increase, overt vigilance can only be accomplished at the expense of feeding (Lima & Bednekoff 1999). Birds are known to change their foraging behavior and habitat use and increase their vigilance rate under increasing predation risk (Lima 1982, Lendrem 1983, Lima & Dill 1990, Suhonen 1993, Barbosa 1997).

Flocking has well known antipredator advantages, such as high collective vigilance and efficient escape flights or freezing behaviors (Morse 1970, Pulliam 1973, Powell 1985, Elgar 1989, Master *et al.* 1993). Permanent tropical forest flocks have highly vigilant leaders and interspecific responsiveness to their mutual alarm calls (Jullien & Thiollay 1998). Observations of encounters between these mixed flocks and forest raptors (e.g., forest falcons, *Micrastur* spp.) also strongly suggested that flocks had a deterrent effect on predators which rarely tried to attack them, as already documented in an African rain forest (Thiollay 1984).

Behavioral correlates of flocking propensity. The presence, or fear of predators may constrain foraging behavior and/or foraging sites, and increase the tendency of birds to flock (Curio 1976, Morse 1977, Schneider 1984, Elgar

1989, Lima & Dill 1990, Suhonen 1993). This relationship was documented in temperate ecosystems but not yet in tropical forests, where the diversity, if not the density, of predators may be higher (Greene 1988).

It seems that the most regular mixed-species flock of insectivorous birds in tropical forest understories may share a unique set of foraging behaviors, substrates and/or microhabitats that make them more conspicuous or exposed and less vigilant than ecologically similar, but solitary foragers. This possibly higher susceptibility to predation could explain their strong association with mixed flocks because of the antipredator protection afforded by such flocks, and especially their sentinels. The hypothesis was supported by the consistent correlation between flocking propensity and expected determinants of vulnerability or predation risk.

The results suggest that, from solitary foragers to occasional and obligate flock members, the overall conspicuousness of birds increased significantly (decreasing concealment by surrounding vegetation, increasing habitat openness and frequency of movements), while their potential vigilance decreased (increasing proportion of foraging time spent moving and/or searching). On the contrary, species foraging always or regularly alone were either still or slow-moving hunters in open understory, or faster and frequently moving species in dense vegetation or low over the ground. In fact, most birds foraging out of flocks were almost always in pairs, an intermediate behavior between flocking and true solitariness. This is typical of many solitary species in tropical forests (pers. observ.) and is likely to provide an increased safety through shared vigilance and experience. Additionally, most of them had surprisingly secretive and inconspicuous behaviors.

A general theory. Predation events are very rarely observed in the field and the actual

threat from diversified predators (snakes, birds, mammals), or the fear they may inspire are difficult to quantify. So, the predation risk, behaviors roused by fear, or antipredator benefits, are difficult to assess and the related hypotheses are uneasy to test directly. Any feeding enhancement, from information transfer to increasing foraging success, can be a cause as well as a consequence of flocking. Hypotheses are only testable on facultative flock members whose behaviors should be compared in and out of flocks in similar environmental conditions. But how to deal with species that are always solitary foragers or obligate flock members? The contrasting behavioral syndromes of solitary and flocking foraging birds suggest a complementary explanation that may be called the vulnerability hypothesis, stated as follows.

Facultative flocking species would join flocks to benefit from the collective vigilance, and/or experience of flock mates. In doing so, they may reduce the time lost scanning, increase their feeding rate, and/or decrease their predation risk. Additionally, when foraging in flocks, they could adopt more vulnerable, but more successful behaviors, or they could use more dangerous microhabitats or prey types, while keeping below a safety threshold. When reversing to solitary foraging, they may tend to use more inconspicuous tactics and less exposed sites, reminiscent of antipredator adaptations. Permanent (obligate) flock members should stay in groups because their conspicuous and little vigilant foraging behavior and semi-open habitat would put them too much at risk, if they were foraging alone. I hypothesize that this foraging syndrome is fixed and not a mere consequence of being in the safety of a flock. For these obligate flock members, it would be the best, if not only alternative, to compensate for their unsafe foraging behaviors if they are actually unable to use different foraging strategies to do without protective sentinels.

Moreover, flocking would also allow them to use resources (microhabitats, substrates or prey types) not safely accessible to solitary foragers. This could give them a competitive advantage decisive enough to maintain their flocking behavior on an evolutionary time scale.

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APPENDIX 1. Indices of conspicuousness and vigilance in foraging birds. Means \pm SD from all observation periods. Visibility = cumulative detection distances of foraging individuals along six orthogonal directions (range = 0–12, see methods); velocity = number of hops + flights/min; success = number of capture attempts/min; move = % of total foraging time spent moving (hops + flights + capture attempts); search = % time spent searching (observing or manipulating substrate + handling prey); scan = % time spent scanning (stopped and looking around). Species are listed from group F₀ to F₂, as in Tables 1–3.

	Visibility	Velocity	Success	Move	Search	Scan
SOLITARY FORAGERS						
White-tailed Trogon (<i>Trogon viridis</i>)	6.9 \pm 1.0	0.7 \pm 0.5	0.3 \pm 0.5	1.8 \pm 1.6	0.6 \pm 0.7	97.6 \pm 2.0
Blue-crowned Motmot (<i>Momotus momota</i>)	8.4 \pm 1.4	0.6 \pm 0.5	0.6 \pm 0.2	1.1 \pm 0.5	0.2 \pm 0.4	98.7 \pm 0.6
Yellow-billed Jacamar (<i>Galbula albirostris</i>)	9.3 \pm 1.0	0.3 \pm 0.2	0.6 \pm 0.5	1.8 \pm 1.0	1.3 \pm 1.0	96.9 \pm 1.9
White-chested Puffbird (<i>Malacoptila fusca</i>)	9.1 \pm 1.0	0.3 \pm 0.2	0.1 \pm 0.1	1.0 \pm 0.0	0.3 \pm 0.4	98.7 \pm 0.5
Mouse-colored Antshrike (<i>Thamnophilus murinus</i>)	4.1 \pm 1.4	5.5 \pm 3.5	0.3 \pm 0.3	4.0 \pm 2.0	4.9 \pm 2.0	91.1 \pm 3.2
Warbling Antbird (<i>Hylocichla ustulata</i>)	4.3 \pm 1.4	13.9 \pm 4.0	0.7 \pm 0.6	8.7 \pm 2.3	8.7 \pm 3.8	82.6 \pm 4.4
Spot-winged Antbird (<i>Pernostola leucostigma</i>)	4.5 \pm 0.5	8.0 \pm 2.3	0.2 \pm 0.2	5.6 \pm 1.2	5.9 \pm 1.8	88.5 \pm 1.7
Spot-backed Antbird (<i>Hylophylax naevia</i>)	6.1 \pm 1.0	7.1 \pm 2.7	0.5 \pm 0.3	5.7 \pm 1.5	3.4 \pm 2.0	90.9 \pm 3.3
Scale-backed Antbird (<i>Hylophylax poecilonota</i>)	6.6 \pm 1.1	2.2 \pm 1.3	0.4 \pm 0.3	2.5 \pm 1.0	3.8 \pm 3.6	93.6 \pm 4.1
Golden-crowned Spadebill (<i>Platyrinchus coronatus</i>)	7.2 \pm 1.2	2.5 \pm 1.2	0.2 \pm 0.2	2.2 \pm 1.1	0.4 \pm 0.5	97.4 \pm 1.1
Ruddy-tailed Flycatcher (<i>Terenotricus erythrurus</i>)	5.1 \pm 0.8	4.2 \pm 2.3	0.6 \pm 0.3	4.5 \pm 1.9	2.1 \pm 1.1	93.5 \pm 2.8
Collared Gnatwren (<i>Microbates collaris</i>)	2.8 \pm 0.7	20.7 \pm 4.8	0.5 \pm 0.3	11.8 \pm 2.4	4.1 \pm 1.7	84.1 \pm 3.0
OCCASIONAL FLOCK MEMBERS						
Black Nunbird (<i>Monasa atra</i>)	9.1 \pm 1.6	0.5 \pm 0.3	0.3 \pm 0.2	1.8 \pm 0.9	1.9 \pm 2.4	96.3 \pm 2.8
Ruddy Foliage-gleaner (<i>Automolus rubiginosus</i>)	2.5 \pm 0.7	13.4 \pm 7.4	0.5 \pm 0.4	6.9 \pm 3.2	19.6 \pm 4.6	73.5 \pm 5.8
Wedge-billed Woodcreeper (<i>Glyphorhynchus spirurus</i>)	4.9 \pm 1.4	38.0 \pm 17.2	0.9 \pm 0.7	21.5 \pm 8.5	73.9 \pm 8.8	4.6 \pm 2.0
Fasciated Antshrike (<i>Cymbilaimus lineatus</i>)	1.4 \pm 0.5	9.8 \pm 3.6	0.2 \pm 0.3	5.9 \pm 1.8	18.6 \pm 6.6	75.6 \pm 7.4
Amazonian Antshrike (<i>Thamnophilus amazonicus</i>)	2.4 \pm 0.5	12.3 \pm 3.9	0.2 \pm 0.2	7.1 \pm 1.8	13.9 \pm 3.5	78.9 \pm 4.3
Rufous-bellied Antwren (<i>Myrmoderus guttata</i>)	4.9 \pm 1.4	14.9 \pm 4.8	0.7 \pm 0.6	9.7 \pm 2.8	15.7 \pm 4.8	74.6 \pm 6.0
Dot-winged Antwren (<i>Microrhopias quixensis</i>)	2.0 \pm 1.0	20.7 \pm 6.2	0.8 \pm 0.4	12.7 \pm 3.5	14.4 \pm 4.3	72.9 \pm 4.1
Gray Antbird (<i>Cercomacra cinerascens</i>)	2.3 \pm 0.8	13.9 \pm 5.5	0.5 \pm 0.6	7.9 \pm 2.7	17.4 \pm 5.6	74.7 \pm 7.1
McConnell's Flycatcher (<i>Mionectes macconnelli</i>)	7.4 \pm 2.2	4.4 \pm 2.0	0.5 \pm 0.2	4.7 \pm 1.8	0.9 \pm 0.4	94.4 \pm 1.9
Olivaceous Flatbill (<i>Rhynchocyclus olivaceus</i>)	4.6 \pm 1.1	6.0 \pm 3.0	0.5 \pm 0.4	7.0 \pm 2.7	1.6 \pm 1.2	91.4 \pm 2.8
Coraya Wren (<i>Thryothorus coraya</i>)	1.2 \pm 1.1	20.1 \pm 7.0	0.5 \pm 0.3	11.1 \pm 3.5	70.5 \pm 4.7	18.4 \pm 5.4
Long-billed Gnatwren (<i>Rampboacaenus melanurus</i>)	3.2 \pm 0.9	23.5 \pm 5.3	0.4 \pm 0.3	12.2 \pm 3.2	10.1 \pm 4.4	77.7 \pm 4.3

APPENDIX 1. Continuation.

	Visibility	Velocity	Success	Move	Search	Scan
Fulvous-crested Tanager (<i>Tachyphonus surinamus</i>)	7.6 ± 1.6	4.0 ± 1.8	0.2 ± 0.3	3.1 ± 1.6	5.9 ± 2.8	91.0 ± 4.2
OBLIGATE FLOCK MEMBERS						
Rufous-rumped Foliage-gleaner (<i>Philydor erythrocerus</i>)	6.2 ± 1.4	18.9 ± 7.9	0.5 ± 0.4	11.4 ± 3.8	85.2 ± 4.0	3.4 ± 1.3
Olive-backed Foliage-gleaner (<i>Automolus infuscatus</i>)	5.8 ± 1.1	13.6 ± 4.9	0.4 ± 0.4	8.4 ± 2.4	84.5 ± 3.4	7.2 ± 2.8
Plain Xenops (<i>Xenops minutus</i>)	5.7 ± 0.9	20.1 ± 7.0	0.5 ± 0.4	12.0 ± 3.5	81.2 ± 3.3	6.8 ± 1.7
Chestnut-rumped Woodcreeper (<i>Xiphorhynchus pardalotus</i>)	5.5 ± 1.4	30.1 ± 9.2	0.5 ± 0.5	16.8 ± 4.8	79.0 ± 5.1	4.2 ± 1.6
Curve-billed Scythebill (<i>Campyloramphus procurvoides</i>)	5.4 ± 1.1	27.2 ± 8.9	0.4 ± 0.4	15.6 ± 5.0	80.0 ± 5.9	4.4 ± 1.3
Dusky-throated Antshrike (<i>Thamnomanes ardesiacus</i>)	7.5 ± 1.5	4.6 ± 2.7	0.6 ± 0.5	5.2 ± 2.1	2.8 ± 2.6	92.0 ± 3.5
Cinereous Antshrike (<i>Thamnomanes caesius</i>)	7.2 ± 1.4	3.0 ± 1.4	0.5 ± 0.5	3.9 ± 1.8	2.0 ± 2.0	94.1 ± 3.4
Brown-bellied Antshrike (<i>Myrmotherula gutturalis</i>)	6.2 ± 1.4	16.7 ± 7.6	0.5 ± 0.4	10.5 ± 4.3	85.7 ± 4.2	3.8 ± 1.6
White-flanked Antwren (<i>Myrmotherula axillaris</i>)	5.4 ± 2.0	21.1 ± 9.1	0.8 ± 0.5	13.0 ± 4.6	79.3 ± 11.5	4.7 ± 1.7
Long-winged Antwren (<i>Myrmotherula longipennis</i>)	7.0 ± 1.2	25.4 ± 7.8	0.9 ± 0.6	15.5 ± 4.6	80.9 ± 4.3	3.6 ± 1.0
Gray Antwren (<i>Myrmotherula menetriesii</i>)	7.6 ± 1.2	22.5 ± 7.7	1.0 ± 0.6	14.1 ± 4.1	82.4 ± 4.0	3.5 ± 0.6
Sulphur-rumped Flycatcher (<i>Myiobius barbatus</i>)	8.0 ± 1.7	14.1 ± 8.2	0.7 ± 0.5	9.8 ± 4.5	17.0 ± 5.8	73.2 ± 6.7

