Comparison of Foraging Behaviors and Movement Patterns of the Wedge-Billed Woodcreeper (*Glyphorynchus spirurus*) Traveling Alone and in Mixed-Species Flocks in Amazonian Ecuador

Author(s): Abigail J. Darrah and Kimberly G. Smith

COMPARISON OF FORAGING BEHAVIORS AND MOVEMENT PATTERNS OF THE WEDGE-BILLED WOODCREEPER (*GLYPHORYNCHUS SPIRURUS*) TRAVELING ALONE AND IN MIXED-SPECIES FLOCKS IN AMAZONIAN ECUADOR

Abigail J. Darrah[1] and Kimberly G. Smith

Department of Biological Sciences, University of Arkansas, SCEN 632, 1 University of Arkansas, Fayetteville, Arkansas 72701, USA

Abstract.—Attendants of Neotropical mixed-species flocks are hypothesized to benefit primarily by gaining protection from predators, while potential costs have received little attention. The Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) frequently joins mixed-species understory flocks but also often forages alone. We hypothesized that, because of the significant vertical component of its foraging behavior, the primary cost to flock-following might be a decrease in foraging efficiency associated with conforming to flock movement patterns. We compared the foraging behavior and microhabitat use of Wedge-billed Woodcreepers in and out of flocks at Tiputini Biodiversity Station, eastern Ecuador, during January–March, 2010–2012. We measured foraging height range, time spent per trunk, vertical movement rate, distance flown between trunks, extent of foliage cover around the focal bird, hitch rate, and peck rate. We tracked birds in 2012 using radiotelemetry to measure horizontal movement rates and to record the locations of flock-joining and -leaving. Wedge-billed Woodcreepers in flocks foraged in more exposed microhabitats, moved vertically at a faster rate despite a decrease in foraging height range, and exhibited greater hitch rates than individuals foraging alone. Peck rates, peck:hitch ratio, and distance flown between trunks did not differ between situations. Horizontal movement rate did not differ in and out of flocks, but the length of flock-following sessions was negatively correlated with movement rate above a threshold of 4 m min^{-1}. These observations are consistent with an antipredator benefit of flocking for this species and suggest an energetic or foraging efficiency cost associated with conforming to flock movement patterns. *Received 25 May 2013, accepted 13 September 2013.*

Key words: flocking propensity, foraging efficiency, movement rate, predation, Tiputini, utilization distribution, vigilance.

Comparación de los Comportamientos de Forrajeo y los Patrones de Movimiento entre *Glyphorynchus spirurus* que Viajan Solos o en Bandadas Mixtas en la Amazonía Ecuatoriana

Resumen.—Se cree que las aves neotropicales que se unen a bandadas mixtas se benefician principalmente en recibir protección ante depredadores, mientras que los costos potenciales han recibido poca atención. *Glyphorynchus spirurus* frecuentemente se une a bandadas mixtas del sotobosque pero también suele forrajear solo. Planteamos la hipótesis de que, debido al alto componente vertical de su comportamiento de forrajeo, el costo primario de unirse a una bandada mixta podría ser una disminución en la eficiencia de forrajeo asociada a conformarse con los patrones de movimiento de la bandada. Comparamos el comportamiento de forrajeo y uso del microhábitat de *G. spirurus* dentro y fuera de bandadas mixtas en la estación de biodiversidad Tiputini, Ecuador oriental, entre enero y marzo de 2010 a 2014. Medimos el rango en la altura de forrajeo, el tiempo invertido en cada tronco, la tasa de movimiento vertical, la distancia volada entre troncos, la cantidad de cobertura vegetal alrededor del ave focal, la tasa de enganche y la tasa de picoteo. En 2012 seguimos a las aves usando radiotelemetría para medir las tasas de movimiento horizontal e identificar los momentos de unión y separación de la bandada. Al estar en bandadas, *G. spirurus* forrajeó en microhábitats más expuestos, se movió verticalmente a una tasa mayor a pesar de una disminución en el rango en la altura de forrajeo y tuvo mayores tasas de picoteo que los individuos que forrajeaban solos. Las tasas de picoteo, la relación picoteo:captura y la distancia volada entre troncos no fueron diferentes entre ambas situaciones. La tasa de movimiento horizontal no fue diferente dentro y fuera de las bandadas, pero la duración de los periodos de seguimiento de las bandadas estuvo correlacionada negativamente con la tasa de movimiento por encima de un umbral de 4 m min-1. Estas observaciones son consistentes con el beneficio antidepredatorio de unirse a bandadas en esta especie, y sugieren un costo energético o en la eficiencia de forrajeo asociado con conformarse con los patrones de movimiento de la bandada.

[1]Present address: University of Arizona, School of Natural Resources and the Environment, Biological Sciences East, Tucson, Arizona 85721, USA.
  E-mail: adarrah@email.arizona.edu

Mixed-species bird flocks are prevalent year round throughout much of the world's lowland rainforests (Partridge and Ashcroft 1976, Munn and Terborgh 1979, Diamond 1987, Goodale and Kotagama 2005), and they are particularly diverse in the Neotropics (Powell 1985). Mixed-species flocks of understory insectivores in the Amazon Basin generally consist of one or two antshrike (*Thamnomanes*) species and 10–12 "core" species that share a common territory that is defended against other conspecifics (Munn and Terborgh 1979, Wiley 1980, English 1998, Jullien and Thiollay 1998). The core species are considered obligate flock-followers, rarely or never seen foraging away from flocks. In addition, 30 or more species are facultative flock-followers, joining these flocks for varying lengths of time but also regularly foraging away from them (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998).

Most hypothesized benefits of flocking fall under two categories: increased foraging efficiency and protection from predators. These types of benefits are not mutually exclusive, particularly when decreased time spent in vigilance allows for more time spent feeding (Dolby and Grubb 1998, Fernández-Juricic et al. 2004, Sridhar et al. 2009). Flock members may gain foraging benefits by copying information from other flock members about successful patches or by taking prey flushed by others (Powell 1985, Terborgh 1990, Greenberg 2000). However, many members of tropical mixed-species insectivore flocks engage in stereotyped, species-specific behaviors that are not conducive to social learning (Henderson 1989, Hutto 1994), and furthermore, typically only one individual or family group per species is present in a flock (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998). In addition, with the exception of the Bluish-slate and Cinereous antshrikes (*Thamnomanes schistogynus* and *T. caesius*, respectively), there is little evidence that Neotropical understory flock members frequently take prey flushed by other flock members (Munn 1986, English 1998).

Antipredator benefits are generally believed to be a more important function than foraging enhancement for individuals in tropical mixed-species insectivore flocks, particularly for species that engage in foraging maneuvers that require the forager to focus attention on nearby substrates (Jullien and Clobert 2000). Predators may capitalize on this vulnerable behavior; for instance, Sharp-shinned Hawks (*Accipiter striatus*) preferentially attack foraging over vigilant birds and solitary over grouped individuals (Roth et al. 2006). Similarly, experimental evidence on group-foraging fish demonstrated that some foraging behaviors increased response time during a predatory attack, and individuals engaged in these maneuvers were preferentially attacked by predators (Krause and Godin 1996). Flock-following may incur antipredator benefits via a number of mechanisms, including collective vigilance, decreased probability of the individual being selected during an attack, and creation of confusion for an attacking predator (Powell 1985, Terborgh 1990, Greenberg 2000). Improved vigilance, by either the actions of sentinel species or the presence of many individuals, has been cited as the most likely mechanism operating in mixed-species forest flocks (Terborgh 1990, Greenberg 2000). Improved vigilance allows many individuals to spend less time scanning the environment when they are in flocks than when they are alone (Alves and Cavalcanti 1996, Dolby and Grubb 1998, Fernández-Juricic et al. 2004, Sridhar et al. 2009). Additionally, some species have been recorded foraging in more exposed situations in flocks than alone (Munn 1984, Dolby and Grubb 2000, Tubelis et al. 2006), and experimental studies in aquatic systems suggest that denser or more structurally complex vegetation reduces predation rates (Crowder and Cooper 1982, Warfe and Barmuta 2004).

Relatively few studies have examined the possible costs associated with joining a mixed-species flock, and the cost–benefit balance likely influences how frequently a given species associates with flocks. Because of the presence of species-specific foraging niches, competition costs are likely reduced for members of mixed-species flocks compared to similar-sized single-species flocks (Gradwohl and Greenberg 1980). In fact, several recent studies have documented significant positive associations among species pairs within mixed-species flocks (Arbeláez-Cortés et al. 2011, Sridhar et al. 2012). A likely cost for members of mixed-species flocks that has received less attention is that species must conform to the movement pattern of the entire flock, which could result in the use of suboptimal movement patterns and reduced foraging efficiency for some species (Partridge and Ashcroft 1976, Hutto 1988). For instance, babblers (Timaliidae) in Ceylon frequently lagged behind the other flocking species and had to interrupt foraging to catch up to the departing flock (Partridge and Ashcroft 1976).

The Wedge-billed Woodcreeper (*Glyphorynchus spirurus*) is a facultative flock-follower of the lowland Neotropics, frequently joining mixed-species understory flocks but also regularly foraging alone (Munn and Terborgh 1979, English 1998, Jullien and Thiollay 1998), which makes it a good model species on which to conduct comparative behavioral observations. Like most other woodcreepers, it forages by moving vertically along trunks and gleaning arthropods from the bark (Marantz et al. 2003). This behavior confers a large vertical component to its movement pattern that is lacking in the majority of core flock species, most of which glean insects from leaves (English 1998). Therefore, to keep up with a moving flock, a Wedge-billed Woodcreeper might need to make one or more of the following behavioral modifications: reduce the height range searched per trunk, increase the vertical movement rate, or increase the distance flown between trunks. Any of these modifications might represent an energetic cost if there is not a compensatory increase in prey intake rate. This hypothesized cost is likely to be reduced or absent when a flock is stationary or moving slowly.

The purpose of the present study was to compare the foraging behavior of Wedge-billed Woodcreepers in and out of flocks to determine the most likely costs and benefits derived by this facultative flock-follower. If the main benefit gained from flock-following is antipredator vigilance, we hypothesized that Wedge-billed Woodcreepers would forage in more dense cover away from flocks than in flocks. We hypothesized that the primary cost to flock-following is an increase in movement rate that compromises foraging efficiency. Therefore, we expected one or more of the following behavioral changes: (1) an increase in either horizontal or vertical movement rates, or both, while following flocks; (2) a decrease in attack to search maneuver ratio in flocks; and (3) a decrease in time spent with a flock as a function of flock movement rate. We further hypothesized that, if the primary cost to flock-following is reduced foraging efficiency because of modifications to movement patterns, there should be a threshold rate below which movement rate has little effect on the length of time the individual spends with the flock.

METHODS

Study area.—Our study was conducted at Tiputini Biodiversity Station (0°38′15″S, 76°08′59″W) in Orellana Province, Ecuador. The station encompasses 638 ha of rainforest within the 1,682,000-ha UNESCO Yasuni Biosphere Reserve. The forest is composed mainly of undisturbed terra firme rainforest, with a strip of varzea (seasonally flooded forest) bordering the Tiputini River. The mean elevation at the station is ~220 m above sea level, and the region receives ~3,200 mm of rainfall annually, with a relatively dry period from January to February. The current project was conducted on two ~100-ha plots within the reserve, separated by ~1.5 km (Blake 2007). Both plots consisted primarily of mature terra firme forest, with one plot characterized by a more dissected topography and the other plot flatter overall (although with a similar mean elevation; Blake 2007) with relatively more treefalls and swampy depressions. Abundance of Wedge-billed Woodcreepers and the core flock members Cinereous and Dusky-throated antshrikes (*Thamnomanes ardesiacus*) were similar in both plots (Blake 2007), and there was greater within-plot variation in canopy height and understory openness than between-plot variation (A. J. Darrah unpubl. data).

Field methods.—We conducted foraging observations during all daylight hours from 12 January to 5 March 2010, 17 January to 7 February 2011, and 14 January to 27 March 2012. In 2010, we systematically searched the plot trails for Wedge-billed Woodcreepers (hereafter "woodcreepers"). When we encountered flocks, we conducted observations on the first woodcreeper spotted in the flock. Only one individual per flock was observed unless other individuals were identifiable by color bands. In 2011 and 2012, we conducted observations opportunistically on unmarked and radio-tagged individuals during radiotracking sessions (see below).

Each foraging observation was categorized as "no flock" or "flock." We considered woodcreepers to be in a flock if they were actively foraging inside a flock or ≤10 m from the edge of a flock (maximum nearest-neighbor distance in Wiley 1980). We began an observation when the focal individual flew to a new tree and continued until the observer lost track of the bird. For observations that included a complete bout on a trunk (bird was seen both alighting on and departing from a trunk), we visually estimated start height and end height to the nearest 0.5 m, and we recorded the time spent on the trunk (2010, 2012). We estimated the distance flown between trunks to the nearest 1 m in 2010. We categorized cover within a 1-m-radius sphere of the foraging individual as open (<25% cover), medium (25–75%), or dense (>75%). In 2010, we dictated foraging maneuvers continuously into a digital voice recorder. Maneuvers were categorized as pecks (any movement where the bill struck the surface of the trunk) and hitches (one hitch = single hop resulting in an upward movement along the trunk). We divided the number of pecks and hitches by the observation time to measure peck and hitch rates (number min^{-1}). We calculated peck:hitch ratio as peck rate divided by hitch rate.

We captured woodcreepers in both study plots in 2012 using 2.6-m mist nets (36-mm mesh) as part of a long-term demographic study of understory birds (for additional details, see Blake and Loiselle 2012). We captured 23 individuals between 10 January and 17 March 2012 and fitted each with a radiotransmitter (0.45 g BD-2N without tubes; Holohil Systems, Carp, Ontario) using a thigh harness (Rappole and Tipton 1991) made from either cotton or elastic thread (~0.5 mm diameter). The thread was attached to the body of the transmitter with superglue. Individuals were released at the site of capture.

We tracked woodcreepers during all daylight hours in 2012 using Advanced Telemetry Systems Field Master receivers and hand-held three-element Yagi antennas for 2–3 h per day, beginning at least 24 h after capture. We randomized the order of tracking each day such that we tracked all individuals during morning, afternoon, and early evening hours. We determined the location of the woodcreeper by approaching either until it was seen or until the lack of directionality in the signal indicated close proximity (~10 m; technicians were trained with the transmitters prior to tracking in order to calibrate their abilities to judge distances using the equipment). This rarely resulted in flushing the bird, and we believe that our presence had negligible effects on movement patterns. We recorded location using a GPS unit every 15 min during the tracking sessions, along with the time and location of any flock-joining or flock-leaving. We occasionally recorded location at shorter time intervals if the focal individual changed direction multiple times while traveling a long distance (e.g., >100 m), or if a focal individual moved away and then returned to the same spot during the 15-min interval.

Statistical analysis.—We compared flight distance between trunks, hitch rate, peck rate, peck:hitch ratio, height range, start height, end height, time spent per trunk, cover use, and vertical movement rate of woodcreepers foraging in and out of flocks. We pooled data from multiple years and from both plots. We used the Shapiro-Wilk test to determine whether data were normally distributed and ln-transformed the data if necessary. We used nonparametric statistics for data that remained non-normally distributed after transformation (hitch and peck rates, peck:hitch ratio, distance between trunks, and height range). We used a *t*-test or Mann-Whitney *U*-test to compare each variable between flocking and nonflocking situations. We used log-linear regression to model the effect of flocking situation on the frequency of cover category use. In addition, because the foraging data likely contained some repeated observations on unmarked birds, we pooled repeated observations from 11 marked individuals in 2010 and 2012 and used an analysis of variance (ANOVA) to determine the effects of individual identity on height range, time spent per trunk, and vertical movement rate. We performed all statistical analyses in R, version 2.15.1 (R Development Core Team 2012), at $\alpha < 0.05$.

We measured distances and times between consecutive locations within tracking sessions for each individual using the Movement Path Metrics feature in Geospatial Modeling Environment (GME; Beyer 2009) and categorized each location as "in flock" or "no flock." We used the distances and times to calculate the horizontal movement rate (m min^{-1}) between points. To test the hypothesis that movement rates differed in flocks and out of flocks, we conducted an ANOVA on movement rate with the factors flock, individual, and flock × individual interaction. To test the hypothesis that time spent with a flock decreases as a function of flock movement rate, we grouped the data for each individual into flock sessions (single events of joining and then leaving a flock), with the time spent in the flock and the average movement rate calculated for each session. We fit a linear mixed-effects model of the effect of movement rate on flock session length using residual maximum likelihood methods in R, with individual included as a random effect. To determine whether there was a threshold movement rate

below which there is little effect of movement rate on flock session length, we performed a two-dimensional Kolmogorov-Smirnov test and compared the observed maximum difference between the two distributions (D_{BKS}) with the D_{BKS} values obtained from 5,000 randomizations of the data using the Ez2dks script (available from J. E. Garvey; Garvey et al. 1998).

If time spent with a flock was found to be negatively correlated with movement rate, there are two likely explanations: (1) the woodcreeper may leave the flock because of the energetic cost of keeping up, or (2) a high movement rate may simply result in reaching the edge of the woodcreeper's home range more quickly. To distinguish between these possibilities, we explored the relationships among flock-joining locations, flock-leaving locations, and session length. We estimated the utilization distribution (UD) for each individual in both years in GME using fixed-kernel density estimation, with the smoothing parameter chosen using the least squares cross-validation method (Seaman and Powell 1996). For each individual, we measured the volume of the UD at each cell of the kernel density raster by generating percent volume contours (1–99%; Kertson and Marzluff 2011) using the Contour tool in GME. We converted this to a raster of UD volume measurements in ARCMAP (ESRI, Redlands, California) using the Feature to Raster tool in ARCTOOL BOX. The UD volume represents a space-use probability surface of the home range, with higher values of the UD corresponding to a higher probability of use by the individual. Because the UD volume is typically highest within the core of the home range and lowest toward the edges, it can be used to indicate relative position within the home range, with low UD values indicating proximity to the home-range edge. We then plotted the locations of flock-joining and flock-leaving for each individual onto that individual's UD volume raster and extracted the volume of the UD at each flock-joining or -leaving point. We fit linear mixed-effects regressions with individual as a random effect in R to investigate the effects of flock-joining location on flock-leaving location and session length. We expected the following patterns to be evident if woodcreepers join flocks and follow them all the way to the edge of their home range: (1) no strong relationship between start and end UD, because woodcreepers depart at the home-range edge (low UD) regardless of start location; and (2) session length would be weakly negatively correlated with UD volume because joining a flock in the home-range edge (low UD) might allow the woodcreeper to remain with the flock longer (if it travels the full length of the home range) than if it joins in the home range core (high UD), although this relationship would be weakened by joining flocks near the edge that traverse only a small section of the home range. Results are presented as means ± SE.

Results

Foraging behavior.—There was no significant individual effect for height range (F = 0.8, df = 10, P = 0.65), time spent per trunk (F = 1.49, df = 9, P = 0.23), or vertical movement rate (F = 1.1, df = 9, P = 0.39). Woodcreepers spent less time per trunk while foraging in flocks than when foraging alone (F = 18.3, df = 1 and 3, P < 0.001; Table 1). In 2010, hitch rate was greater in flocks (U = 59.0, P = 0.03), whereas differences in peck rate were nonsignificant (U = –19.0, P = 0.43; Table 1). The increase in hitch rate did not result in a significant decrease in peck:hitch

TABLE 1. Means (with SE in parentheses) of foraging and habitat variables recorded for Wedge-billed Woodcreepers foraging in and out of flocks (asterisk indicates significant difference) from January to March 2010 and 2012 at Tiputini Biodiversity Station, Orellana Province, Ecuador.

	Alone	Flock
Height range (m)	2.6* (0.4), n = 32	1.5* (0.2), n = 44
Start height (m)	1.1 (0.5), n = 32	1.4 (0.5), n = 44
End height (m)	1.9* (0.6), n = 32	1.6* (0.5), n = 44
Time on trunk (s)	112.9* (15.9), n = 35	48.6* (6.3), n = 44
Vertical movment rate (s m^{-1})	74.1* (10.7), n = 32	46.4* (9.5), n = 44
Peck rate (number min^{-1})	16.4 (5.7), n = 13	10.6 (3.5), n = 17
Hitch rate (number min^{-1})	14.8* (2.5), n = 13	26.1* (4.1), n = 17
Peck:hitch ratio	1.3 (0.4), n = 13	0.5 (0.2), n = 17
Distance between trunks (m)	5.6 (4.6), n = 10	5.5 (1.1), n = 21

ratio (U = –296.0, P = 0.12; Table 1). Woodcreepers used a smaller height range per trunk while foraging in flocks than alone (U = –2,194.5, P < 0.05), as a result of a decrease in end height (t = 2.3, df = 74, P = 0.02) in flocks and no change in start height (t = –1.7, df = 75.6, P = 0.09; Table 1). Vertical movement rate was greater in flocks than alone (t = 2.4, df = 61.8, P = 0.02). There was no difference in flight distance between trunks (U = –9.5, P = 0.70) in flocks or alone (Table 1). Woodcreepers used less cover when foraging in flocks than when foraging alone (χ^2 = 12.7, df = 2, P = 0.002; Fig. 1).

Horizontal movement rates and flock sessions.—Horizontal movement rates of woodcreepers did not differ in and out of flocks (F = 1.7, df = 1 and 24, P = 0.19). Mean individual movement rates varied from 1.3 ± 0.2 m min^{-1} to 2.9 ± 0.3 m min^{-1}, with an
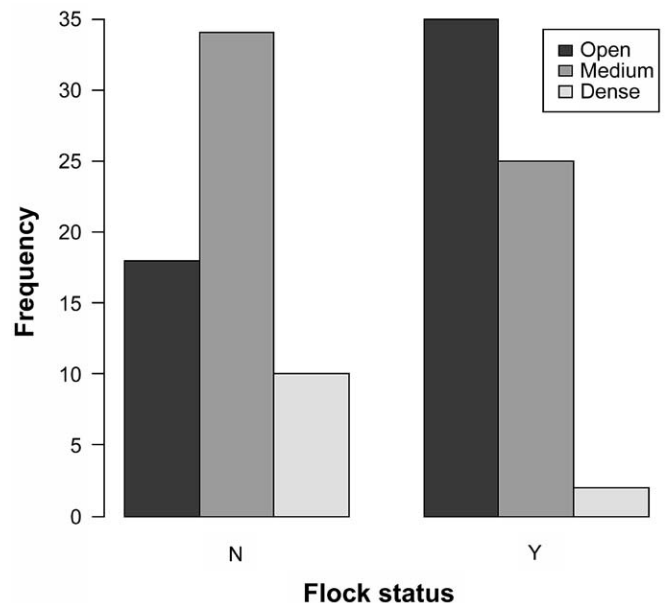

FIG. 1. Frequency of cover category use (density of vegetation within a 1-m radius of foraging individual; dense > 75%, medium = 25–75%, open < 25%) of Wedge-billed Woodcreepers observed foraging in (Y) and out (N) of flocks from January to March, 2010–2012, at Tiputini Biodiversity Station, Orellana Province, Ecuador.

overall mean of 2.2 ± 0.5 m min^{-1} out of flocks and 2.4 ± 0.1 m min^{-1} in flocks. Mean flock-following session length was 36.1 ± 2.3 min (range: 5.0–210.0 min), with a mean of 91.7 ± 5.6 m (range: 0.0–377.0 m) traveled per session. Session length was inversely related to movement rate ($\hat{\beta}$ = −0.2 ± 0.1, t = −2.3, df = 150, P = 0.02; Fig. 2), with a threshold movement rate of 4.0 m min^{-1} (D_{BKS} = 0.1, P = 0.02). Location of flock-leaving was positively correlated with location of flock-joining (t = 12.1, df = 150, P < 0.001; Fig. 3), which suggests that woodcreepers left the flock in the same general area as they joined. Flock session length was positively correlated with join location UD (t = 2.13 df = 150, P = 0.03), which suggests that an individual stayed with a flock longer when it joined the flock in the core than at the edge of the home range, although the effect size was small ($\hat{\beta}$ = 0.004 ± 0.002; Fig. 4).

DISCUSSION

Wedge-billed Woodcreepers' vertical movement rate was greater in flocks than alone, despite a concurrent decrease in height range used in flocks as a result of departing trunks at a lower height. The increased search movement (hitch) rate was not mirrored by an increase in prey attack (peck) rate, resulting in a decreased peck:hitch ratio in flocks, although the difference was not statistically significant. However, in order to counteract the smaller area per trunk searched (and searched at a faster rate), peck:hitch ratio would need to increase in order to maintain foraging efficiency, assuming that attack rate is an appropriate index for prey capture rate (Norberg 1977, Robinson and Holmes 1982). These results suggest that woodcreepers may incur a cost in terms of reduced foraging efficiency associated with behavioral modifications to keep up with a moving flock. Similarly, Thiollay (2003) documented no
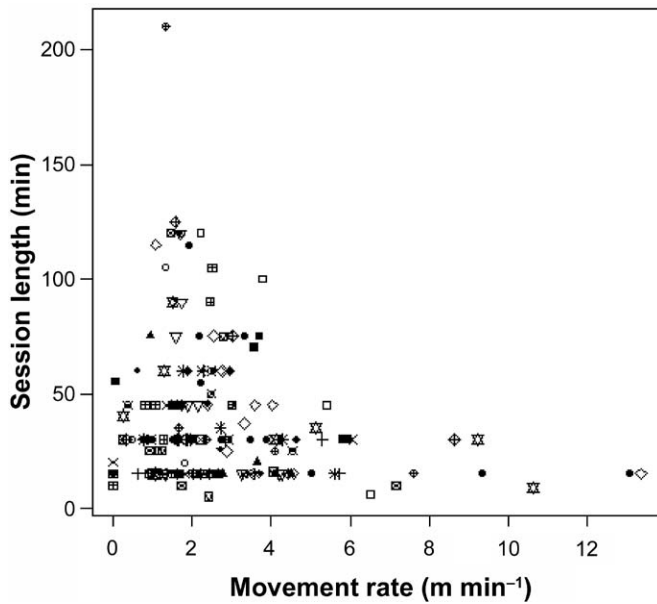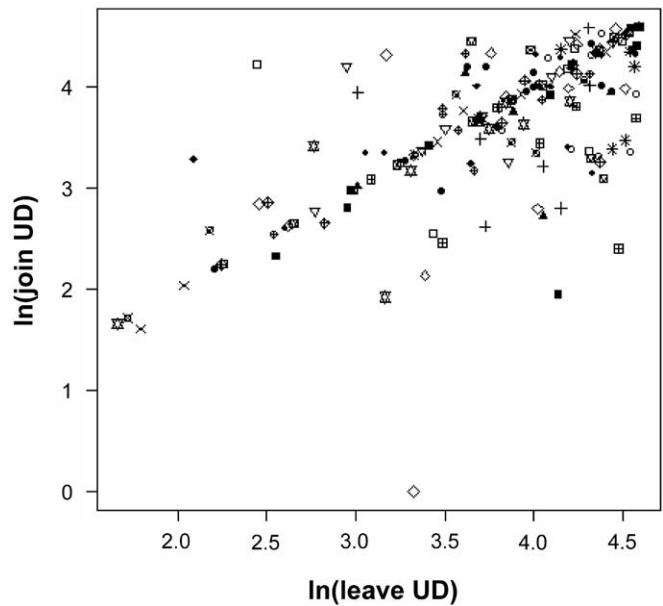

FIG. 3. Relationship between relative flock-joining and -leaving locations (measured as the utilization distribution [UD] volume within home ranges; low values indicate proximity to home-range edge) of 23 individual Wedge-billed Woodcreepers tracked using radiotelemetry from January to March, 2012, at Tiputini Biodiversity Station, Orellana Province, Ecuador. Individuals are represented by unique symbols.

FIG. 2. Relationship between horizontal movement rates (m min^{-1}) and flock-following session lengths (min) of 23 individual Wedge-billed Woodcreepers tracked using radiotelemetry from January to March, 2012, at Tiputini Biodiversity Station, Orellana Province, Ecuador. Individuals are represented by unique symbols.
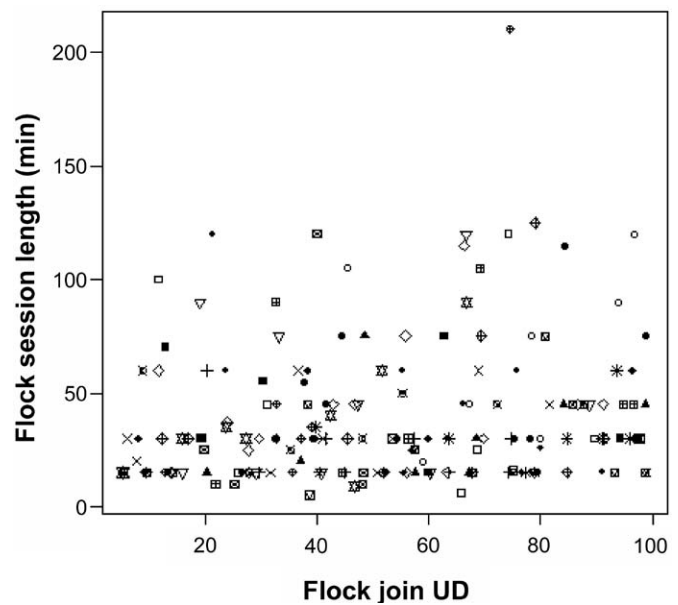

FIG. 4. Relationship between flock sessions length (m min^{-1}) and relative flock-joining locations (measured as the utilization distribution [UD] volume within home ranges; low values indicate proximity to home-range edge) of 23 individual Wedge-billed Woodcreepers tracked using radiotelemetry from January to March, 2012, at Tiputini Biodiversity Station, Orellana Province, Ecuador. Individuals are represented by unique symbols.

change in prey attack rate in this species in flocks versus alone, and, in a study on mixed-species flocks in Panama, Pomara et al. (2003) found that Slate-throated Redstarts (*Myioborus miniatus*) increased movement rates but not attack rates when foraging in flocks. Pomara et al. (2003) attributed this change to a shift from sit-and-wait flycatching to a more active foraging strategy suitable for keeping up with a moving flock. Unfortunately, it was not possible to measure prey capture rate directly in the Wedge-billed Woodcreeper because of its rapid movements and the often tiny prey consumed (English 1998, Marantz et al. 2003), and it is possible that woodcreepers could compensate for increased search rate without an increase in attack rate by taking only larger, more profitable prey items (Giraldeau and Caraco 2000). To further complicate matters, it is probable that some proportion of "pecks" constituted search behavior rather than prey attack, although if this proportion is similar while foraging alone and in flocks, then the failure to increase peck rates along with search rates still suggests a decrease in foraging efficiency.

Although vertical movement rate was greater in flocks, horizontal movement rate (m min^{-1}, generally measured over a 15-min period) did not differ in flocks or without. This may be due, in part, to the different time scales over which these variables were measured; the horizontal-movement-rate data reveal broader-scale movements that would not capture finer-scale variation due to visiting consecutive trunks in a nonlinear pattern. However, horizontal movement rate was negatively correlated with flock session length, with a threshold rate of 4 m min^{-1}, above which session length was most strongly negatively correlated with movement rate, and below which there was little correlation. This provides further support for the hypothesis that woodcreepers incur an energetic cost as a result of behavioral shifts while following flocks, and suggests that this cost may be minimal when the flock is stationary or moving at a rate less than 4 m min^{-1}. An alternative explanation not explored in our study is the possibility that flocks move rapidly through areas that offer poor foraging opportunities, and that woodcreepers drop out in order to remain inside preferred foraging patches, rather than because of movement rate per session.

The negative relationship between movement rate and flock-following session length was not a result of reaching the edge of the woodcreeper's home range more quickly. Although woodcreepers spent more time in a flock when they joined within the core part of the home range, the relative positions of flock-joining and flock-leaving locations were positively correlated, which suggests that woodcreepers generally did not travel from one edge of their home range to the other in a flock and regularly left flocks that were present in the core of their home range (>50% volume; Fig. 4). This differs from the observations of Pomara et al. (2007) of four passerine species in Panama, which were observed following flocks as long as the flock was present within the follower's home range. This has often been assumed to be the case for flock-followers in Amazonia (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Jullien and Thiollay 1998, Marantz et al. 2003), but our results demonstrate that, for the Wedge-billed Woodcreeper, additional factors besides flock presence within the home range have an important influence on an individual's decision to join or leave a flock. As demonstrated here, movement rate appears to be one important factor; additional possibilities are that Wedge-billed

Woodcreepers may leave flocks to stay within preferred foraging patches or to carry food to young (although only 5 of 23 individuals were known to be breeding during the 2012 study season).

Wedge-billed Woodcreepers foraged in more exposed microhabitats when in flocks than when alone, which is consistent with the antipredator hypothesis of flock function. This is contrary to the findings of Thiollay (2003) for this species, although that author did document a shift to more exposed sites in flocks for the White-flanked Antwren (*Myrmotherula axillaris*). However, Thiollay (2003) used a different method to quantify foliage density, so our results may not be directly comparable. Many animals respond to increases in predation risk by foraging in more protected areas, even if these areas are less profitable (Sih 1982, Lima and Dill 1990, Suhonen 1993, Jordan et al. 1997). The reduced predation risk associated with flocking may release the Wedge-billed Woodcreeper from such constraints, allowing individuals to forage on a wider range of trunk surfaces. However, this assumes that more exposed trunks are riskier for the Wedge-billed Woodcreeper. While experiments using fish indicate that structural complexity reduces the efficiency of predators in aquatic ecosystems (Crowder and Cooper 1982, Warfe and Barmuta 2004), this assumption is more difficult to test directly using terrestrial vertebrates. More studies on the behavior of Neotropical rainforest predators are needed to determine the relative risk of predation from raptors, mammals, and snakes in a variety of habitats. Anecdotal evidence suggests that snakes may capture Wedge-billed Woodcreepers at least opportunistically (Greene 1997). It is possible that dense microhabitats harbor a separate suite of predators and are therefore not considerably safer than areas of open understory.

We categorized social behavior as "with flock" or "without flock." Although this ignores variation in flock size and composition, we believe this dichotomy to be adequate for the purposes of the present study. First, the presence and number of core species varied little over spatial or temporal scales (English 1998; A. J. Darrah and K. G. Smith pers. obs.). All flocks contained both species of *Thamnomanes*, three or more antwren species (*Myrmotherula* and *Epinecrophylla*; generally at least Long-winged Antwren [*M. longipennis*], White-flanked Antwren, and Gray Antwren [*M. menetriesii*]), one or more foliage-gleaners (*Automolus* and *Phylidor* spp.), and one or two woodcreepers (*Xyphorynchus* spp.). A large source of variation in flock size and composition that may be of interest for future investigation is the concurrent presence or absence of a canopy flock (Munn and Terborgh 1979, English 1998), which would affect the average height of flock members and, thus, possibly the height range used by attendant Wedge-billed Woodcreepers. If the primary benefit of joining a flock is to gain an antipredator benefit, larger flocks may offer increased protection via the "many eyes" or predator-confusion mechanisms. On the other hand, several studies have documented that the movement rate of flocks increases with total flock size (Powell 1985, Greenberg 2000); thus, the total size of the flock may affect the length of time a Wedge-billed Woodcreeper follows the flock.

It is likely that our foraging behavior contains some repeated observations from unmarked individuals, particularly in the 2010 data. However, the lack of a significant individual effect observed in height range, time spent per trunk, and vertical movement rate suggests that foraging behavior is more variable within individuals

than between individuals. Furthermore, given the high density of this species at our study area (Blake and Loiselle 2012), it is unlikely that repeated observations of unmarked individuals constitute a large portion of our data. We therefore believe that our foraging data are robust and that any repeated observations hidden in our data have not significantly affected our conclusions.

The primary cost of flock-following to Wedge-billed Woodcreepers appears to be a reduction in foraging efficiency associated with the need to modify movement patterns to keep up with a moving flock; this cost likely increases with flock movement rate and could account for the negative relationship between flock-following session length and movement rates above a threshold rate of 4 m min⁻¹. Under the assumption that exposed trunks are riskier foraging sites, Wedge-billed Woodcreepers appear to benefit from flocks by gaining some protection from predators, which could represent an indirect foraging benefit by allowing them to exploit additional foraging patches. Wedge-billed Woodcreepers do not typically follow flocks up to the home-range boundary, which suggests that factors (including movement rate) other than flock presence influence an individual's decision to join or leave a flock.

Acknowledgments

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