GROUNDED GROUND BIRDS AND SURFING CANOPY BIRDS: VARIATION OF FORAGING STRATUM BREADTH OBSERVED IN NEOTROPICAL FOREST BIRDS AND TESTED WITH SIMULATION MODELS USING BOUNDARY CONSTRAINTS

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Abstract.—Vertical stratification of bird species has been intensively studied in temperate as well as tropical forest bird communities. One question that has received less attention is the variation of foraging stratum breadth. Hypotheses trying to explain that variation are based on differences in perception, evasion, adaptation, competition, and environmental and geometric boundary constraints. Although some predict that foraging strata near the ground should be narrower than those near the canopy, others predict that strata in the midstory should be broadest. These hypotheses were tested using observational data of 92 rainforest bird species. Observations were made from or near a 40 m high canopy crane situated close to the Surumoni River (3°10′N, 65°40′W) near Esmeralda, Estado Amazonas, southern Venezuela (Surumoni-Crane-Project). I found a highly significant parabolic relationship between mean foraging height and its standard deviation showing that midstory bird species foraged in a broader stratum than either understory or canopy species. Using a conservative comparative method, I also showed that the relationship was not the result of the phylogenetic relatedness of the species involved. Analysis of previously published data supports the relationship for two other tropical avifaunas. Because the ground and the outer canopy represent geometric boundaries to the movement of most forest birds, two simulation models were used to test whether midstory species may simply have a broader stratum because they are less constrained in their movements than species near the boundaries. The ''random model'' allowed individuals to move randomly between the two boundaries. It illustrated that boundary constraints alone cannot explain the observed parabolic relationship. In the ''preference model,'' individuals tended to move back to their preferred height within the forest column. That model simulated the observed parabolic relationship once a sufficient number of time steps had been reached, suggesting that a simple combination of geometric boundaries and preference for a specific foraging height may generate narrower strata near the boundaries. The other hypotheses only explain the parabolic relationship if other factors (e.g. vegetation density) are vertically distributed in such a way as to generate the observed parabolic pattern. Finally, I briefly discuss the advantages and disadvantages of using raw data in across-species analyses versus corrected data in phylogenetically-controlled analyses. *Received 29 January 2001, accepted 15 April 2002.*

Resumen.—Las estratificación vertical de especies de aves ha sido estudiada intensamente en comunidades de aves tanto templadas como tropicales. Una pregunta que ha recibido menor atención es la variación de la amplitud de los estratos de forrajeo. Las hipótesis que intentan explicar esta variación están basadas en las diferencias en la percepción, evasión, adaptación, competencia y en las restricciones impuestas por los límites ambientales y geométricos. A pesar de que algunas hipótesis predicen que los estratos de forrajeo cercanos al suelo deberían ser más estrechos que aquellos cercanos al dosel, otras predicen que los estratos de forrajeo en el dosel medio deberían ser los más amplios. Puse a prueba estas hipótesis utilizando observaciones de 92 especies de aves de selva lluviosa. Las observaciones fueron realizadas desde o cerca de una grúa de dosel localizada cerca del río Surumoni (3°10′N, 65°40′O) cerca de Esmeralda, Estado Amazonas, sur de Venezuela. Encontré una relación parabólica altamente significativa entre la altura media de forrajeo y su desviación estándar, lo que muestra que las especies del dosel medio forrajean en un estrato más amplio

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que las del sotobosque o el dosel. Utilizando un método comparativo conservador, mostré que la relación encontrada no fue resultado de las relaciones filogenéticas de las especies involucradas. Análisis de datos previamente publicados apoyan la relación para otras dos avifaunas tropicales. Debido a que el sotobosque y el dosel exterior representan límites geométricos para el movimiento de la mayoría de las aves de bosque, utilicé dos modelos de simulación para determinar si las aves del dosel medio tienen estratos más amplios simplemente debido a que están menos restringidas en sus movimientos que especies cercanas a los límites. El ''modelo azaroso'' permitió a los individuos moverse al azar entre los dos límites. Éste mostró que las restricciones impuestas por los límites no pueden explicar la relación parabólica observada por sí solas. En el ''modelo de preferencia'' los individuos tendieron a moverse hacia sus alturas preferidas dentro de la columna del bosque. Este modelo simuló la relación parabólica observada una vez que un número suficiente de intervalos de tiempo fue alcanzado, sugiriendo que una combinación simple entre los límites geométricos y preferencia por una altura de forrajeo específica puede generar estratos más estrechos cerca de los límites. Las otras hipótesis sólo explican la relación parabólica si otros factores (e.g. densidad de la vegetación) se encuentran verticalmente distribuidos de tal manera que pueden generar el patrón parabólico observado. Finalmente, discuto brevemente las ventajas y desventajas de utilizar datos crudos en análisis entre especies contra datos corregidos mediante análisis filogenéticamente controlados.

THE STRUCTURE of forest bird communities depends on the habitat use and interactions of its members. Many factors shape forest communities, including resource availability, vegetation structure, and abiotic factors such as the weather (Cody 1985, Wiens 1989). Factors that are known to change with forest height are, for example, evaporation, temperature, wind (Longman and Jenik 1974, Richards 1996), ambient light (Endler 1993), foliage density, and resource, predator, and parasite abundance (references in Pearson 1971, Terborgh 1980, Walther et al. 1999). These factors may explain the phenomenon of vertical stratification of bird species that has been documented in temperate as well as tropical forest bird communities (Orians 1969, Pearson 1971, Smith 1973, Cody 1974, Anderson et al. 1979, Terborgh 1980, Greenberg 1981, Bell 1982, Cody 1985, Haffer 1988, Marra and Remsen 1997). Bird species remain in their respective strata presumably because they have adapted to the specific environmental conditions of each stratum. For example, the predominant availability of fruits in the canopy or as mast on the ground is a likely reason for most frugivores to be rather strict canopy birds or ground feeders (Terborgh 1980, Bell 1982).

Whereas many studies have documented the stratification of bird species, only a few studies have tried to explain the variation in the vertical breadth of foraging strata. The hypotheses that try to explain that variation are based on differences in perception, evasion, adaptation, competition, and environmental and geometric boundary constraints.

Based on observations showing that species near the ground have narrower strata than species living in the canopy (Orians 1969, Cody 1974, Anderson et al. 1979, Terborgh 1980), Cody (1974) hypothesized that this pattern may be explained by differently sized visual stimuli. Given that the just-perceivable differences between two visual stimuli should be proportional to the absolute magnitudes of those stimuli, he suggested that ''many important variables involved in displacement patterns, such as habitat variables, food sizes, and foraging heights, are discriminated by birds on the basis of relative rather than absolute magnitudes.'' Although the mechanisms leading from stimulus detection to behavioral choices remain unclear (see below), Cody suggested two outcomes. The first one assumes that the size differences of the visual stimuli increase with height, and therefore foraging strata become increasingly broader with a species' foraging height (Cody 1974). The second one assumes that the visual size differences vary with vegetation density and predicts that strata become broader in layers of lower vegetation density (M. Cody pers. comm.).

Another reason for this pattern may be that species living in the canopy move more vertically to evade light and heat stress. Tropical forest birds often shift downwards during midday when light levels and temperatures are highest (Pearson 1971, 1977; Bell 1982; Walther

2002). If canopy birds have a greater need to shift downwards than understory birds, the strata of canopy birds should be wider than those of understory birds.

Terborgh (1980) suggested further reasons for such a pattern. The first one is based on species being adapted to perform certain foraging techniques that consequently lead to differently broad foraging strata. For example, ground birds can usually only walk horizontally on the ground whereas woodpeckers climb up and down vertically on tree trunks. Thus, the vertical distribution of adequate foraging substrates may cause species to have different stratum breadths. Similarly, the vertical distribution of resources (e.g. food) may cause differential competition between species so that species may become more specialized and pack into narrower strata wherever resource availability is high (Marra and Remsen 1997).

Alternatively, Terborgh (1980) suggested that both the ground and canopy effectively are boundaries where several environmental factors change much more rapidly than in the midstory. He argued that the ground and canopy have an essentially ''two-dimensional character'' whereas the midstory provides a much more ''complex three-dimensional environment'' that may cause midstory species to have broader strata than either ground or canopy species. That hypothesis relies not on change in one, but several factors that change most rapidly at those environmental boundaries.

Terborgh (1980) finally hinted at another reason for that pattern, stating that stratum breadths are ''constrained within boundaries'' and ''maximum latitude is permitted to a species that chooses a mean position in the middle tier.'' The profound effect of geometric boundaries on distributional patterns of species richness has recently been realized (Colwell and Lees 2000). Geometric boundaries constrain the placement of distributional ranges of species, and a similar effect may influence stratum breadths in that individuals are not free to move beyond the boundary, thus constraining the breadth of their movements. Therefore, individuals of species foraging near a boundary (e.g. ground or canopy) would be constrained into smaller stratum breadths than individuals foraging in the midstory. To test possible out-comes of this novel hypothesis, two simulation models were developed. In the ''random model,'' individuals move randomly between the two boundaries, whereas in the ''preference model'' individuals tend to move back to their preferred foraging height within the forest column.

The perception, adaptation, and competition hypotheses cannot make any prediction about the vertical variation of stratum breadths without additional information about the vertical distribution of the size of visual stimuli, foraging substrates, or resources. Given certain assumptions (as stated above), all three hypotheses may predict an increase in stratum breadth with forest height. The evasion hypothesis, on the other hand, predicts that foraging strata are broader towards the canopy simply because the canopy is most exposed to light and heat increases during the day. On the other hand, both boundary hypotheses predict a completely different outcome in that strata should be broadest in the midstory and narrowest near the boundaries.

In this study, I use the results from two simulation models, observational data from my study site in a lowland Amazonian tropical forest, and data from two previously published studies to investigate whether predicted and observed variation of stratum breadths correspond with any of the hypotheses.

STUDY SITE AND METHODS

Study site.—Fieldwork was conducted in lowland tropical forests located in the catchment area of the upper Orinoco near Esmeralda, Estado Amazonas, southern Venezuela (65°32′W, 3°11′N, elevation ~110 m above sea level). Esmeralda lies within a patch of lowland grassland and scrub surrounded by lowland and flooded tropical evergreen, river-edge, river island, gallery, palm, and second-growth forests (cf. Stotz et al. 1996). Most soils are extremely poor in nutrients (arenolatosols and plinthi-humi-geric ferrosols). Low-lying areas are swampy and become regularly flooded during the rainy season because river levels can rise up to 4 m (Anhuf and Winkler 1999, Anhuf et al. 1999). Esmeralda is located almost at the centre of the Alto Orinoco-Casiquiare Biosphere Reserve (87,000 km²), which has so far been spared from extensive human disturbance. The only anthropogenic influences are hunting and slash-and-burn agriculture of the local native populations (Anhuf and Winkler 1999). Average daily temperatures are around 26°C, relative humidity ranges from 40–100%, and average annual precipitation is around

3,000 mm, ranging between 1,000–4,000 mm (Anhuf and Winkler 1999). The dry season usually lasts from December to March, and the rainy season from April to November with two precipitation peaks during May–July and September–October.

Most observations (~70%) were made from or near the 40 m high canopy crane situated ~15 km west of Esmeralda close to the mouth of the Surumoni river (65°40′W, 3°10′N, elevation ~105 m above sea level; Anhuf and Winkler 1999). The crane plot is characterized by lowland (*terra firme*) and flooded tropical evergreen forest. The forest canopy is usually between 15–30 m high, but some trees may be as tall as 35 m, although almost no emergents occur. Its structure is heterogeneous with small and large gaps, whereas the undergrowth is relatively dense (up to 10,000 stems >1 cm ha⁻¹). The remaining observations were made at six other forest sites near Esmeralda that covered a variety of forest habitats (lowland and flooded tropical evergreen, river edge, gallery, and second-growth forests).

Data collection.—All behavioral observations were made during two field seasons (May–June 1998, February–April 1999) between 0620 and 1830 h from either the ground or the crane. On the ground, observations were made during slow walks along narrow forest trails, covering all trails at least once during any observation day (trails covered a length of 400–1,000 m at each site). Whenever flocks of birds were encountered, they were followed as long as possible or until all species had been observed. The crane was operated by remote control from the cabin that can be moved to any point within the 1.5 ha study plot covered by the crane's 40 m jib and its 100 m long railtracks. Because of the crane's great mobility, flocks can be actively pursued. If necessary, I moved the cabin towards the bird or the flock and made observations as long as possible or until all species had been observed. The behavior of birds was not obviously disturbed by the crane's movements because no avoidance behavior was evident even when the cabin was within 10 m of a bird. I chose different observation points during the day, so that at least half the plot was covered during any observation day. Although most observations were made within and above the canopy because of the better view, the midstory was also regularly observed at various points within the plot wherever the forest structure allowed the cabin to be lowered into the midstory.

The overall goal was to establish when and where each species forages in a mature forest with a closed canopy. Any observations made at gap, edge, or secondary habitats were therefore excluded. Foraging was defined as any behavior that may lead to food consumption (e.g. searching, catching, and manipulating food, and movement within a flock). Unless it was clear that a species was resting (e.g. all vultures), sitting was interpreted as a food searching activity. Only behaviors that were obviously not food related

(e.g. preening, long-distance flying, nesting, or displaying to mates) were excluded. Likewise, all behaviors induced by the observer (e.g. reaction to song playback or evasion from the observer) were disregarded. Because of the great number of birds to be observed, especially during flock encounters, the instantaneous scan sampling method was used (Altmann 1974). Once a species had been observed, no new records were taken until 1 h had passed. For each observation, I recorded two measures of foraging height:

(1) *Stratum (categorical).*—The ground was defined as the soil, the leaf litter, and fallen tree trunks. The understory was defined to be the space between the ground and 3 m up. The midstory was defined as the space between the understory and the canopy. The canopy was defined as the space above 18 m or the space within the crown of the highest trees. In the analyses, the four strata are given the scores from 0 to 3; a score of 2.5, for example, means that the species occurs in both midstory and canopy. This classification was adopted from Parker et al. (1996).

(2) *Relative height (continuous).*—Relative height of the individual was calculated by dividing the height of the bird by the height of the forest canopy in the immediate vicinity of the bird (both in meters). Using relative instead of absolute height circumvents the problem of variable canopy height (Terborgh 1980). Estimates of height made from the crane are reliable because the crane's structure can be used to estimate height. Estimates made from the ground are less reliable, especially for the height of the canopy. However, estimates of relative height should still be reliable because any error would enter both height estimates. For these reasons, estimates of relative and not absolute height were used.

Other data sources.—Two previously published data sets contain data on absolute foraging heights of tropical bird species observed in Peru (Pearson 1971) and New Guinea (Bell 1982). These data are presented in such a way that, for each species, I could calculate the mean and the range of absolute foraging heights. Both data sets present percentage observations in each stratum (defined as height intervals in meters). I used the midrange of each stratum interval for calculations. For the New Guinean data set, 37.5 m was estimated for emergents (cf. fig. 3 in Bell 1982), and five aerial foragers were excluded (*Eurystomus orientalis*, *Collocalia esculenta*, *Collocalia vanikorensis*, *Hemiprocne mystacea*, *Merops ornatus*) for reasons outlined below (see below). I calculated the mean by multiplying the percentage observations in each stratum with its midrange, then summing over all strata and dividing by 100. I calculated the range by subtracting the minimum midrange from the maximum midrange. Unfortunately, these data did not allow the calculation of the standard deviation (see below).

To test for the possible influence of vegetation density on stratum breadth, I obtained data on the vertical distribution of vegetation density at my study site from N. Ellinger (pers. comm.). Using the crane, he descended on a rope and passed a 1 m stick in a horizontal circle at 1 m intervals. At each height, the number of leaves touching the stick was counted. Twenty-seven descents were made at regular 10 m intervals within a 90 × 30 m grid within the crane plot, and data from all descents were then averaged.

Analyses.—Location and dispersion of frequency distributions can be calculated in a number of ways (Sokal and Rohlf 1995, Zar 1996), but the most widely used statistics are the mean and standard deviation (Fowler and Cohen 1986). I used those statistics because they were also used in a previous analysis of the relationship between the mean and the standard deviation of foraging height (Terborgh 1980).

Because two hypotheses consider the ground and the outer canopy as boundaries, and the effects of such boundaries on stratum breadth are tested in the simulation models (see below), I needed to restrict the analysis to those species that are actually constrained in their foraging movements by those boundaries. All bird species are constrained in their movements by the ground, which is a nonpermeable boundary. However, the outer canopy is a permeable boundary because birds can cross the boundary to enter the airspace above it. Nevertheless, for most species, the outer canopy represents a foraging boundary because they never enter the airspace above it for the purpose of foraging. However, several species among the 92 species of the original data set (Table 1) use the airspace above the canopy for foraging. Those species typically sit on some exposed outer branch from which they sally out to catch insects. Therefore I excluded *Chelidoptera tenebrosa*, *Galbula leucogastra*, *Iodopleura isabellae*, and five flycatchers (*Empidonomus varius*, *Griseotyrannus aurantioatrocristatus*, *Myiodynastes maculatus*, *Myiozetes luteiventris*, *Tyrannus melancholicus*) from the analyses.

Because it is reasonable to expect that the error variances of the residuals near the boundaries are smaller than the error variances away from the boundaries, a weighted least-squares regression was used to fit a parabolic model ($y = b_2x^2 + b_1x + b_0$) to the data, using the program STATISTICA, version 5.1. That method applies the inverse values of the variances for the residuals as weights and computes weighted least-square estimates. I used that method for the across-species analysis. Such analyses have been criticized for disregarding the effects of phylogenetic relatedness of species on statistical tests and the resulting deductive logic (Harvey and Pagel 1991, Harvey et al. 1995, Nee et al. 1996). I nevertheless present such an analysis because it allows a direct graphical depiction of the relationship, and it may have ecological relevance (see below). However,

to control for the potential influence of phylogenetic relatedness of species on statistical results (i.e. to avoid pseudoreplication) and to understand how evolution proceeded, a phylogenetically controlled analysis should be performed (Harvey and Pagel 1991). Because of the problem of estimating ancestral states (Björklund 1997, Losos 1999), especially for ecological variables such as stratum use, I restricted the analysis to a comparison of extant sister taxa (Read and Nee 1995). To avoid assumptions about the magnitude of evolutionary change in relation to branch lengths, I analyzed the directions of sister taxa comparisons with a one-sample sign test. That is one of the most conservative methods to test comparative hypotheses because it makes the least assumptions about how evolution proceeds, considering only whether evolution in two characters repeatedly and independently proceeded in the same direction or not.

Sister taxa comparisons were generated within genera, families, and orders using published phylogenies (Forshaw 1973; S. M. Lanyon 1985; W. E. Lanyon 1985, 1988; Prum and Lanyon 1989; Ridgely and Tudor 1989, 1994; Hackett and Rosenberg 1990; Sibley and Ahlquist 1990; Birt et al. 1992; Helm-Bychowski and Cracraft 1993; Winkler et al. 1995; Burns 1997; Prum 1997; Espinosa de los Monteros 1998; Gerwin and Zink 1998; Miyaki et al. 1998; Bates et al. 1999; Lanyon and Omland 1999; Prum et al. 2000) and the program CAIC (Purvis and Rambaut 1995). In the subroutine Brunch, CAIC automatically selects sister taxa comparisons within the phylogeny in such a way that the lines linking compared species never meet or cross. Thus all comparisons are independent of each other.

Simulation model.—The model simulates the vertical movements of individual birds through the forest column and registers the locations of successive perches, but ignores the movements made between perches (e.g. flights above the canopy). Its main assumption is that the ground and the outer canopy represent geometric boundaries (*sensu* Colwell and Lees 2000) for perch availability. The second assumption is that individuals only make one of three choices: either move to a perch at the same height as the previous one, or move to a perch just below or above. I divided the forest column in 31 different perching heights (the number was chosen for good graphical depiction and because the forest at my study site is ~30 m high) of equal vertical distance from each other, with zero representing the ground and 30 representing the uppermost canopy. Each perching height represented the starting point for an individual's simulated movement through the forest column, resulting in 31 individuals moving through the forest column.

To determine the movements of individuals, I defined three probabilities; P_{up}, P_{down}, and P_{stay}, which respectively define the probabilities of moving to a

higher perch, a lower perch, or staying at the same level in a single time step. At each time step, an individual moves to a lower perch, stays at the same height, or moves to a higher perch if a random number generated by my simulation model falls within the respective probability interval (see Appendix for details).

I considered two variations of this basic model. The random model assumes that the probability of moving in any given direction is independent of current perching height (Fig. 1A), that is, an individual's preference for staying or moving up or down does not change with perching height. However, an individual perching on one of the boundaries effectively increases its probability of remaining at the boundary because it cannot move beyond the boundary. For example, if the individual is on the ground and the random number indicates it should move lower, it remains on the ground. To take into account that an individual can only choose between two instead of three new perches at the boundary, I additionally assume that probabilities of movement at each boundary are adjusted so that the probability previously associated with moving outside of the boundary (e.g. into the ground) is divided proportionately between the other two probabilities. That guarantees that the ratio between the original and the newly calculated probabilities remains the same.

The preference model assumes that each individual has a preferred perching height and that the probability of moving in any particular direction depends on its current perching height relative to its preferred height. This model assumes that preferences for individuals to move back towards their preferred perching height increase linearly with increased distance from the preferred perch, and that all individuals starting from different preferred perching heights have the same distance-related preferences. For example, for a ground bird (preferred height = 0), the adjusted probability of moving to a lower perch, P'_{down}, would increase from P_{down} at ground level to 1 at the top of the canopy whereas the adjusted probability of moving upwards, P'_{up}, would decrease from P_{up} at ground level to 0 at the top of the canopy (Fig. 1B). For individuals at preferred perching heights between the two boundaries, P'_{down} and P'_{up} change at the same linear rate, but never reach 0 or 1 (Fig. 1C). Like the random model, the preference model also adjusts the probabilities at the boundaries to take into account the impossibility of moving beyond the boundary.

Each simulation run registered the successive perches of 31 individuals starting from 31 different perching heights. For the preference models, the preferred height of each individual was assumed to be that individual's initial perching height. The total number of successive perches is the number of time steps for which the model was run. The mean and standard deviation were calculated for each indivi-

dual's successive perches. All simulation runs used the same set of random numbers so that a run with a higher number of perch changes initially used the same random numbers used by a run with a lower number of perch changes.

RESULTS

Across-species analysis.—I restricted the analysis to species that were observed at least 5 or 10 times (a total of 1,518 or 1,266 observations of 92 or 53 species, respectively). The resulting data set is presented in Table 1. Those species should, with few exceptions (e.g. very cryptic or nocturnal species), be the most abundant species at my study site. They should thus represent the core avifauna whose species are presumably the best adapted to the local ecological conditions (Remsen 1994).

For both measures of foraging height, stratum and relative height, the standard deviation is a parabolic function of the mean, with the maximum point close to the middle of the range of stratum and relative height (Fig. 2). A better fit is achieved for relative height than for stratum (explaining 73–79% vs. 60–64% of the variation, respectively). Likewise, plots of the mean versus the range of absolute height calculated from the data sets of Peruvian (Pearson 1971) and New Guinean (Bell 1982) birds also showed a highly significant parabolic relationship (Fig. 3).

At my study site, vegetation density was highest in the understory and the canopy and lowest in the midstory (Fig. 4), thus being the reverse of the relationships above. Dividing vegetation density into dense (>mean density) and open (<mean density) vegetation, Figure 4 shows that dense vegetation is found from 0.0–3.0 m and 20.5–30.0 m, and open vegetation is found in the much broader layer between those intervals. Consequently, vegetation density at the mean relative height of each species is negatively correlated with the standard deviation of the species' relative height (Fig. 5), meaning that species in denser vegetation have narrower foraging strata.

Phylogenetically controlled analysis.—For the comparative analysis, I needed a categorical variable to perform the sign test (see below). Therefore, I categorized each species into one of three relative height categories (Table 1). All comparative analyses were performed on those height categories.

Table 1. Ninety two bird species observed inside closed mature tropical evergreen forests near Esmeralda, Estado Amazonas, southern Venezuela.

Species	Sister taxa	Stratum	Relative height	Relative height category
Picumnus spec.[a]	1[4]	2.4 ± 0.2 (5), 2.0–3.0	0.73 ± 0.07 (5), 0.52–0.89	2
Veniliornis spec.[b]	2[6]	2.6 ± 0.1 (14), 2.0–3.0	0.76 ± 0.05 (14), 0.47–0.94	3
Piculus chrysochloros	2[6]	2.8 ± 0.2 (5), 2.0–3.0	0.74 ± 0.09 (5), 0.40–0.90	2
Celeus grammicus		2.5 ± 0.2 (10), 2.0–3.0	0.74 ± 0.04 (10), 0.57–0.93	2
Celeus elegans	3	2.1 ± 0.1 (15), 1.0–3.0	0.46 ± 0.06 (15), 0.10–0.85	2
Celeus flavus	3	3.0 ± 0.0 (5), 3.0–3.0	0.81 ± 0.07 (5), 0.57–0.96	3
Celeus torquatus		2.4 ± 0.2 (5), 2.0–3.0	0.745 ± 0.07 (5), 0.64–0.93	2
Capito niger	4[4]	2.8 ± 0.1 (75), 1.0–3.0	0.78 ± 0.03 (73), 0.08–0.97	3
Pteroglossus azara	4[4]	2.7 ± 0.1 (20), 2.0–3.0	0.74 ± 0.04 (20), 0.24–0.94	2
Ramphastos culminatus	5	2.7 ± 0.1 (27), 2.0–3.0	0.749 ± 0.06 (24), 0.14–1.00	2
Ramphastos cuvieri	5	2.8 ± 0.1 (21), 2.0–3.0	0.83 ± 0.04 (21), 0.42–1.00	3
*Galbula leucogastra**	1[4]	2.9 ± 0.1 (24), 2.0–3.0	0.83 ± 0.02 (23), 0.55–1.00	3
Notharchus macrorhynchos		3.0 ± 0.0 (17), 3.0–3.0	0.88 ± 0.02 (17), 0.72–1.00	3
Notharchus tectus		3.0 ± 0.0 (6), 3.0–3.0	0.89 ± 0.04 (5), 0.73–0.96	3
Monasa atra	6[4]	2.0 ± 0.1 (22), 1.0–3.0	0.39 ± 0.05 (18), 0.08–0.96	2
*Chelidoptera tenebrosa**	6[4]	3.0 ± 0.0 (15), 3.0–3.0	0.99 ± 0.01 (14), 0.88–1.00	3
Trogon melanurus	7[4]	2.7 ± 0.1 (5), 2.5–3.0	0.79 ± 0.05 (4), 0.72–0.93	3
Trogon viridis		2.5 ± 0.1 (25), 2.0–3.0	0.68 ± 0.04 (23), 0.20–0.93	2
Trogon violaceus		2.6 ± 0.2 (9), 1.0–3.0	0.68 ± 0.09 (9), 0.08–0.96	2
Momotus momota	7[4]	1.9 ± 0.2 (22), 0.5–3.0	0.42 ± 0.06 (20), 0.04–0.96	2
Coccyzus americanus	8[4]	2.3 ± 0.2 (9), 2.0–3.0	0.69 ± 0.04 (9), 0.57–0.97	2
Piaya melanogaster	8[4]	2.8 ± 0.2 (17), 0.5–3.0	0.77 ± 0.05 (16), 0.04–0.97	3
Ara macao		3.0 ± 0.0 (5), 3.0–3.0	0.97 ± 0.02 (5), 0.93–1.00	3
Brotogeris cyanoptera		3.0 ± 0.0 (12), 3.0–3.0	0.90 ± 0.02 (7), 0.80–0.95	3
Pionites melanocephala		3.0 ± 0.0 (13), 3.0–3.0	0.96 ± 0.02 (12), 0.72–1.00	3
Amazona farinosa		3.0 ± 0.0 (16), 3.0–3.0	0.92 ± 0.02 (11), 0.80–1.00	3
Phaethornis ruber		1.2 ± 0.1 (17), 1.0–2.0	0.15 ± 0.04 (17), 0.03–0.72	1
Thalurania furcata		2.0 ± 0.2 (14), 1.0–3.0	0.43 ± 0.08 (14), 0.06–0.83	2
Heliothryx aurita		2.2 ± 0.2 (16), 1.0–3.0	0.51 ± 0.07 (16), 0.10–0.88	2
Leptotila rufaxilla		0.4 ± 0.2 (9), 0.0–2.0	0.04 ± 0.02 (9), 0.0–0.16	1
Harpagus bidentatus	9[4]	3.0 ± 0.0 (9), 3.0–3.0	0.89 ± 0.02 (9), 0.80–0.96	3
Buteo magnirostris	9[4]	2.6 ± 0.2 (7), 2.0–3.0	0.69 ± 0.12 (5), 0.33–1.00	2
Zimmerius gracilipes		3.0 ± 0.0 (6), 3.0–3.0	0.94 ± 0.01 (6), 0.90–1.00	3
Tyrannulus elatus		3.0 ± 0.0 (14), 3.0–3.0	0.94 ± 0.01 (14), 0.86–1.00	3
Myiopagis gaimardii		3.0 ± 0.0 (5), 3.0–3.0	0.87 ± 0.04 (5), 0.73–0.96	3
Myiopagis caniceps		2.9 ± 0.1 (8), 2.5–3.0	0.85 ± 0.04 (8), 0.71–0.97	3
Lophotriccus galeatus	10[1]	1.9 ± 0.2 (5), 1.0–2.5	0.40 ± 0.11 (5), 0.08–0.70	2
Tolmomyias sp.[c]	10[1]	3.0 ± 0.0 (7), 3.0–3.0	0.90 ± 0.03 (7), 0.80–1.00	3
Myiobius erythrurus	11[4]	2.1 ± 0.2 (7), 1.5–3.0	0.41 ± 0.11 (7), 0.12–0.80	2
Laniocera hypopyrra	12[2,7]	1.7 ± 0.2 (7), 1.0–2.0	0.31 ± 0.07 (7), 0.07–0.52	2
*Tyrannus melancholicus**		3.0 ± 0.0 (6), 3.0–3.0	0.99 ± 0.01 (6), 0.97–1.00	3
*Empidonomus varius**		2.9 ± 0.1 (8), 2.5–3.0	0.96 ± 0.03 (8), 0.75–1.00	3
*Griseotyrannus aurantioatrocristatus**		3.0 ± 0.0 (8), 3.0–3.0	0.98 ± 0.01 (8), 0.89–1.00	3
*Myiodynastes maculatus**		3.0 ± 0.0 (8), 3.0–3.0	0.80 ± 0.04 (8), 0.64–1.00	3
*Myiozetetes luteiventris**	11[4]	2.8 ± 0.2 (6), 2.0–3.0	0.87 ± 0.06 (6), 0.60–1.00	3
Pachyramphus marginatus	13[7]	2.6 ± 0.1 (11), 2.0–3.0	0.74 ± 0.06 (11), 0.37–0.97	2
Tityra cayana	13[7]	3.0 ± 0.0 (8), 3.0–3.0	0.91 ± 0.04 (8), 0.64–0.97	3
*Iodopleura isabellae**	*12*[2,7]	3.0 ± 0.0 (16), 3.0–3.0	0.99 ± 0.01 (16), 0.92–1.00	3
Lipaugus vociferans	14[7]	2.3 ± 0.2 (5), 2.0–3.0	0.47 ± 0.09 (5), 0.25–0.80	2
Cotinga cayana		3.0 ± 0.0 (7), 3.0–3.0	0.88 ± 0.03 (7), 0.72–0.96	3
Xipholena punicea	14[7]	3.0 ± 0.0 (19), 3.0–3.0	0.95 ± 0.01 (14), 0.88–1.00	3
Cephalopterus ornatus		2.9 ± 0.1 (7), 2.0–3.0	0.87 ± 0.06 (7), 0.53–1.00	3
Pipra filicauda		1.7 ± 0.1 (16), 1.0–2.5	0.30 ± 0.04 (16), 0.07–0.62	2
Pipra erythrocephala		2.1 ± 0.1 (47), 1.0–3.0	0.48 ± 0.03 (46), 0.03–0.95	2
Pipra pipra	15[2,7]	1.4 ± 0.2 (5), 1.0–2.0	0.14 ± 0.02 (5), 0.08–0.20	1
Tyranneutes stolzmanni	15[2,7]	2.1 ± 0.1 (5), 2.0–2.5	0.46 ± 0.09 (5), 0.25–0.72	2
Thamnophilus aethiops	16	1.6 ± 0.3 (6), 0.5–2.0	0.13 ± 0.03 (6), 0.01–0.18	1
Thamnophilus amazonicus	16	2.2 ± 0.1 (17), 1.5–3.0	0.52 ± 0.05 (15), 0.16–0.80	2

TABLE 1.   Continued.

Species	Sister taxa	Stratum	Relative height	Relative height category
Pygiptila stellaris	17[3]	2.3 ± 0.1 (20), 2.0–3.0	0.62 ± 0.04 (20), 0.40–0.93	2
Thamnomanes caesius	18[3,5]	1.7 ± 0.1 (53), 1.0–2.5	0.27 ± 0.025 (47), 0.06–0.70	2
Myrmotherula guttata		1.0 ± 0.1 (10), 0.5–2.0	0.04 ± 0.01 (10), 0.01–0.16	1
Myrmotherula haematonota	17[3]	1.1 ± 0.1 (8), 1.0–2.0	0.08 ± 0.01 (8), 0.04–0.17	1
Myrmotherula axillaris		1.8 ± 0.1 (41), 1.0–3.0	0.27 ± 0.02 (41), 0.04–0.60	2
Myrmotherula longipennis		1.1 ± 0.1 (6), 1.0–1.5	0.10 ± 0.02 (6), 0.06–0.16	1
Myrmotherula menetriesii		1.8 ± 0.1 (17), 1.0–2.0	0.35 ± 0.05 (17), 0.03–0.65	2
Herpsilochmus dorsimaculatus	18[3,5]	2.9 ± 0.1 (16), 2.0–3.0	0.83 ± 0.024 (16), 0.64–0.97	3
Hypocnemis cantator		1.0 ± 0.0 (5), 1.0–1.0	0.08 ± 0.02 (4), 0.04–0.11	1
Hypocnemoides melanopogon		1.0 ± 0.1 (12), 0.5–1.5	0.07 ± 0.01 (10), 0.01–0.12	1
Hylophylax punctulata		1.4 ± 0.2 (5), 1.0–2.0	0.11 ± 0.04 (5), 0.02–0.20	1
Dendrocincla fuliginosa		1.8 ± 0.2 (5), 1.0–2.0	0.23 ± 0.08 (5), 0.01–0.44	1
Xiphorhynchus obsoletus		2.2 ± 0.1 (13), 2.0–3.0	0.47 ± 0.07 (13), 0.10–0.96	2
Xiphorhynchus guttatus		2.0 ± 0.0 (17), 2.0–2.0	0.38 ± 0.05 (17), 0.10–0.82	2
Formicarius colma		0.1 ± 0.1 (7), 0.0–0.5	0.00 ± 0.00 (7), 0.0–0.03	1
Viero olivaceus		3.0 ± 0.0 (25), 3.0–3.0	0.91 ± 0.01 (21), 0.77–0.97	3
Cyanocorax violaceus		2.9 ± 0.1 (8), 2.5–3.0	0.78 ± 0.03 (6), 0.70–0.89	3
Thryothorus leucotis		1.3 ± 0.2 (13), 1.0–3.0	0.13 ± 0.05 (10), 0.01–0.52	1
Dendroica striata	19[4]	3.0 ± 0.0 (16), 3.0–3.0	0.88 ± 0.02 (16), 0.75–0.96	3
Hemithraupis flavicollis		2.9 ± 0.0 (93), 2.0–3.0	0.87 ± 0.01 (93), 0.40–1.00	3
Tachyphonus cristatus		2.9 ± 0.0 (58), 2.0–3.0	0.84 ± 0.02 (57), 0.44–1.00	3
Thraupis palmarum		2.8 ± 0.1 (15), 2.0–3.0	0.83 ± 0.05 (14), 0.36–1.00	3
Euphonia rufiventris		3.0 ± 0.0 (13), 3.0–3.0	0.93 ± 0.02 (13), 0.80–1.00	3
Tangara velia		3.0 ± 0.0 (19), 3.0–3.0	0.93 ± 0.02 (19), 0.80–1.00	3
Dacnis flaviventer		3.0 ± 0.0 (18), 3.0–3.0	0.97 ± 0.01 (17), 0.90–1.00	3
Dacnis cayana		3.0 ± 0.0 (64), 2.0–3.0	0.90 ± 0.01 (64), 0.60–1.00	3
Chlorophanes spiza		3.0 ± 0.0 (18), 3.0–3.0	0.90 ± 0.02 (18), 0.72–1.00	3
Cyanerpes nitidus	20	3.0 ± 0.0 (57), 2.0–3.0	0.89 ± 0.01 (56), 0.54–1.00	3
Cyanerpes caeruleus	20	2.7 ± 0.1 (15), 2.0–3.0	0.68 ± 0.05 (15), 0.40–1.00	2
Pitylus grossus	19[4]	1.5 ± 0.6 (5), 0.0–3.0	0.35 ± 0.20 (5), 0.0–0.93	2
Psarocolius viridis		3.0 ± 0.0 (13), 3.0–3.0	0.94 ± 0.01 (12), 0.85–1.00	3
Gymnostinops bifasciatus		3.0 ± 0.0 (31), 2.0–3.0	0.91 ± 0.03 (27), 0.32–1.00	3
Cacicus cela		2.9 ± 0.1 (35), 2.0–3.0	0.82 ± 0.03 (29), 0.32–1.00	3
Icterus chrysocephalus		3.0 ± 0.0 (12), 3.0–3.0	0.95 ± 0.02 (9), 0.88–1.00	3

Names are taken from Sibley and Monroe (1990). Species with <5 observations for ''stratum'' were excluded. For stratum and relative height, mean ± 1 SE (sample size) and range (as minimum–maximum) are given. The last column gives the relative height category of each species whereby the three categories (1) ''ground and understory'', (2) ''midstory'', and (3) ''canopy'' were defined as the intervals 0.0–0.02499, 0.25–0.7499, and 0.75–1.0 of relative height (see text), respectively. The 20 sister taxa generated by the CAIC program (see text) and differing in the relative height category (last column) are indicated with successive numbers. References used for determining sister taxa were: [1]Lanyon 1988, [2]Prum and Lanyon 1989, [3]Hackett and Rosenberg 1990, [4]Sibley and Ahlquist 1990, [5]Ridgely and Tudor 1994, [6]Winkler et al. 1995, and [7]Prum et al. 2000. Congenerics were assumed to be sister taxa. Note that for the *Celeus elegans–Celeus flavus* comparison, the standard errors do not reflect the magnitudes of the standard deviations whose magnitude is reversed (i.e. the standard deviations of relative height are 0.06 and 0.02 for *C. elegans* and *C. flavus*, respectively). Species that foraged in the airspace above the canopy are marked with an asterisk (*). Because the data given for those species in this table only relate to their perches in the canopy, the data do not reflect the true breadth of their foraging strata. Therefore, these species were excluded from the analyses (see also text). Because all observations were based on visual and sometimes vocal identifications, three taxa could only be identified to the genus level because the presence of very similar congenerics could not be excluded.

[a] Only *Picumnus exilis* has so far been determined with certainty at the study site, but the presence of *P. lafresnayi* or *P. pumilus* cannot be excluded. These three species are almost impossible to distinguish visually in the field (Winkler et al. 1995).

[b] Because of the uncertain taxonomic status of *Veniliornis affinis* and *V. cassini* (Sibley and Monroe 1990), observations of both species were lumped.

[c] *Tolmomyias* species could be present at my study site (*T. assimilis*, *T. poliocephalus*, and *T. sulphurescens*), but they are almost impossible to distinguish visually in the field (Ridgely and Tudor 1994).

I found that certain families predominated in each height category (Table 2). Near the ground, antbirds and relatives (Thamnophilidae, Furnariidae, Formicarridae) made up 70% of all species. However, they only represented 22% of species in the midstory and dropped to 2% in the canopy. Almost absent from the understory, flycatchers and relatives (Tyrannidae) represented the largest family in the midstory and canopy with 25 and 32% of species, respectively. Furthermore, tangers and relatives (Fringillidae) represented a further 30% of can-
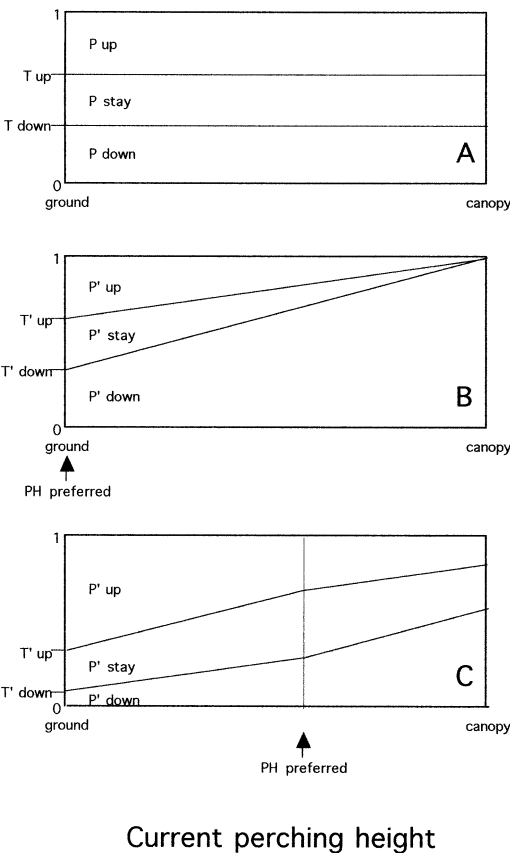
Current perching height

FIG. 1.   Plots of probability ranges. (A) In the random model, probability ranges are equal for all current perching heights. (B) Probability ranges for a ground bird (PH$_{preferred}$ = 0) in the preference model. Whereas P'_{down} increases linearly with current perching height, P'_{up} decreases linearly. (C) Probability ranges for individuals at preferred perching heights between the two boundaries ($0 <$ PH$_{preferred} < 1$) in the preference model. P'_{down} and P'_{up} change at the same linear rate as in (B), but never reach 0 or 1.

opy species, but were hardly found in the midstory and were absent in the understory. Those examples indicate that the parabolic relationship described above (Figs. 2 and 3) may be inflated by related species foraging at the same relative height.

Therefore, a phylogenetically controlled analysis was performed. Given that the midstory category typically had a broader stratum than the other two categories (cf. Table 1; mean relative height of ground and understory category = 0.22 ± 0.20 (mean ± 1 SD), midstory category = 0.53 ± 0.17, and canopy
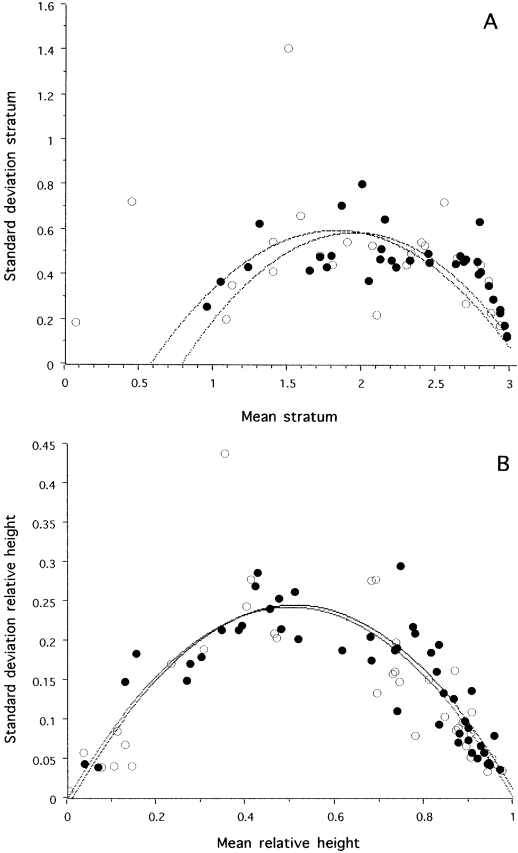

FIG. 2.   Plots of the mean versus the standard deviation of (A) stratum and (B) relative height for 84 and 82 South American tropical forest bird species, respectively. See text for definitions of stratum and relative height. Species with $n \geq 5$ or $n \geq 10$ observations are depicted with open and filled circles, respectively. All weighted least-squares regression models fits were significant at the $P < 0.0001$ level (stratum for $n \geq 5$ or $n \geq 10$ observations, respectively: $y = -0.38x^2 + 1.39x - 0.67$, maximum point at (1.83, 0.60), $F = 61.4$, df = 2 and 81, $r^2 = 0.60$, and $y = -0.43x^2 + 1.68x - 1.05$, maximum point at (1.94, 0.58), $F = 41.0$, df = 2 and 46, $r^2 = 0.64$; relative height for $n \geq 5$ or $n \geq 10$ observations, respectively: $y = -0.97x^2 + 0.97x + 0.001$, maximum point at (0.50, 0.24), $F = 108.7$, df = 2 and 79, $r^2 = 0.73$, and $y = -0.98x^2 + 1.00x - 0.009$, maximum point at (0.51, 0.24), $F = 80.1$, df = 2 and 44, $r^2 = 0.79$).

category = 0.89 ± 0.06; mean standard deviation of ground and understory category = 0.07 ± 0.06, midstory category = 0.22 ± 0.06, and canopy category = 0.09 ± 0.05), I expected the taxon foraging in the midstory to forage in a broader stratum than its sister tax-
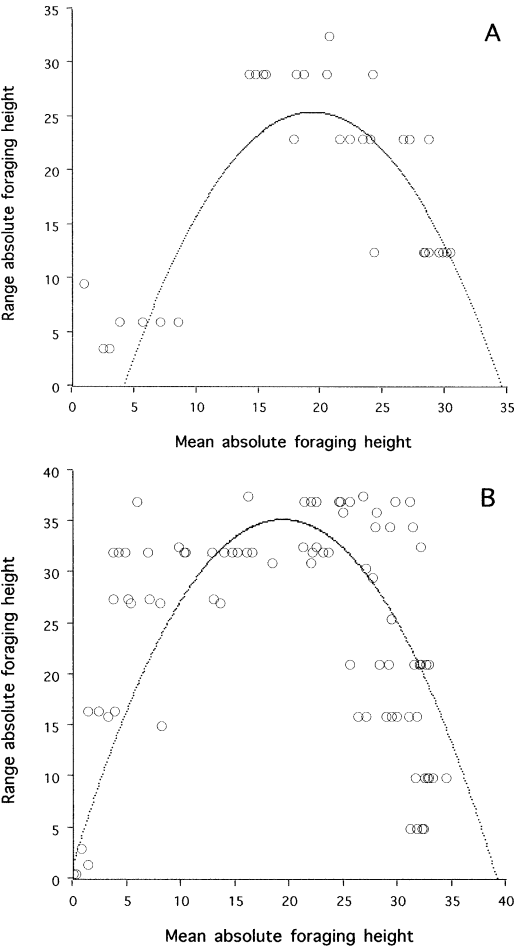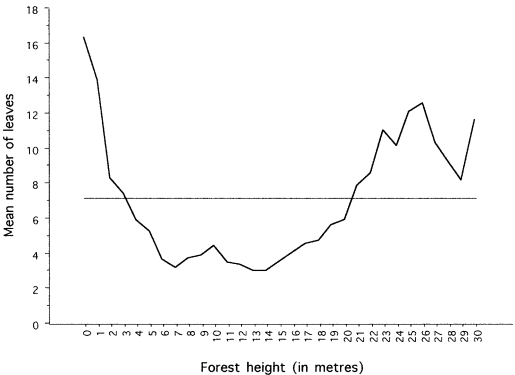
FIG. 4. Plot of forest height versus vegetation density, that is, the mean number of leaves. Data points were smoothed by averaging over a symmetrical 3 m interval. The thin line indicates mean density which was 7.0 ± 3.7 (mean ± 1 SD).

opy or the ground taxon (one sample sign test, $n = 16$, $P = 0.0005$).

Simulation model.—I used three different thresholds $T_{down} = 1/6$, $1/3$, and $1/2$ for all models. I found the results for all thresholds to be similar, except that the overall effects were observed at lower numbers of time steps if T_{down} increased. Therefore, I only present results for $T_{down} = 1/3$ in which case $P_{down} = P_{stay} = P_{up}$. I increased the number of time steps four-fold (16, 64, 256, 1,024, 4,096, and 16,384) because I found that model effects could thus be more easily depicted.

With 4,096 time steps or higher, all runs of the random model ended up with all individuals covering the entire range (0–30) of avail-

FIG. 3. Plots of the mean versus the range of absolute height (both in meters) for (A) 37 Peruvian ($y = -0.11x^2 + 4.03x - 11.4$, maximum point at (18.3, 25.5), $F = 38.7$, df = 2 and 34, $r^2 = 0.70$), and (B) 95 New Guinean tropical forest bird species ($y = -0.09x^2 + 3.30x + 5.03$, maximum point at (18.3, 35.3), $F = 42.1$, df = 2 and 92, $r^2 = 0.48$). Both weighted least squares regression model fits were significant at the $P < 0.0001$ level.

on foraging either in the canopy or near the ground. Twenty-five sister taxa comparisons were inconclusive because both taxa foraged in the same relative height category (Table 1). Among the remaining 20 sister taxa comparisons, four comparisons were excluded because one sister taxon foraged in the airspace above the canopy (see above). Of the remaining 16 comparisons, 15 showed that the standard deviation for relative height was larger for the midstory taxon than for either the can-
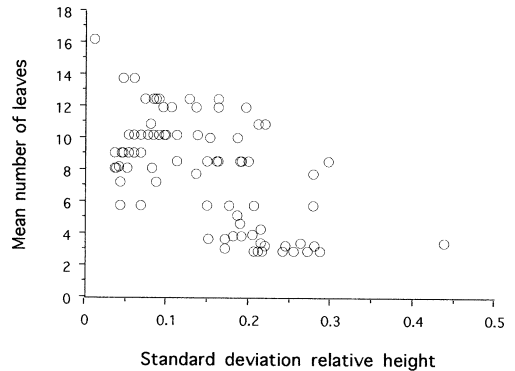

FIG. 5. Plot of vegetation density (mean number of leaves) versus the standard deviation of relative height for 82 bird species (model I linear regression, $F = 43.5$, df = 1 and 80, $r^2 = 0.35$, $P < 0.0001$).

TABLE 2. Number of species in each family (as defined by Sibley and Monroe 1990) for three relative height categories (defined in Table 1).

Number of species	Family
	Relative height category
	Ground and understory
7	Thamnophilidae
1	Trochilidae, Columbidae, Tyrannidae, Furnariidae, Formicariidae, Certhiidae
	Midstory
8	Tyrannidae
5	Picidae, Thamnophilidae
2	Ramphastidae, Trogonidae, Trochilidae, Furnariidae, Fringillidae
1	Bucconidae, Momotidae, Coccyzidae, Accipitridae
	Canopy
15	Tyrannidae
14	Fringillidae
4	Psittacidae
3	Bucconidae
2	Picidae, Ramphastidae
1	Galbulidae, Trogonidae, Coccyzidae, Accipitridae, Thamnophilidae, Vireonidae, Corvidae

able perches, that is, the range was equal for all individuals. Therefore, the range is not an appropriate statistic for a large number of time steps. Instead, I used the standard deviation as the dependent variable as in the analyses above.

The results show a clear difference between the random and the preference model (Table 3). The random model only produced a parabolic relationship for a medium number of time steps, but that relationship was not apparent at a low or high number of time steps. On the other hand, the preference model consistently produced a strong parabolic relationship very similar to the relationships depicted in Figures 2 and 3 as soon as the number of time steps passed 256.

DISCUSSION

This study provides evidence that midstory species of tropical rainforests forage in a broad-

TABLE 3. Weighted least-squares regression models for the relationship between the mean (independent variable varying from 0–30) and the standard deviation (dependent variable) of relative perching height.

Time steps	Model equation	Maximum (x, y)	r^2 value	F value	P value
		Random model			
16	$y = -0.002x^2 + 0.05x + 0.98$	14.9, 1.37	0.06	0.85	0.44
64	$y = -0.005x^2 + 0.12x - 1.97$	12.9, 2.77	0.19	3.31	0.05
256	$y = -0.022x^2 + 0.63x + 1.32$	14.4, 5.86	0.38	8.66	0.001
1,024	$y = -0.048x^2 + 1.47x - 3.20$	15.3, 8.09	0.69	30.5	<0.0001
4,096	$y = -0.032x^2 + 0.94x + 1.55$	14.8, 8.47	0.14	2.33	0.12
16,384	$y = 0.016x^2 - 0.39x + 10.8$	12.0, 8.49	0.07	0.99	0.39
		Preference model			
16	$y = -0.001x^2 + 0.03x + 1.01$	14.1, 1.20	0.04	0.62	0.55
64	$y = -0.001x^2 + 0.02x + 1.94$	8.42, 2.01	0.07	1.11	0.34
256	$y = -0.006x^2 + 0.17x + 1.70$	14.8, 2.98	0.33	6.80	0.004
1,024	$y = -0.007x^2 + 0.22x + 1.47$	15.5, 3.17	0.58	19.4	<0.0001
4,096	$y = -0.008x^2 + 0.26x + 1.49$	15.2, 3.49	0.83	67.5	<0.0001
16,384	$y = -0.007x^2 + 0.22x + 1.76$	14.9, 3.42	0.87	93.0	<0.0001

Results from two different simulation models (random and preference) are presented, whereby each model was run for different numbers of time steps (see text). For each number of time steps, the model equation and its maximum point are given as well as the r^2 value, F value and overall P value (for all models, $n = 31$ and df = 2 and 28).

er stratum than either understory or canopy species. Those results held regardless of which measure of foraging height (stratum or relative height) was used. They also held if a different measure of location (the median) was used (B. A. Walther unpubl. results). In addition, they were insensitive to different sample sizes and were confirmed if phylogenetic relatedness of species was taken into account. One may also question whether the rare species that were excluded from the analysis due to low sample sizes may change the observed relationship. This possibility remains to be investigated. However, I found a similar although weaker relationship when I included all species with sample sizes $n \geq 3$ (B. A. Walther unpubl. results).

The results also suggest that relative height is a better estimate of stratification than either stratum or absolute height. Stratum is necessarily a coarser measure because it is a categorical variable instead of a continuous one. The relationships were weaker for stratum than for relative height as indicated by the lower r^2 values (Fig. 2). Absolute height is also a poorer measure than relative height because of the variable height of the forest (Terborgh 1980). Nevertheless, the relationship between the mean and the range for absolute height among both Peruvian and New Guinean birds had the same overall shape (Fig. 3).

Terborgh (1980) suggested that such a parabolic relationship could have also been found in his Peruvian avifauna, but he was unable to substantiate it because his ground-based observations of the canopy were ''biased downwards due to poor visibility.'' In this study, this shortcoming of many previous studies of tropical bird communities (Munn and Loiselle 1995) was circumvented by using a crane for detailed observations of canopy birds. Access to the canopy was absolutely essential for establishing the observed relationship. Many canopy species are usually invisible from the ground within continuous forest, but could be easily observed from the crane. Despite considerably improving observational opportunities, having access to just one canopy crane cannot eliminate the problem of pseudoreplicating observations of territorial species (Munn 1985). However, whenever canopy species were observed at alternative forest sites (which are included in all analyses), they did not behave differently from those observed at the crane site.

Diurnal and seasonal variation of foraging height has been observed in tropical forest birds (Pearson 1971, 1977; Bell 1982). This study includes observations made during all daylight hours over five months. Although the species at that study site showed diurnal shifts in foraging heights (Walther 2002), those variations were not substantial enough to change the overall relationship reported here. I also found no disjunct distributions (e.g. species foraging for fruit and nectar in the canopy and for insects in lower strata) like those that Bell (1982) reported.

It may not be easy to disentangle the reasons for the observed parabolic relationship because several mutually nonexclusive hypotheses may explain it. Clearly, the two-boundary hypotheses both explicitly predict the observed pattern. Terborgh's (1980) hypothesis assumes that a whole suite of environmental factors changes most rapidly at the boundaries, causing the layers of suitable microhabitats to be narrower at the boundaries (Orians 1969 provides similar arguments). Direct measurements of many variables would be the ideal way of testing that hypothesis, but such measurements are extremely difficult to obtain in rainforests (Terborgh 1980). Instead, Terborgh (1980) used the ''mildly circular procedure of guild analysis.'' I will not repeat his analysis, but I agree with Terborgh (1980) that the predominance of certain families at each relative foraging height category (Table 2) suggests that combinations of structures, resources and conditions are most amenable to certain guilds at particular foraging heights.

For example, it is rather obvious that walking ground birds are ''grounded'' by their very style of movement. Most understory antbirds use the narrow, but dense layer of small vertical stems for foraging. That layer, however, impedes sallying flycatchers that are more abundant in the more open midstory and canopy. Likewise, trunks for foraging woodpeckers and vegetational structures for dead-leaf foraging antbirds are found throughout the midstory, often extending into the understory and canopy. On the other hand, tanagers are mostly found in the narrow canopy layer where fruits can be found. To most canopy birds, the outer canopy probably represents a two-dimensional surface over which to ''surf'' in search of food (Orians 1969, Pearson 1971, Terborgh 1980). That sup-

position is supported by the observation that many canopy birds are also found outside continuous forest in scrub and other more open habitats that have environmental conditions similar to those of the canopy (Orians 1969, Terborgh and Weske 1969, Pearson 1971, Greenberg 1981). Observation supports that supposition. Of the 92 observed species, only 4 of 45 species (9%) foraging below the canopy (relative height categories 1 and 2, see Table 1), but 14 of 47 species (30%) foraging in the canopy (relative height category 3) were also observed outside continuous forest, for example in scrub or gardens (whereby these percentages are low estimates because observations in other habitats were only made incidentally). The different stratum breadths may thus result from each species' foraging requirements being found in narrow layers near the ground and in the outer canopy, but in a much broader layer in the midstory.

However, the simulation models suggest another intriguing possibility for the observed relationship. The simple combination of geometric boundaries and preference for a specific foraging height may generate narrower strata near the boundaries (Table 3). Whereas the preference for a specific foraging height would presumably be the result of specific foraging adaptations (as outlined above), the different breadths of the foraging strata need not be the result of several environmental factors acting in concert, but would be the result of a single environmental variable. That variable is the presence of geometric boundaries constraining the random movements around the preferred foraging height. Equal preferences to move back to the initial foraging height cause vertical movements to be more confined near the boundaries than in the middle section of the forest column.

The random model does not consistently generate the observed relationship. Individuals without any preferred foraging height may end up foraging in any part of the forest column, following a path of Brownian motion through the forest column. Consequently, given a sufficient number of time steps in the random model, all individuals cover the entire range between the boundaries. However, at a medium number of time steps, even the random model yields a parabolic relationship because individuals starting near the boundary bump more often into the boundary than individuals starting further away from the boundary. Therefore, the parabolic relationship may even be the result of individuals choosing the same initial foraging height every morning, after which they may move completely randomly. As long as their rate of movement is such that individuals starting near the boundary do not escape its constraining effects, even a simple preference for an initial foraging height may result in narrower strata near the boundaries. Without a preference of some kind, however, no parabolic relationship would be observed.

The behavioral mechanism behind this relationship could be very simple. Individuals simply monitor their approximate height within the forest, and return to their preferred height whenever they stray too far from it. There is no need for Terborgh's (1980) claim that understory and canopy species "are behaviorally specialized in the sense that they occupy narrower foraging zones." Rather, their behavioral decisions may all be equal, but through the interaction with the boundaries, the consequences of their decisions lead to narrower strata.

As outlined above, none of the other hypotheses explicitly predict the parabolic relationship. However, with the exception of the evasion hypothesis, the perception, adaptation, and competition hypothesis may also explain the observed relationship given that the vertical distribution of the size of visual stimuli, foraging substrates, or resources are distributed in such a way as to generate the observed pattern. One variable that has been mentioned in connection with all three hypotheses is vegetation density. Because the dense vegetation layers in the understory and canopy in the present study plot are narrower than the more open layer in the midstory (Fig. 4), and vegetation density is correlated with stratum breadths (Fig. 5), vegetation density may very well explain the differences in stratum breadths. Vegetation density, of course, cannot explain the stratification of species itself, because similar vegetation densities in the canopy and understory are not occupied by the same but by different species.

The adaptation hypothesis may explain the parabolic relationship if vegetation density is one of the important variables controlling foraging choices. For example, gleaners may prefer dense understory vegetation and salliers

may prefer open midstory vegetation (Terborgh 1980). Individuals would simply monitor whether they are still within their preferred vegetation density. Likewise, the competition hypothesis (Marra and Remsen 1997) may explain the observed pattern if vegetation density is correlated with resource availability. The denser layers in the understory and canopy would allow denser species packing, with more specialized species occupying narrower strata. Other studies have observed similar packing of related species in the same foraging stratum (Pearson 1971, Greenberg 1981, Terborgh 1985, Haffer 1988).

Although it is relatively easy to imagine that vegetation density may correlate with the distribution of foraging substrates or resources, the perception hypothesis is based on the much more tentative assumption that vegetation density correlates with the just noticeable differences of visual stimuli. Although these results are inconsistent with Cody's (1974) original hypothesis that predicted broader strata with increasing foraging height, they are consistent with his second hypothesis involving vegetation density (M. Cody pers. comm.). However, whether birds really scale their visual environment in the way Cody (1974) imagined can only be determined experimentally. His hypothesis also assumes that all bird species perceive their visual environment in a similar manner, which is rather unlikely (Goldsmith 1990, Thompson et al. 1992). Moreover, Cody's hypotheses lack a clear behavioral mechanism that leads from stimulus detection to different stratum breadths. To illustrate that problem, it is helpful to imagine that individual birds move through layers of high and low vegetation density of equal breadth. Cody's hypothesis would require that an individual remains within a smaller stratum in the high-density layer than in the low-density layer. Starting from an initial foraging height, individuals would have to continuously monitor how far they are away from their initial perch, for example by counting the number of visual stimuli they have passed. Although such a mechanism may be possible, a much more straightforward mechanism would be if individuals simply stay within their preferred vegetation density (as in the adaptation hypothesis).

The observed relationship certainly does not support the evasion hypothesis. Even though tropical forest birds shift downwards during midday when light levels and temperatures are highest (Pearson 1971, 1977; Bell 1982; Walther 2002), such movements are either too restricted to affect the observed relationship or are performed by all bird species except for those very close to the ground.

Although vegetation density may be one of the explanatory factors of the observed relationship, it is unlikely to be the only one. Terborgh (1985) cautioned that "in the association between avian diversity and structural complexity of the habitat, one does not find a cause and effect relationship, merely a seductive correlation." Because birds generally choose habitats on the basis of resource availability and shelter from abiotic factors, predators, and parasites, vegetation density is probably just a correlate of some more vital factor. Most likely, overall stratification of species is due to adaptation and specialization of species to the various environmental conditions found in each specific forest stratum. Variation in stratum breadth, however, may be due to species near the boundaries having narrower strata either because several environmental factors change more rapidly at the boundaries, causing favorable conditions to be found in narrower layers near the boundaries, or because species are simply more constrained in their movements by geometric boundaries as they move around a preferred foraging height. The problem is that the geometric boundaries coincide with the environmental boundaries. It may therefore be difficult to distinguish between these two hypotheses. It is noteworthy, however, that species from different families (and therefore presumably from different foraging guilds) all had similar stratum breadths at equal foraging heights, which may not be expected if species mapped various environmental factors (which would presumably differ for different foraging guilds), but which would be expected from the preference model.

The random model and preference model could both be said to be null models (*sensu* Gotelli and Graves 1996) in that they describe the pattern that should be observed given minimal assumptions. Of course, one could imagine more complicated models. For example, given the lower vegetation density in the midstory, perch distances may not be equally spaced, but further apart in the midstory, which may lead

to broader strata. Certainly, studying the effect of boundary constraints on the movement of individuals will lead to many other nonintuitive conclusions, just as in the study of species richness patterns (Colwell and Lees 2000).

This study is the first to provide a phylogenetically controlled analysis of the parabolic relationship to back up the across-species analysis using raw species data. Both types of analyses have their advantages and disadvantages, and a formidable war of words has been raging over the question whether ecological questions need to take into account the evolutionary history of the species examined (e.g. Harvey et al. 1995, Westoby et al. 1995, Nee et al. 1996, Björklund 1997, and references therein). At the risk of adding to the fusillade, it should be pointed out that across-species analyses are informative because they may reveal an overall pattern that may be harder to discern in comparative analyses (thus avoiding a Type II error). Furthermore, the overall raw species pattern may have ecological significance. For example, a species that ranges in a broader stratum may encounter more prey, predators, or parasites. Likewise, predators interact with the present distribution of species in the forest, regardless of their evolutionary history (Walther et al. 1999). Finally, using raw species data may avoid errors introduced by the comparative methodology itself (Losos 1999), especially when the raw data values vary so much that comparative methods seem unwarranted (Björklund 1997). However, across-species analyses can never completely control for the possibility of pseudoreplication, because related species may share unknown characters that cause them to do similar things (thus creating a Type I error). Therefore, it is much more convincing and satisfying to determine independent evolutionary events that confirm that an associative pattern has evolved several times (Harvey and Pagel 1991, Read and Nee 1995, Nee et al. 1996). Both types of analyses should be used until it has been firmly established when comparative methods need to be used and how they should be applied. If results from both analyses disagree, further data and analysis may be needed. However, in this study, results from both analyses are in agreement, and the phylogenetically controlled analysis used one of the most conservative methods to test comparative hypotheses.

To summarize, I found a highly significant parabolic relationship showing that midstory bird species forage in a broader stratum than either understory or canopy species. Although similar parabolic relationships were observed in two other tropical avifaunas, it may be premature to assess the generality of that relationship. However, even in temperate forests, access to the canopy is crucial to resolve this or any other question relating to patterns of stratification (e.g. Walther et al. 1999). Therefore, the establishment of a worldwide network of canopy cranes or other methods of canopy access would significantly advance the study of stratification patterns (Stork 1997).

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Associate Editor: S. J. Hackett

APPENDIX. Consider a forest column divided into n different perching heights of equal vertical distance from each other, with zero representing the ground and $n - 1$ representing the uppermost canopy. Each perching height represents the starting point for an individual's simulated movement through the forest column, hence there are n individuals moving through the forest column.

Movements of individuals are defined according to probabilities of moving up, down, or remaining stationary. Let P_{up}, P_{down}, and P_{stay} be the probabilities of moving up a single perch, down a single perch, or remaining on the same perch, respectively. Because

those are the only possible actions that an individual can make in a single time step, these probabilities sum to one. These probabilities are used to define two thresholds T_{down} and T_{up}, which partition the interval (0,1). The two models differ in the way that these threshold values are calculated (see below).

At each time step, a random number u is chosen for each individual and its movement is simulated according to the following decision rule.

If

$$u < T_{down} \qquad \text{individual moves to a lower perch,}$$

$$T_{down} \leq u \leq T_{up} \quad \text{individual stays on perch,}$$

$$u > T_{up} \qquad \text{individual moves to a higher perch.} \qquad (1)$$

All random numbers were generated using the ''ran1'' function (Press 1989) that has a uniform distribution between 0 and 1.

The random model assumes that the probabilities remain constant over all current perching heights (Fig. 1A), that is, an individual's preference for staying or moving down or up do not change regardless of its current perching height. Hence,

$$T_{down} = P_{down},$$

$$T_{up} = P_{down} + P_{stay} = 1 - P_{up}. \qquad (2)$$

In addition, it was assumed that the probability of moving up or down is the same, that is, $P_{down} = P_{up}$ so that the thresholds are symmetrical, that is, $T_{down} = 1 - T_{up}$.

It was also assumed that probabilities change at each boundary to account for the fact that movement cannot be made past the boundaries. The probability of moving outside of the boundary is reassigned proportionately among the other two probabilities, so that the ratio between the original and the newly calculated probabilities remains the same. Hence, at the lower boundary,

$$T'_{down} = P_{down} = 0,$$

$$T'_{up} = P_{stay} = \frac{T_{up} - T_{down}}{1 - T_{down}}, \qquad (3A)$$

and at the upper boundary,

$$T'_{down} = P_{down} = \frac{T_{down}}{T_{up}},$$

$$T'_{up} = P_{down} + P_{stay} = 1, \qquad (3B)$$

where, T_{up} and T_{down} are as defined in Equation 2.

The preference model assumes that the probabilities change as a linear function of the distance between an individual's current perching height and its preferred perching height (Fig. 1B–C). Let x_{ph} be an individuals preferred perching height. Then,

$$T'_{down}(x) = \begin{cases} T_{down}\dfrac{(x_{ph} - x)}{n}, \\[1ex] \quad \text{if } (x_{ph} - x) \geq 0 \\[2ex] T_{down} + (1 - T_{down})\dfrac{(x_{ph} - x)}{n}, \\[1ex] \quad \text{if } (x_{ph} - x) < 0 \end{cases} \qquad (4A)$$

and

$$T'_{up}(x) = \begin{cases} T_{up}\dfrac{(x_{ph} - x)}{n}, \\[1ex] \quad \text{if } (x_{ph} - x) \geq 0 \\[2ex] T_{up} + (1 - T_{up})\dfrac{(x_{ph} - x)}{n}, \\[1ex] \quad \text{if } (x_{ph} - x) < 0 \end{cases} \qquad (4B)$$

where x is the current height of the individual and n is the total number of perches. In the simulations presented in this study, n was set to 31. It was also assumed that the probabilities change at the boundaries in the same way as in the random model. Hence, thresholds for the preference model are calculated using Equation 4 with the thresholds at the boundaries subsequently adjusted using Equation 3.