

## **Vertical stratification and use of vegetation and light habitats by Neotropical forest birds**

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### **Summary**

The vertical stratification of bird species has been intensively studied in both temperate and tropical bird communities. I investigated the vertical stratification of bird species and their use of vegetation structures and light habitats using observation data from 92 rainforest species. Most observations were made from a 40 m high canopy crane situated close to the Surumoni river (65°40'W, 3°10'N) near Esmeralda, Estado Amazonas, southern Venezuela. Further observations were made at several forest sites nearby. Previous analyses had shown that bird species foraged in stratified vertical niches, with wider niches for midstorey birds than for either canopy or understorey birds. In this study, I used across-species as well as phylogenetically-controlled analyses to correlate the vertical position of bird species with variables relating to vegetation structures and the amount of illumination. I found that species which foraged low in the forest were mostly found in small gap and forest shade light habitats, while species that foraged high were mostly found in large gap and woodland shade light habitats. Furthermore it was the lower-foraging species that were more often found in dimmer light conditions inside denser cover. In correspondence with their wider vertical niches, midstorey birds foraged in a wider range of light habitats and illumination than either canopy or understorey birds. While preserving their overall stratification, species actively moved within their preferred stratum, e. g. downwards and into denser vegetation during hours of strong sunlight and around midday when temperatures are highest. Bird activity appeared to be lowest shortly after midday, as I discovered when controlling for the effects of chance encounters with multi-species flocks. These observations are important not only for the determination of foraging niches, but also for the study of crypsis and the conspicuousness of a bird species in relation to its foraging stratum.

**Keywords:** Amazon, bird community, niche, vegetation density, diurnal behavioural changes.

### **Zusammenfassung**

#### **Vertikale Stratifizierung und die Benutzung der Vegetation und der Lichthabitate von südamerikanischen Waldvögeln**

Die vertikale Stratifizierung von Vogelarten ist sowohl in temperaten als auch in tropischen Vogelmgemeinschaften intensiv untersucht worden. Ich untersuchte die vertikale Stratifizierung von Vogelarten und deren Benutzung von Vegetationsstrukturen und Licht-

habitaten mit Beobachtungsdaten von 92 Regenwaldarten. Die meisten Beobachtungen wurden von einem 40 m hohen Baumkronenkranz aus gemacht, welcher sich in der Nähe des Surumoni-Flusses (65°40'W, 3°10'N) nahe der Ortschaft Esmeralda, Estado Amazonas, Süd-Venezuela befindet. Weitere Beobachtungen wurden in Wäldern der näheren Umgebung gemacht. Frühere Analysen hatten gezeigt, dass Vogelarten in stratifizierten vertikalen Nischen nach Futter suchen, wobei die Nischen für Vögel der mittleren Straten größer waren als die Nischen der Vögel der oberen und unteren Straten. In dieser Studie konnte ich durch zwei verschiedene vergleichende Analysen zeigen, dass die vertikale Position von Vogelarten mit Variablen korreliert war, die sowohl Vegetationsstrukturen als auch die einfallende Lichtmenge beschreiben. Ich beobachtete, dass Arten der tieferen Straten meistens in „small gap“ und „forest shade“ Lichthabitaten nach Futter suchten, während Arten der höheren Straten meistens in „large gap“ und „woodland shade“ Lichthabitaten beobachtet wurden. Arten der tieferen Straten wurden außerdem öfter im Schatten und in dichter Vegetation beobachtet. Übereinstimmend mit ihren größeren vertikalen Nischen suchten Arten der mittleren Straten in einem weiteren Bereich von Lichthabitaten und Sonneneinfall nach Futter als die Arten der höheren und tieferen Straten. Obwohl die Arten ihre generelle Stratifizierung beibehielten, wanderten sie doch aktiv innerhalb ihres bevorzugten Stratum, z. B. nach unten und in dichtere Vegetation während Sonneneinfalls und zur Mittagszeit, wenn die Temperaturen am höchsten sind. Die Aktivität der Vögel erschien am geringsten kurz nach der Mittagszeit, nachdem ich die Anzahl der beobachteten Vogeltrupps berücksichtigt hatte. Diese Beobachtungen sind nicht nur wichtig, um die Futternischen zu bestimmen, sondern auch für die Untersuchung der Tarnung und Auffälligkeit von Vogelarten in Bezug auf ihr Futterstratum.

### Introduction

The structure of forest bird communities depends on the habitat use and interactions of their members. Many factors combine to shape forest communities, e. g. resource availability, vegetation structure and abiotic factors such as weather (Cody 1985, Wiens 1989). One factor that has been studied intensively in temperate as well as tropical forest communities is the influence of forest height on the vertical stratification of bird species (Orians 1969, Terborgh & Weske 1969, Pearson 1971, Smith 1973, Cody 1974, Anderson et al. 1979, Terborgh 1980, Greenberg 1981, Bell 1982, Cody 1985, Haffer 1988, Marra & Remsen 1997). Variables that are known to change with forest height are, for example, evaporation, temperature, wind (Longman & 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). In this study, I focus on

the use of vertical foraging niches by Neotropical forest birds in relation to vegetation and light habitats.

Vegetation structures and densities change with forest height (Pearson 1971, Terborgh 1980, Richards 1996). In several studies, vegetation density has been shown to be highest in the canopy and understorey, with more open spaces in the midstorey (Terborgh & Weske 1969, Pearson 1971, Terborgh 1980, Bell 1982, but see Pearson 1975 for different foliage profiles). Vegetation structures also change, with tree trunks and dead leaves being found in the under- and midstorey, and most flowers and fruits in the canopy (Terborgh 1980, Marra & Remsen 1997).

While vegetation may change seasonally within a forest, ambient light and temperature change rapidly during the course of the day, often within minutes (Longman & Jenik 1974, Yoda 1974, Pukkala et al. 1991, Endler 1993, Richards 1996). Therefore, daytime, weather

conditions, and indeed the height within the forest, all influence the quantity and quality of the ambient light. On a cloudless day, incident light increases rapidly in the morning, is constant at noon and rapidly decreases in the afternoon (Doley et al. 1988). Cloud cover, however, can reduce light levels to less than a fifth (Hutchison & Matt 1977). With decreasing forest height, both the total amount and the temporal variation of ambient light also decrease dramatically (Yoda 1974, Doley et al. 1988, Pukkala et al. 1991, Endler 1993, Terborgh & Mathews 1999). Moreover, the spectral composition of ambient light changes as the amount of direct sunlight and reflected light changes with forest height (Endler 1993). These changes are due to vegetation structures blocking direct sunlight and increasing the amount of mostly yellow-green light reflected by plant surfaces.

Endler (1993) defined four light habitats which are found in most forests: large gaps are associated with white light which is virtually indistinguishable from direct sunlight as no vegetation blocks it. Woodland shade is associated with blue-grey light as a significant fraction of the incident light comes from the sky, but direct sunlight is blocked by vegetation. Forest shade is associated with yellow-green light as most incident light is reflected by vegetation surfaces. Lastly, small gaps are associated with reddish light as most incident light comes directly from the sun with little light coming from the blue sky or green plant surfaces. Endler (1993) measured the vertical distribution of ambient light using a canopy tower and found a shift from large gap via woodland shade to forest shade light with decreasing height. In view of the vertical structure of the forest, it is likely that, overall, the vertical distribution of light habitats progresses from large gap via woodland shade and small gap to forest shade. Thus, these four light habitat categories probably correlate with forest height, and birds foraging at a particular height ought also to be found in the corresponding light habitat. Likewise, illumination with direct sunlight ought to

decrease with forest height (see references above) so that understory birds are lit by direct sunlight less often than canopy birds. I used behavioural data of 92 bird species observed in a lowland Amazonian tropical forest in southern Venezuela to test these ideas.

Using these data, Walther (in press) also showed that all frequently observed species maintained a preferred vertical foraging stratum or niche. Furthermore, the vertical width of these foraging niches was greater for midstorey birds than for either canopy or understory birds. Walther (in press) discusses possible reasons for this phenomenon, such as environmental and geometrical constraints. Since midstorey birds had a wider vertical niche, in this study I examined whether midstorey birds were also found in a wider range of light habitats and illuminations.

In response to diurnal increases in sunlight and temperature, tropical forest birds often shift vertically downwards or reduce their activity (Pearson 1971, Pearson 1977, Bell 1982). Therefore, I also examined changes in activity, vertical foraging height, use of vegetation and light habitats by bird species in relation to daytime and incident light.

This study thus defines where in the forest a bird species is usually found in relation to height within the forest, vegetation structures and ambient light. This kind of information is crucial not only for the determination of foraging niches (Walther, in press), but also for the study of crypsis and conspicuousness of bird species in relation to their foraging stratum (Walther et al. 1999).

## 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 Vene-

zuela (65°32'W, 3°11'N, altitude ~110 m. a. s. l.). 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 as river levels can rise by up to four metres (Anhuf & Winkler 1999, Anhuf et al. 1999). Esmeralda is located almost at the centre of the Alto Orinoco-Casiquiare Biosphere Reserve (87,000 km<sup>2</sup>), which has so far been spared extensive human disturbance. The only anthropogenic influences are the hunting and the slash-and-burn agriculture of the local native populations (Anhuf & Winkler 1999).

Average daily temperatures are around 26 °C, relative humidity ranges from 40–100 %, and average annual precipitation is around 3000 mm, ranging between 1000–4000 mm (Anhuf & Winkler 1999). The dry season usually lasts from December to March, the rainy season from April to November with two precipitation peaks during May–July and September–October. However, large fluctuations in precipitation patterns were recorded, partly as a result of large climatic events such as the La Niña and El Niño phenomena in 1996 and 1997–98 (Rütger Rollenbeck, pers. commun.).

I made most observations (approximately 70 %) from or near the 40 m high canopy crane situated approximately 15 km west of Esmeralda close to the mouth of the Surumoni river (65°40'W, 3°10'N, altitude ~105 m. a. s. l.; Anhuf & Winkler 1999). The crane plot is characterised 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, while the undergrowth is relatively dense (up to 10000 stems > 1 cm/ha). The remaining observations were made at six other forest sites near Esmeralda which covered a variety of forest habitats (lowland and flooded tropical evergreen, river-edge, gallery and second-growth forests).

### Observation procedures

All behavioural observations were made during two field seasons (May–June 1998, February–April

1999) between 0620 and 1830 hours from either the ground or the crane. On the ground, I made observations during slow walks along narrow forest trails, covering all trails at least once during any observation day (trails covered a length of 400–1000 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 which can be moved to any point within the 1.5 hectare study plot covered by the crane's 40 m jib and its 100 m long track. Because of the great mobility of the crane, flocks can be actively pursued. When the need arose, 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 behaviour of observed birds was not manifestly disturbed by the movement of the crane, since no avoidance behaviour 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 midstorey was also regularly observed at various points within the plot wherever the forest structure allowed the cabin to be lowered into the midstorey. Because of the limited availability of the crane during both field seasons, I scheduled my crane periods mostly in the morning when more behavioural observations can be made (see Results).

The overall goal was to establish when and where each species forages in a mature forest with a closed canopy. Because of the great number of birds to be observed, especially during flock encounters, I used the instantaneous scan sampling method (Altmann 1974). For each observation, I tried to record the following information for each bird species (in cases of flocks or fast-moving birds, some information could not be recorded, which explains the variable sample sizes in the analyses, cf. Table 1–3):

Foraging behaviour: foraging was defined as any behaviour which 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 behaviours which were obviously not food-related (e. g. preening, long-distance flying, nesting, or displaying to mates) were excluded. Likewise, all behaviours induced by the observer (e. g. reaction to

song playback or evasion from the observer) were disregarded.

**Time of day:** to test for diurnal influences on bird behaviour, I scored the variable 'time of day' as minutes from midday (scored as zero) in both directions, i. e. towards the morning and towards the evening.

**Habitat:** I included only observations made in mature closed forest, excluding observations from gap, edge or degraded habitat as these habitats have different light conditions.

**Forest stratum:** 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 midstorey was defined as the space between the canopy and the understory. The canopy was defined as the space above 18 m and/or the space within the crown of the highest trees. In the analyses, the four strata are given scores from 0 to 3; a score of 2.5, for example, means that the species occurs in both midstorey and canopy (cf. Parker III et al. 1996).

**Relative height:** the 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 metres). 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.

**Tree position:** the position of the individual within the tree was categorised as (0) on the trunk, (1) nearer to the trunk than to the outer reaches, (2) nearer to the outer reaches than to the trunk, or (3) on the outer reaches.

**Percentage leaf cover:** the leaf cover of the tree used by a given bird was categorised as having (0) no foliage, (1) 1–25 %, (2) >25–50 %, (3) >50–75 %, or (4) >75–100 % foliage cover.

**Percentage cover:** visual cover within a 1 m radius of the individual was categorised as (0) no cover, (1) 1–25 %, (2) >25–50 %, (3) >50–75 %, or (4) >75–100 % cover.

**Leaf position:** the position of the bird in relation to the nearest dense vegetation (categories 3 and 4

above) was categorised as (0) under, (1) in, (2) on top of the vegetation, (3) more than 5 m away from dense vegetation.

**Incident light:** categorised as (1) direct sunlight from clear blue sky, (2) direct sunlight, but clouds in the sky, (3) occluded sunlight, but some blue sky still visible, (4) sunlight occluded by complete cloud cover. The following two variables could only be recorded in sunny conditions (categories 1 and 2).

**Light habitat:** categorised as (1) large gap, (2) woodland shade, (3) small gap, and (4) forest shade. Since it was impossible to measure ambient light for each observation, light habitat was assessed by the position of the bird within the forest and the kind of illumination it received (cf. Fig. 3 in Endler 1993). In many cases birds moved through two light habitat categories with consecutive ranks; in those cases I assigned them a midrange value, e. g. a score of 3.5 means that the species moved through both small gap and forest shade. Whenever a bird could not be assigned to any of the categories unambiguously, I excluded the observation.

**Illumination:** each individual was categorised as (1) fully illuminated, (2) ~50 % illuminated, or (3) fully shaded.

The variables stratum, relative height, tree position, percentage leaf cover, percentage cover and illumination can be thought of as discrete rank orders, so I present the mean and standard error for these variables. Leaf position and light habitat, however, are categorical variables; therefore I only present the mode.

When calculating the mean and mode values for each species (cf. Appendix 1), I excluded all observations of a species made within 60 minutes of the last included observation of that species. In this way, I tried to avoid pseudoreplication through repeated observations of the same individual. However, when I estimated bird activity by counting the number of individuals or species observed per hour (see Results), I included all observations. I also counted the number of flocks observed per hour. A flock was defined as a cohesive multi-species group of birds in which all members of which were evidently moving in the same general direction while foraging.

## Analyses

I present two types of species analyses, across-species as well as phylogenetically-controlled

analyses. The former type has been criticised as disregarding the effects of phylogenetic relatedness of species on statistical tests and the resulting deductive logic (Harvey & Pagel 1991, Harvey et al. 1995). I nevertheless present such an analysis because (1) it allows a direct graphical depiction of the relationship, and (2) it may have ecological relevance. For example, if species richness is correlated with overall abundance (e. g. Wiens 1989, Siemann et al. 1996), bird abundance in a certain stratum may be correlated with the strength of interactions, e. g. with seeds or predators (e. g. Walther et al. 1999).

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 done (Harvey & Pagel 1991). Because of the problem of estimating ancestral states (Losos 1999), especially for ecological variables such as stratum use, I restricted the analysis to a comparison of extant sister taxa (Read & Nee 1995). To avoid assumptions about the magnitude of evolutionary change in relation to branch lengths, I analysed the directions of sister taxa comparisons with a one-sample sign test. As far as I am aware, this is the most conservative method of testing comparative hypotheses as it makes the fewest 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, Lanyon 1985a, Lanyon 1985b, Lanyon 1988, Prum & Lanyon 1989, Ridgely & Tudor 1989, Hackett & Rosenberg 1990, Sibley & Ahlquist 1990, Birt et al. 1992, Helm-Bychowski & Cracraft 1993, Ridgely & Tudor 1994, Burns 1997, Prum 1997, Espinosa de los Monteros 1998, Gerwin & Zink 1998, Miyaki et al. 1998, Bates et al. 1999, Lanyon & Omland 1999, Prum et al. 2000) and the program CAIC (Purvis & Rambaut 1995).

## Results

### Behavioural patterns emerging from species comparisons

The data set is presented in Appendix 1. To reduce error due to small sample sizes, I restricted the following analyses to species which were observed at least 5 times (a total of 1518 observations of 92 species representing 19 families). These species should, with few exceptions, represent the most abundant species at our site. They should thus embody the core avifauna whose species are presumably the best adapted to the local ecological conditions (Remsen 1994). All species analyses below use the mean or mode values shown in Appendix 1.

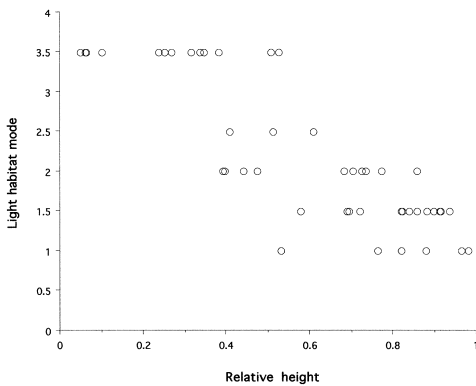
Stratum and relative height were highly correlated across species ( $n = 92$  species,  $r^2 = 0.94$ ,  $p < 0.0001$ ). I restricted further analyses to relative height because (1) results are very similar for both variables, (2) relative height is a continuous and not a discrete variable like stratum, and (3) relative height is a more accurate measure of vertical stratification (Walther, in press).

Across-species analyses revealed that relative height was highly correlated with five out of six variables representing the position of the bird within the forest (Table 1). Specifically, species which foraged at low heights in the forest were mostly found in small gap and forest shade light habitats, while species that foraged high were mostly found in large gap and woodland shade light habitats (Fig. 1). Consequently, species foraging at lower levels were found at lower illuminations than species foraging higher up. Moreover, species foraging lower were the ones more often found in trees with dense leaf cover, and the ones more often found foraging in dense cover, and the ones more often found foraging close to the trunk of the tree. The only variable not correlated with relative height was leaf position, i. e. foraging height had no influence on whether the bird species foraged above or below dense vegetation.

**Table 1.** Correlations of relative height with six variables representing the position of the bird species within the forest. For analyses of across-species correlations a Spearman-Rank test was applied (numbers given are sample size, rho-value and p-value; a minus sign in front of the rho value indicates a negative relationship). Sister-taxa comparisons were analysed on the basis of a one-sample sign test (numbers given are the number of positive, negative, or neutral relationships, followed by the p-value).

**Tab. 1.** Korrelationen der relativen Höhe mit sechs Variablen, die die Position der Vogelart im Wald beschreiben. Korrelationen über Arten hinweg wurden mit einem Spearman-Rank Test analysiert (Zahlenangaben sind Stichprobengröße, rho-Wert und p-Wert; ein Minuszeichen vor dem rho-Wert bezeichnet eine negative Beziehung). Vergleiche zwischen verwandten Arten wurden mit einem One-Sample Sign Test analysiert (Zahlenangaben sind die Anzahl der positiven, negativen und neutralen Beziehungen, gefolgt vom p-Wert).

Variable	across-species correlation	sister-taxa comparison
light habitat	46, -0.78; < 0.0001	2,13,8; 0.007
illumination	46, -0.83; < 0.0001	5,18,0; 0.01
% leaf cover	92, -0.65; < 0.0001	11,27,8; 0.01
% cover	92, -0.29; 0.005	15,31,0; 0.03
tree position	92, 0.81; < 0.0001	23,14,9; 0.19
leaf position	92, 0.09; 0.40	12,10,24; 0.83



**Fig. 1.** Relationship between mean relative height and the mode of light habitat for 46 South American tropical forest bird species (see Table 1 for statistics).

**Abb. 1.** Beziehung zwischen der durchschnittlichen relativen Höhe und dem Mode des Lichthabitats für 46 südamerikanische tropische Waldvogelarten (siehe Tab. 1 für statistische Angaben).

On being tested by comparison with sister-taxa, four out of the five relationships were again significant (Table 1). The exception was the relationship between relative height and tree position which, despite having the same direction, was no longer significant.

As midstorey birds had a wider vertical foraging niche than either canopy or understorey birds (Walther, in press), it seemed plausible that they would also have a wider range of light habitats and illuminations. Using a polynomial regression model, I found that midstorey birds were indeed found in a wider range of light habitats and illuminations (Table 2, Fig. 2).

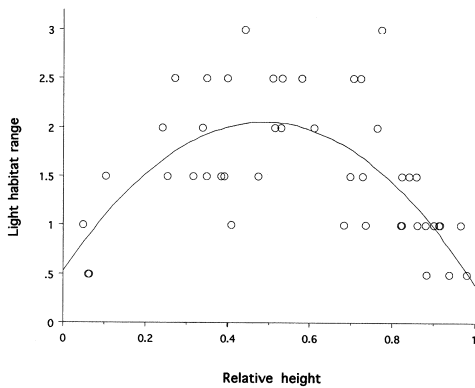
**Behavioural patterns using individual observations**

In the following analyses, I included only species which were observed at least 10 times so that sample sizes were sufficient for the analyses. For each species I used a multiple linear regression model to determine the influence of two independent variables (time of day and incident light) on 5 dependent variables representing the position of the bird within the forest (Table 3). I found that significantly more species foraged lower in the forest and in denser foliage at midday than in the morning or evening. The three remaining variables (percentage leaf cover, tree position, leaf position) were not significantly correlated with the independent variable 'time of day'. In sunshine

**Table 2.** Polynomial regression models of the second order for the relationship between the mean relative height (x-value) and (a) the range or (b) the standard deviation (y-value) of light habitat and illumination. Partial p-values are given for the respective model parameters ( $x^2$ ,  $x$  and the constant) and overall p-values for the entire model.

**Tab. 2.** Polynomiales Regressionsmodell der zweiten Potenz für die Beziehung zwischen der durchschnittlichen relativen Höhe (x-Wert) und (a) der Ausbreitung oder (b) der Standardverteilung (y-Wert) des Lichthabitates und der Illumination. Partielle p-Werte werden für die jeweiligen Modellparameter ( $x^2$ ,  $x$  und die Konstante) angegeben sowie die universellen p-Werte für das gesamte Modell.

variable	Model	d. f.	F	$r^2$	partial p-values	overall p-value
<b>(a)</b>						
light habitat	$y = -6.37 x^2 + 6.24 x + 0.53$	2,43	14.4	0.40	< 0.0001, < 0.0001, 0.13	< 0.0001
illumination	$y = -2.21 x^2 + 2.97 x + 0.46$	2,43	4.59	0.18	0.04, 0.02, 0.12	0.02
<b>(b)</b>						
light habitat	$y = -2.31 x^2 + 2.22 x + 0.21$	2,43	18.8	0.47	< 0.0001, < 0.0001, 0.06	< 0.0001
illumination	$y = -1.26 x^2 + 1.43 x + 0.21$	2,43	5.94	0.22	0.002, 0.001, 0.04	0.005



**Fig. 2.** Relationship between mean relative height and the range of light habitat for 46 South American tropical forest bird species (see Table 2 for statistics).

**Abb. 2.** Beziehung zwischen der durchschnittlichen relativen Höhe und der Ausbreitung der Lichthabitats für 46 südamerikanische tropische Waldvogelarten (siehe Tab. 2 für statistische Angaben).

conditions significantly more species foraged lower in the forest and closer to the trunk. In addition, species were more often found in trees with denser foliage. However, neither the percentage of cover nor leaf position correlated significantly with the independent variable ‘incident light’.

To quantify bird activity, I counted the number of all individuals and all species observed during one-hour periods as well as the number of flocks encountered. Even though the 165 flock encounters only lasted on average  $8.5 \pm 0.9$  (mean  $\pm$  1 S. E.) minutes, the number of flocks encountered was by far the best predictor of the number of individuals (Type I linear regression,  $n = 200$  one-hour periods,  $r^2 = 0.31$ ,  $p < 0.0001$ ) or species ( $r^2 = 0.32$ ,  $p < 0.0001$ ) observed per hour. Since the chance event of encountering a flock would bias any estimate of bird activity, I needed to control for this effect to quantify overall bird activity. This was achieved by calculating residuals from the linear regression model. A polynomial regression model explained the then remaining variation better than a simple linear regression model. Although most variation remained unexplained, bird activity was definitely lowest shortly after midday (Fig. 3).

### Discussion

Not surprisingly, the vertical position of a bird species predetermined to some extent the vegetation structures and ambient light in which it foraged. Using species data as well as sister taxa comparisons, I found that bird species which foraged at lower levels in the forest

**Table 3.** Multiple regression models for 49 tropical forest bird species with  $n \geq 10$  observations of relative height. For each regression model, I noted only whether the relationship between the independent and the dependent variable was positive, negative, or neutral (in the case of too little variation for model analysis). Thus, each species contributed one relationship, and the resulting 49 relationships were analysed by use of a one-sample sign test. Numbers given are the number of positive, negative, or neutral relationships, followed by the p-value.

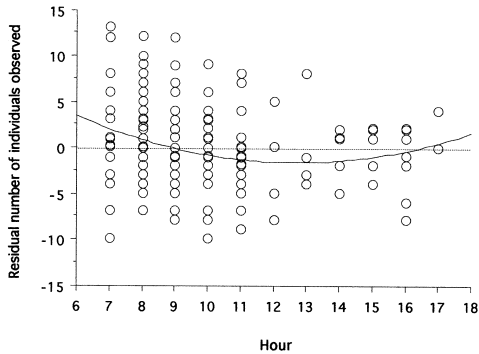
**Tab. 3.** Multiple Regressionsmodelle für 49 tropische Vogelarten mit  $n \geq 10$  Beobachtungen der relativen Höhe. Für jedes Regressionsmodell habe ich lediglich aufgezeichnet, ob die Beziehung positiv, negativ oder neutral (im Falle von zu geringer Variation für Modellanalyse) war. Dadurch hat jede Art nur eine Beziehung beigetragen, und die resultierenden 49 Beziehungen wurden mit einem One-Sample Sign Test analysiert. Zahlenangaben sind die Anzahl der positiven, negativen und neutralen Beziehungen, gefolgt vom p-Wert.

independent variables	time of day	incident light
dependent variables:		
relative height	37,12,0; 0.0005	13,36,0; 0.001
% leaf cover	20,25,4; 0.55	30,15,4; 0.04
% cover	16,33,0; 0.02	27,22,0; 0.57
tree position	23,17,9; 0.43	11,29,9; 0.006
leaf position	27,19,3; 0.30	17,29,3; 0.10

were found in habitats with denser vegetation and less light. These correlations are probably a result of the vertical distribution of forest vegetation. For example, species foraging lower were more often found in trees with dense leaf cover. This observation may result from the fact that canopy trees often lose many leaves (e. g. as response to water stress in drier periods, which can be quite pronounced in the study area; Anhuf & Winkler 1999, Anhuf et al. 1999), whereas almost no leafless trees are found in the understorey. However, during periods of sufficient water resources at our study site, foliage density was highest in the canopy and understorey and lowest in the midstorey (Walther In review). Thus, vegetation density appears to be more variable in the canopy than in the understorey. This variation may also explain why bird species which foraged lower were more often observed foraging in dense cover. However, in this particular case, a sampling bias may also explain the result. From the canopy crane, one has a wide view of the surroundings so even distant birds can be observed. These distant birds can in most cases be observed only when they are foraging in the open, which leads to a spurious correlation be-

tween relative height and the cover in which a foraging bird is observed. Future sampling procedures should try to control for this possible bias.

The negative correlations between relative height and light habitat categories and illumination, however, is not thought to be due to sampling bias but to reflect the fact that progressively more light is blocked by the vegetation in the lower strata of the forest, as many studies have shown (Yoda 1974, Hutchison & Matt 1977, Doley et al. 1988, Pukkala et al. 1991, Endler 1993, Terborgh & Mathews 1999). Therefore, understorey birds have to forage in less ambient light and light habitats of different spectral qualities than canopy birds. My results are also consistent with the notion that the vertical distribution of the four light habitats ought to be in the rank order in which the categories were assigned (cf. Introduction): large gap habitats are generally found above woodland shade habitats, which are often found above small gap habitats, while forest shade habitats are predominantly found in the lowest strata. However, this proposed vertical layering of light habitats needs to be confirmed by spectral measurements.



**Fig. 3.** Relationship between time of day (in hours) and the residual number of bird individuals observed. Residuals were taken from a linear regression of flock number as the independent variable against number of individuals observed. A polynomial regression model of the second order is significant for both number of individuals ( $n = 200$  one-hour periods,  $r^2 = 0.06$ ,  $p = 0.003$ ; this plot) and species ( $r^2 = 0.03$ ,  $p = 0.04$ ; not shown) observed per hour.

**Abb. 3.** Beziehung zwischen Tageszeit (in Stunden) und der residuellen Anzahl der beobachteten Vogelindividuen. Residuelle Werte wurden von einer linearen Regression gewonnen, bei der die Anzahl der Vogeltrupps als unabhängige Variable gegen die Anzahl der beobachteten Individuen aufgetragen wurde. Ein polynomiales Regressionsmodell der zweiten Potenz ist signifikant sowohl für die Anzahl der Individuen ( $n = 200$  1-Stunde-Perioden,  $r^2 = 0.06$ ,  $p = 0.003$ ; diese Graphik) als auch für die Anzahl der Arten ( $r^2 = 0.03$ ,  $p = 0.04$ ; nicht abgebildet), die pro Stunde beobachtet wurden.

While the above results were confirmed by both species data and sister taxa comparisons, the positive correlation between relative height and tree position was only significant for species data (Table 1). This correlation is probably due to tree topology as understorey birds foraging in a tree are often restricted to the trunk (tree position = 0), while canopy birds can use all four tree positions. The non-significant result with sister-taxa comparisons suggests that many of the species involved in this correlation are closely related, e.g. trunk-foraging woodpeckers. Thus the use of closely related species in across-species analyses can in-

flate sample size and lead to spurious correlations (Harvey & Pagel 1991). For these reasons, comparative analyses (e.g. sister-taxa comparisons) should be used to back up across-species analyses.

Since most bird species are confined to a specific vertical foraging niche, especially the canopy and understorey birds which forage in narrower vertical niches than midstorey birds (Walther, in press), they are equally confined to the vegetation and light conditions which are predominant in their preferred forest stratum. However, within their stratum, they can and do actively choose favourable microhabitats. For example, dead-leaf foraging birds differed not only in foraging height, but also in the size or type of leaves searched (Rosenberg 1997), and understorey birds differed in the type and density of vegetation used (Marra & Remsen 1997). Similarly, insectivorous bird species chose light habitats that minimise the reflectance of their mandibles (Burt 1984, Burt 1986), while male manakins preferred light habitats that are optimal for increased conspicuousness during lek displays, but chose light habitats that increase crypsis for other activities (Endler & Théry 1996). In contrast, some understorey birds may avoid crossing areas of open sunlight altogether (Bell 1982), such as *Formicarius colma* at our site. This ground-foraging antthrush appeared actively to avoid patches of sunlight in which the conspicuousness of its reddish head would be greatly increased. The behaviour of individual species is to be the focus of future publications. In the present study it was my intention to investigate general patterns that affect the behaviour of the entire avifauna. It should be emphasised that the behaviour of individual birds or species may deviate entirely from these patterns.

The finding that midstorey birds are to be found in a wider range of light habitats and illuminations than either canopy or understorey birds is consistent with the pattern that midstorey birds also use a wider vertical niche (Walther, in press). Since variation in light

habitats may influence the foraging success of sallying and gleaning species (Pearson 1977, Bell 1982), such variation may have important implications for microhabitat choice, especially since light habitats show not only vertical and horizontal, but also great diurnal variation (Yoda 1974, Hutchison & Matt 1977, Doley et al. 1988, Pukkala et al. 1991, Terborgh & Mathews 1999). In addition, bird species have morphological adaptations to different light habitats, such as non-reflective plumage and beak colours (Burt 1986), large bulbous eyes (Orlans 1969) and conspicuous signalling patches (Marchetti 1993), that are related to their microhabitat use. To test hypotheses relating to the choice of light habitats, independent measurements of the spatial and temporal distribution of light habitats need to be taken which distinguish between birds passively sampling their environment and those actively choosing certain microhabitats within their niche.

Another general pattern to emerge was that bird species moved downwards and into denser vegetation around midday when temperatures are 5–10 °C higher than in the morning or evening (Anhuf & Winkler 1999). Similar results have been reported from other tropical avifaunas (Pearson 1971, Pearson 1977, Bell 1982). Two possible factors may contribute to this phenomenon: diurnal changes of climatic conditions and food abundance (Pearson 1971, Bell 1982). For example, if insects were to shift lower at midday, birds may follow them. However, not only did birds move lower, but they were also less active, which suggests that birds were resting either to avoid harsh light and heat conditions or because they had already fed sufficiently. Another indication that birds did not follow food but avoided light and heat is the observation that birds moved not only downwards and into trees with denser vegetation at times of intense sunlight, but also closer to the trunk of the tree. It seems unlikely that food abundance would shift towards the trunk at these times (except for mobile prey such as large insects). On the other hand, mi-

crohabitats close to the trunk may be more protected from light and heat.

Finally, the significant correlation between flock encounters and the number of individuals and species observed per hour will hardly come as a surprise to anybody who has experience of tropical forests. The explosion of bird life is always spectacular whenever a multi-species flock moves through, only to contrast starkly with the ensuing stillness when the forest again appears almost devoid of any bird life. Controlling for the number of flock encounters revealed that bird activity appeared to be lowest shortly after midday as the number of individuals and species observed was lowest during that period. A similar effect of time of day on bird activity was observed in frugivorous birds feeding on a *Ficus* tree (Walther 2000).

To summarise, I not only found a pronounced vertical “layering” of species, which had previously been observed in many other avifaunas (Walther, in press), but also correlated differences in the position of bird species with respect to vegetation structures and the amount of light. Most of these correlations are probably a consequence of the distribution of vegetation and light within the forest. While preserving their overall stratification, species nevertheless actively moved within their preferred stratum, e.g. downwards and into denser vegetation at midday and in sunshine conditions. These data are not only important for the determination of foraging niches (Walther, in press), but also for the study of crypsis and conspicuousness of bird species, which in turn are dependent not only on the inherent coloration of the bird (Walther et al. 1999), but also on the colour of the background and the ambient light (Endler & Théry 1996).

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**Appendix 1.** Bird species observed inside closed mature tropical evergreen forests near Esmeralda, Estado Amazonas, southern Venezuela. Species with less than 5 observation for forest stratum are excluded. Names were taken from Sibley and Monroe (1990). The first six variables involve the position of each species within the forest, whereas the next two variables involve illumination. Mean  $\pm$  1 S. E. (sample size) and range (as minimum-maximum) are given for all variables except for the two variables 'leaf position' and 'light habitat' for which only the mode (sample size) is presented.

As all observations were based on visual and sometimes vocal identifications, it was necessary to lump observations in the case when congeners could not be distinguished with absolute certainty:

- a) Only *Picumnus exilis* has so far been determined with certainty at the study site, but the presence of *P. lafresnayi* and *P. pumilus* cannot be excluded. These 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), I lumped observations of both.
- c) Three *Tolmomyias* species could be present (*T. assimilis*, *T. poliocephalus*, *T. sulphureus*), but they are almost impossible to distinguish visually in the field (Ridgely and Tudor 1994).

Species	forest stratum	relative height	tree position	% leaf cover	% cover	leaf position	light habitat	illumination
<i>Picumnus spec.</i> <sup>a</sup>	2.4 $\pm$ 0.2 (5), 2.0–3.0	0.73 $\pm$ 0.07 (5), 0.52–0.89	1.8 $\pm$ 0.2 (3), 1.5–2.0	2.5 $\pm$ 0.9 (4), 0.0–4.0	2.0 $\pm$ 0.6 (3), 1.0–3.0	1.0 (1)	1.0 (2)	1.0 $\pm$ 0.2 (2), 1.0–1.0
<i>Veniliornis spec.</i> <sup>b</sup>	2.6 $\pm$ 0.1 (14), 2.0–3.0	0.76 $\pm$ 0.05 (14), 0.47–0.94	1.3 $\pm$ 0.2 (14), 0.0–2.0	2.8 $\pm$ 0.4 (14), 0.0–4.0	1.5 $\pm$ 0.2 (14), 0.0–2.5	0.0 (8)	2.0 (6)	1.9 $\pm$ 0.1 (14), 1.0–3.0
<i>Piculus chrysochloros</i>	2.8 $\pm$ 0.2 (5), 2.0–3.0	0.74 $\pm$ 0.09 (5), 0.40–0.90	1.2 $\pm$ 0.6 (5), 0.0–3.0	3.4 $\pm$ 0.2 (5), 3.0–4.0	1.2 $\pm$ 0.1 (5), 1.0–1.5	0.0 (3)	1.5 (2)	2.0 $\pm$ 0.2 (2), 2.0–2.0
<i>Celeus grammicus</i>	2.5 $\pm$ 0.2 (10), 2.0–3.0	0.74 $\pm$ 0.04 (10), 0.57–0.93	0.7 $\pm$ 0.3 (9), 0.0–2.0	2.8 $\pm$ 0.4 (9), 0.0–4.0	1.9 $\pm$ 0.3 (9), 1.0–3.0	0.0 (2)	2.0 (3)	2.2 $\pm$ 0.3 (6), 1.0–3.0
<i>Celeus elegans</i>	2.1 $\pm$ 0.1 (15), 1.0–3.0	0.46 $\pm$ 0.06 (15), 0.10–0.85	0.3 $\pm$ 0.1 (14), 0.0–1.0	3.3 $\pm$ 0.4 (15), 0.0–4.0	2.1 $\pm$ 0.1 (15), 1.0–3.0	0.0 (4)	2.5 (6)	2.6 $\pm$ 0.2 (8), 2.0–3.0
<i>Celeus flavus</i>	3.0 $\pm$ 0.0 (5), 3.0–3.0	0.81 $\pm$ 0.07 (5), 0.57–0.96	1.1 $\pm$ 0.2 (5), 0.5–2.0	2.6 $\pm$ 0.7 (5), 0.0–4.0	1.7 $\pm$ 0.3 (5), 1.0–2.5	0.0 (4)	2.0 (1)	3.0 $\pm$ 0.0 (1), 3.0–3.0
<i>Celeus torquatus</i>	2.4 $\pm$ 0.2 (5), 2.0–3.0	0.75 $\pm$ 0.07 (5), 0.64–0.93	0.3 $\pm$ 0.2 (5), 0.0–1.0	2.4 $\pm$ 0.7 (5), 0.0–4.0	1.7 $\pm$ 0.3 (5), 1.0–2.5	0.0 (2)	2.5 (2)	2.3 $\pm$ 0.3 (3), 2.0–3.0
<i>Capito niger</i>	2.8 $\pm$ 0.1 (75), 1.0–3.0	0.78 $\pm$ 0.03 (73), 0.08–0.97	1.9 $\pm$ 0.1 (61), 0.0–3.0	3.6 $\pm$ 0.1 (74), 2.0–4.0	2.3 $\pm$ 0.1 (69), 1.0–4.0	1.0 (29)	2.0 (15)	2.2 $\pm$ 0.1 (39), 1.0–3.0
<i>Pteroglossus azara</i>	2.7 $\pm$ 0.1 (20), 2.0–3.0	0.74 $\pm$ 0.04 (20), 0.24–0.94	1.7 $\pm$ 0.1 (14), 1.0–2.0	3.7 $\pm$ 0.1 (18), 3.0–4.0	2.3 $\pm$ 0.2 (17), 1.0–4.0	1.0 (10)	2.0 (3)	1.7 $\pm$ 0.2 (6), 1.0–2.0
<i>Ramphastos culminatus</i>	2.7 $\pm$ 0.1 (27), 2.0–3.0	0.75 $\pm$ 0.06 (24), 0.14–1.00	1.8 $\pm$ 0.2 (15), 1.0–3.0	2.5 $\pm$ 0.3 (23), 0.0–4.0	1.3 $\pm$ 0.2 (23), 0.0–3.0	3.0 (12)	3.5 (3)	2.4 $\pm$ 0.2 (7), 2.0–3.0
<i>Ramphastos cuvieri</i>	2.8 $\pm$ 0.1 (21), 2.0–3.0	0.83 $\pm$ 0.04 (21), 0.42–1.00	1.9 $\pm$ 0.2 (19), 1.0–3.0	2.5 $\pm$ 0.3 (20), 0.0–4.0	1.6 $\pm$ 0.2 (20), 0.0–3.0	3.0 (7)	1.5 (4)	1.9 $\pm$ 0.3 (7), 1.0–3.0

Species	forest stratum	relative height	tree position	% leaf cover	% cover	leaf position	light habitat	illumination
<i>Galbula leucogastra</i>	2.9 ± 0.1 (24), 2.0–3.0	0.83 ± 0.02 (23), 0.55–1.00	2.3 ± 0.1 (24), 1.0–3.0	1.5 ± 0.3 (24), 0.0–4.0	0.6 ± 0.1 (23), 0.0–2.0	3.0 (21)	1.0 (8)	1.2 ± 0.1 (10), 1.0–2.0
<i>Notharchus macrorhynchos</i>	3.0 ± 0.0 (17), 3.0–3.0	0.88 ± 0.02 (17), 0.72–1.00	2.0 ± 0.1 (16), 1.0–3.0	1.9 ± 0.3 (17), 0.0–4.0	1.0 ± 0.2 (17), 0.0–2.0	0.0 (13)	1.0 (3)	1.3 ± 0.2 (7), 1.0–2.0
<i>Notharchus tectus</i>	3.0 ± 0.0 (6), 3.0–3.0	0.89 ± 0.04 (5), 0.73–0.96	2.1 ± 0.1 (6), 2.0–2.5	P3.2 ± 0.4 (6), 2.0–4.0	1.4 ± 0.2 (5), 1.0–2.0	0.0 (6)	–	–
<i>Monasa atra</i>	2.0 ± 0.1 (22), 1.0–3.0	0.39 ± 0.05 (18), 0.08–0.96	1.5 ± 0.2 (8), 1.0–2.0	3.8 ± 0.1 (20), 2.0–4.0	1.1 ± 0.1 (20), 0.0–3.0	3.0 (18)	2.0 (3)	2.4 ± 0.2 (11), 1.0–3.0
<i>Chelidoptera tenebrosa</i>	3.0 ± 0.0 (15), 3.0–3.0	0.99 ± 0.01 (14), 0.88–1.00	2.2 ± 0.3 (15), 0.0–3.0	0.9 ± 0.4 (14), 0.0–4.0	0.3 ± 0.2 (15), 0.0–2.0	3.0 (14)	1.0 (4)	1.0 ± 0 (4), 1.0–1.0
<i>Trogon melanurus</i>	2.7 ± 0.1 (5), 2.5–3.0	0.79 ± 0.05 (4), 0.72–0.93	1.2 ± 0.2 (4), 1.0–2.0	3.8 ± 0.2 (4), 3.0–4.0	1.5 ± 0.3 (4), 1.0–2.0	1.5 (3)	1.5 (1)	3.0 ± 0 (3), 3.0–3.0
<i>Trogon viridis</i>	2.5 ± 0.1 (25), 2.0–3.0	0.68 ± 0.04 (23), 0.20–0.93	1.8 ± 0.1 (18), 1.0–3.0	3.4 ± 0.2 (25), 1.0–4.0	1.3 ± 0.1 (25), 0.0–2.5	3.0 (11)	2.0 (8)	2.6 ± 0.1 (15), 2.0–3.0
<i>Trogon violaceus</i>	2.6 ± 0.2 (9), 1.0–3.0	0.68 ± 0.09 (9), 0.08–0.96	1.9 ± 0.2 (7), 1.5–3.0	3.0 ± 0.5 (9), 0.0–4.0	1.1 ± 0.3 (9), 0.0–3.0	3.0 (6)	1.0 (2)	2.0 ± 0.6 (4), 1.0–3.0
<i>Momotus momota</i>	1.9 ± 0.2 (22), 0.5–3.0	0.42 ± 0.06 (20), 0.04–0.96	1.7 ± 0.2 (6), 1.0–2.0	3.9 ± 0.1 (19), 3.0–4.0	1.5 ± 0.2 (18), 0.0–3.0	3.0 (12)	3.5 (6)	2.8 ± 0.1 (9), 2.0–3.0
<i>Coccyzus americanus</i>	2.3 ± 0.2 (9), 2.0–3.0	0.69 ± 0.04 (9), 0.57–0.97	2.0 ± 0.1 (8), 1.5–2.5	1.9 ± 0.5 (8), 1.0–4.0	1.5 ± 0.3 (8), 1.0–3.0	1.0 (4)	1.5 (7)	2.1 ± 0.1 (7), 2.0–3.0
<i>Piaya melanogaster</i>	2.8 ± 0.2 (17), 0.5–3.0	0.77 ± 0.05 (16), 0.04–0.97	1.8 ± 0.1 (12), 1.0–3.0	3.6 ± 0.2 (16), 2.0–4.0	2.8 ± 0.1 (16), 2.0–4.0	1.0 (10)	1.5 (3)	2.0 ± 0 (4), 2.0–2.0
<i>Ara macao</i>	3.0 ± 0.0 (5), 3.0–3.0	0.97 ± 0.02 (5), 0.93–1.00	2.8 ± 0.2 (5), 2.0–3.0	2.0 ± 0.9 (5), 0.0–4.0	1.2 ± 0.5 (5), 0.0–2.0	3.0 (3)	1.0 (1)	1.0 ± 0 (1), 1.0–1.0
<i>Brotogeris cyanoptera</i>	3.0 ± 0.0 (12), 3.0–3.0	0.90 ± 0.02 (7), 0.80–0.95	1.9 ± 0.2 (7), 1.0–2.5	2.9 ± 0.3 (7), 2.0–4.0	2.1 ± 0.3 (7), 1.0–3.0	0.5 (3)	1.5 (2)	1.8 ± 0.5 (4), 1.0–3.0
<i>Pionites melanocephala</i>	3.0 ± 0.0 (13), 3.0–3.0	0.96 ± 0.02 (12), 0.72–1.00	2.5 ± 0.2 (12), 1.0–3.0	2.7 ± 0.5 (13), 0.0–4.0	1.5 ± 0.3 (13), 0.0–3.0	2.0 (5)	1.0 (4)	1.0 ± 0 (4), 1.0–1.0
<i>Amazona farinosa</i>	3.0 ± 0.0 (16), 3.0–3.0	0.92 ± 0.02 (11), 0.80–1.00	2.1 ± 0.1 (10), 1.5–3.0	2.2 ± 0.5 (11), 0.0–4.0	1.4 ± 0.3 (11), 0.0–3.0	0.0 (4)	1.0 (2)	1.3 ± 0.3 (3), 1.0–2.0
<i>Phaethornis ruber</i>	1.2 ± 0.1 (17), 1.0–2.0	0.15 ± 0.04 (17), 0.03–0.72	–	3.8 ± 0.1 (16), 2.0–4.0	1.2 ± 0.3 (16), 0.0–3.0	3.0 (12)	3.5 (2)	2.2 ± 0.4 (5), 1.0–3.0
<i>Thalurania furcata</i>	2.0 ± 0.2 (14), 1.0–3.0	0.43 ± 0.08 (14), 0.06–0.83	3.0 ± 0.0 (4), 3.0–3.0	3.7 ± 0.2 (14), 1.0–4.0	1.5 ± 0.2 (14), 0.0–2.0	2.0 (7)	3.5 (2)	2.5 ± 0.2 (6), 2.0–3.0
<i>Heliothryx aurita</i>	2.2 ± 0.2 (16), 1.0–3.0	0.51 ± 0.07 (16), 0.10–0.88	1.8 ± 0.2 (2), 1.5–2.0	3.3 ± 0.3 (15), 0.0–4.0	1.3 ± 0.2 (14), 0.0–3.0	3.0 (8)	2.0 (2)	2.4 ± 0.2 (10), 1.0–3.0
<i>Leptotila rufaxilla</i>	0.4 ± 0.2 (9), 0.0–2.0	0.04 ± 0.02 (9), 0.0–0.16	0.8 ± 0.8 (2), 0.0–1.5	4.0 ± 0.0 (8), 4.0–4.0	2.2 ± 0.4 (8), 0.0–4.0	1.0 (3)	4.0 (2)	2.5 ± 0.3 (4), 2.0–3.0
<i>Harpagus bidentatus</i>	3.0 ± 0.0 (9), 3.0–3.0	0.89 ± 0.02 (9), 0.80–0.96	1.9 ± 0.2 (8), 1.0–3.0	1.1 ± 0.5 (9), 0.0–3.0	0.6 ± 0.2 (9), 0.0–1.0	3.0 (6)	2.0 (1)	2.0 ± 0 (1), 2.0–2.0
<i>Buteo magnirostris</i>	2.6 ± 0.2 (7), 2.0–3.0	0.69 ± 0.12 (5), 0.33–1.00	2.3 ± 0.3 (3), 2.0–3.0	3.4 ± 0.4 (5), 2.0–4.0	1.8 ± 0.4 (5), 1.0–3.0	3.0 (2)	2.5 (2)	2.3 ± 0.3 (3), 2.0–3.0
<i>Zimmerius gracilipes</i>	3.0 ± 0.0 (6), 3.0–3.0	0.94 ± 0.01 (6), 0.90–1.00	2.4 ± 0.2 (5), 2.0–3.0	3.7 ± 0.2 (6), 3.0–4.0	2.2 ± 0.4 (5), 1.0–3.0	1.0 (2)	1.5 (2)	2.0 ± 0 (2), 2.0–2.0
<i>Tyrannulus elatus</i>	3.0 ± 0.0 (14), 3.0–3.0	0.94 ± 0.01 (14), 0.86–1.00	2.3 ± 0.1 (14), 1.5–3.0	2.9 ± 0.3 (14), 1.0–4.0	1.7 ± 0.3 (14), 0.0–3.0	1.5 (5)	1.5 (5)	1.8 ± 0.1 (8), 1.0–2.0
<i>Myiopagis gaimardii</i>	3.0 ± 0.0 (5), 3.0–3.0	0.87 ± 0.04 (5), 0.73–0.96	2.1 ± 0.1 (4), 2.0–2.5	3.5 ± 0.3 (4), 3.0–4.0	2.5 ± 0.3 (4), 2.0–3.0	1.0 (4)	1.5 (4)	1.9 ± 0.1 (4), 1.5–2.0
<i>Myiopagis caniceps</i>	2.9 ± 0.1 (8), 2.5–3.0	0.85 ± 0.04 (8), 0.71–0.97	2.2 ± 0.1 (7), 1.5–2.5	3.8 ± 0.2 (8), 2.0–4.0	2.4 ± 0.3 (7), 1.0–3.0	1.5 (4)	1.5 (3)	2.0 ± 0 (4), 2.0–2.0
<i>Lophotriccus galeatus</i>	1.9 ± 0.2 (5), 1.0–2.5	0.40 ± 0.11 (5), 0.08–0.70	1.5 ± 0.0 (2), 1.5–1.5	3.8 ± 0.2 (5), 3.0–4.0	3.0 ± 0.0 (4), 3.0–3.0	1.0 (5)	3.5 (2)	2.3 ± 0.3 (3), 2.0–3.0

Species	forest stratum	relative height	tree position	% leaf cover	% cover	leaf position	light habitat	illumination
<i>Tolmomyias spec.<sup>c</sup></i>	3.0 ± 0.0 (7), 3.0–3.0	0.90 ± 0.03 (7), 0.80–1.00	2.5 ± 0.3 (5), 1.5–3.0	4.0 ± 0.0 (7), 4.0–4.0	2.4 ± 0.2 (6), 2.0–3.0	2.0 (3)	1.0 (1)	1.8 ± 0.6 (3), 1.0–3.0
<i>Myiobius erythrurus</i>	2.1 ± 0.2 (7), 1.5–3.0	0.41 ± 0.11 (7), 0.12–0.80	1.6 ± 0.1 (5), 1.5–2.0	4.0 ± 0.0 (7), 4.0–4.0	1.9 ± 0.3 (6), 1.0–3.0	3.0 (3)	3.5 (4)	2.7 ± 0.2 (6), 2.0–3.0
<i>Laniocera hypopyrra</i>	1.7 ± 0.2 (7), 1.0–2.0	0.31 ± 0.07 (7), 0.07–0.52	1.8 ± 0.2 (2), 1.5–2.0	3.9 ± 0.1 (7), 3.0–4.0	1.8 ± 0.2 (7), 1.0–2.5	3.0 (5)	3.5 (3)	2.8 ± 0.2 (4), 2.0–3.0
<i>Tyrannus melancholicus</i>	3.0 ± 0.0 (6), 3.0–3.0	0.99 ± 0.01 (6), 0.97–1.00	2.8 ± 0.2 (6), 2.0–3.0	2.0 ± 0.7 (6), 0.0–4.0	0.8 ± 0.3 (6), 0.0–2.0	3.0 (5)	1.0 (1)	2.0 ± 0 (1), 2.0–2.0
<i>Empidonomus varius</i>	2.9 ± 0.1 (8), 2.5–3.0	0.96 ± 0.03 (8), 0.75–1.00	2.9 ± 0.1 (7), 2.5–3.0	2.5 ± 0.5 (8), 0.0–4.0	1.1 ± 0.3 (8), 0.0–2.0	3.0 (5)	1.0 (1)	1.5 ± 0.5 (2), 1.0–2.0
<i>Griseotyrannus aurantioatrocristatus</i>	3.0 ± 0.0 (8), 3.0–3.0	0.98 ± 0.01 (8), 0.89–1.00	2.9 ± 0.1 (8), 2.0–3.0	3.0 ± 0.5 (7), 1.0–4.0	1.4 ± 0.3 (7), 0.0–2.0	3.0 (4)	1.5 (1)	2.0 ± 0 (1), 2.0–2.0
<i>Myiodynastes maculatus</i>	3.0 ± 0.0 (8), 3.0–3.0	0.80 ± 0.04 (8), 0.64–1.00	1.9 ± 0.3 (8), 1.0–3.0	2.0 ± 0.6 (8), 0.0–4.0	1.2 ± 0.3 (8), 0.0–2.0	0.0 (3)	1.0 (2)	1.6 ± 0.2 (5), 1.0–2.0
<i>Myiozetetes luteiventris</i>	2.8 ± 0.2 (6), 2.0–3.0	0.87 ± 0.06 (6), 0.60–1.00	2.9 ± 0.1 (4), 2.5–3.0	4.0 ± 0.0 (6), 4.0–4.0	2.0 ± 0.0 (6), 2.0–2.0	2.0 (3)	1.0 (1)	1.0 ± 0 (1), 1.0–1.0
<i>Pachyramphus marginatus</i>	2.6 ± 0.1 (11), 2.0–3.0	0.74 ± 0.06 (11), 0.37–0.97	1.7 ± 0.2 (7), 1.0–2.5	3.8 ± 0.1 (10), 3.0–4.0	2.6 ± 0.2 (9), 2.0–3.0	1.0 (4)	2.0 (5)	2.1 ± 0.1 (6), 2.0–2.5
<i>Tityra cayana</i>	3.0 ± 0.0 (8), 3.0–3.0	0.91 ± 0.04 (8), 0.64–0.97	1.9 ± 0.1 (8), 1.0–2.5	3.1 ± 0.4 (8), 1.0–4.0	1.8 ± 0.2 (8), 1.0–2.5	0.0 (4)	2.0 (3)	2.0 ± 0 (4), 2.0–2.0
<i>Iodopleura isabellae</i>	3.0 ± 0.0 (16), 3.0–3.0	0.99 ± 0.01 (16), 0.92–1.00	2.9 ± 0.1 (16), 2.5–3.0	2.9 ± 0.3 (16), 1.0–4.0	1.6 ± 0.2 (16), 0.0–2.5	2.0 (8)	1.0 (5)	1.4 ± 0.2 (7), 1.0–2.0
<i>Lipaugus vociferans</i>	2.3 ± 0.2 (5), 2.0–3.0	0.47 ± 0.09 (5), 0.25–0.80	2.0 ± 0.0 (1), 2.0–2.0	3.6 ± 0.2 (5), 3.0–4.0	2.1 ± 0.4 (4), 1.0–3.0	2.0 (2)	–	–
<i>Cotinga cayana</i>	3.0 ± 0.0 (7), 3.0–3.0	0.88 ± 0.03 (7), 0.72–0.96	1.8 ± 0.2 (6), 1.0–2.5	2.6 ± 0.5 (7), 0.0–4.0	1.5 ± 0.3 (7), 0.0–2.5	0.0 (3)	1.5 (1)	1.5 ± 0 (1), 1.5–1.5
<i>Xipholena punicea</i>	3.0 ± 0.0 (19), 3.0–3.0	0.95 ± 0.01 (14), 0.88–1.00	1.9 ± 0.2 (12), 1.0–3.0	3.0 ± 0.3 (14), 1.0–4.0	1.4 ± 0.2 (13), 1.0–3.0	0.0 (6)	1.0 (3)	1.5 ± 0.2 (5), 1.0–2.0
<i>Cephalopterus ornatus</i>	2.9 ± 0.1 (7), 2.0–3.0	0.87 ± 0.06 (7), 0.53–1.00	2.2 ± 0.2 (6), 2.0–3.0	2.6 ± 0.6 (7), 0.0–4.0	1.0 ± 0.4 (6), 0.0–2.0	0.0 (3)	2.5 (1)	3.0 ± 0 (1), 3.0–3.0
<i>Pipra filicauda</i>	1.7 ± 0.1 (16), 1.0–2.5	0.30 ± 0.04 (16), 0.07–0.62	–	4.0 ± 0.0 (16), 4.0–4.0	1.8 ± 0.2 (15), 1.0–3.0	3.0 (7)	3.5 (4)	2.6 ± 0.2 (10), 2.0–3.0
<i>Pipra erythrocephala</i>	2.1 ± 0.1 (47), 1.0–3.0	0.48 ± 0.03 (46), 0.03–0.95	1.4 ± 0.1 (21), 0.0–2.5	3.9 ± 0.0 (44), 3.0–4.0	1.9 ± 0.1 (45), 0.0–3.0	3.0 (15)	3.5 (7)	2.7 ± 0.1 (20), 1.0–3.0
<i>Pipra pipra</i>	1.4 ± 0.2 (5), 1.0–2.0	0.14 ± 0.02 (5), 0.08–0.20	–	4.0 ± 0.0 (5), 4.0–4.0	2.1 ± 0.5 (5), 1.0–3.0	1.0 (2)	4.0 (2)	3.0 ± 0 (3), 3.0–3.0
<i>Tyrannetes stolzmanni</i>	2.1 ± 0.1 (5), 2.0–2.5	0.46 ± 0.09 (5), 0.25–0.72	1.0 ± 0.0 (1), 1.0–1.0	4.0 ± 0.0 (5), 4.0–4.0	1.6 ± 0.4 (5), 1.0–3.0	1.5 (2)	2.5 (2)	3.0 ± 0 (4), 3.0–3.0
<i>Thamnophilus aethiops</i>	1.6 ± 0.3 (6), 0.5–2.0	0.13 ± 0.03 (6), 0.01–0.18	–	4.0 ± 0.0 (6), 4.0–4.0	2.7 ± 0.1 (6), 2.5–3.0	1.0 (4)	3.5 (1)	3.0 ± 0 (2), 3.0–3.0
<i>Thamnophilus amazonicus</i>	2.2 ± 0.1 (17), 1.5–3.0	0.52 ± 0.05 (15), 0.16–0.80	1.5 ± 0.1 (9), 1.0–2.0	3.6 ± 0.2 (14), 2.0–4.0	2.2 ± 0.2 (13), 1.0–3.0	1.0 (9)	2.5 (5)	2.4 ± 0.2 (9), 2.0–3.0
<i>Pygiptila stellaris</i>	2.3 ± 0.1 (20), 2.0–3.0	0.62 ± 0.04 (20), 0.40–0.93	2.1 ± 0.4 (4), 1.5–3.0	3.9 ± 0.1 (18), 3.0–4.0	2.9 ± 0.1 (17), 2.0–3.5	1.0 (17)	2.5 (4)	2.2 ± 0.2 (9), 1.0–3.0
<i>Thamnomanes caesius</i>	1.7 ± 0.1 (53), 1.0–2.5	0.27 ± 0.02 (47), 0.06–0.70	1.4 ± 0.1 (9), 1.0–2.0	3.9 ± 0.1 (47), 1.0–4.0	2.0 ± 0.1 (42), 1.0–3.0	3.0 (20)	3.5 (13)	2.5 ± 0.1 (31), 2.0–3.0
<i>Myrmotherula guttata</i>	1.0 ± 0.1 (10), 0.5–2.0	0.04 ± 0.01 (10), 0.01–0.16	–	3.8 ± 0.2 (10), 2.0–4.0	2.5 ± 0.2 (10), 2.0–3.0	1.0 (8)	3.5 (3)	2.9 ± 0.1 (7), 2.0–3.0
<i>Myrmotherula haematonota</i>	1.1 ± 0.1 (8), 1.0–2.0	0.08 ± 0.01 (8), 0.04–0.17	–	4.0 ± 0.0 (8), 4.0–4.0	2.9 ± 0.1 (8), 2.0–3.0	1.0 (8)	3.5 (5)	3.0 ± 0 (6), 3.0–3.0

Species	forest stratum	relative height	tree position	% leaf cover	% cover	leaf position	light habitat	illumination
<i>Myrmotherula axillaris</i>	1.8 ± 0.1 (41), 1.0–3.0	0.27 ± 0.02 (41), 0.04–0.60	1.6 ± 0.2 (5), 1.0–2.0	4.0 ± 0.0 (38), 4.0–4.0	2.7 ± 0.1 (38), 1.0–3.0	1.0 (36)	3.5 (10)	2.5 ± 0.1 (16), 2.0–3.0
<i>Myrmotherula longipennis</i>	1.1 ± 0.1 (6), 1.0–1.5	0.10 ± 0.02 (6), 0.06–0.16	1.0 ± 0.0 (1), 1.0–1.0	3.8 ± 0.2 (6), 3.0–4.0	2.0 ± 0.4 (6), 1.0–3.0	1.0 (6)	3.5 (1)	3.0 ± 0 (1), 3.0–3.0
<i>Myrmotherula menetriesii</i>	1.8 ± 0.1 (17), 1.0–2.0	0.35 ± 0.05 (17), 0.03–0.65	1.5 ± 0.0 (1), 1.5–1.5	3.9 ± 0.1 (14), 3.0–4.0	2.5 ± 0.2 (11), 1.0–3.0	1.0 (15)	3.5 (6)	2.4 ± 0.1 (12), 2.0–3.0
<i>Herpsilochmus dorsimaculatus</i>	2.9 ± 0.1 (16), 2.0–3.0	0.83 ± 0.02 (16), 0.64–0.97	2.1 ± 0.1 (12), 1.5–2.5	3.9 ± 0.1 (15), 3.0–4.0	2.8 ± 0.1 (14), 2.0–3.0	1.0 (7)	1.5 (2)	2.0 ± 0 (3), 2.0–2.0
<i>Hypocnemis cantator</i>	1.0 ± 0.0 (5), 1.0–1.0	0.08 ± 0.02 (4), 0.04–0.11	–	4.0 ± 0.0 (4), 4.0–4.0	2.9 ± 0.1 (4), 2.5–3.0	1.0 (4)	3.5 (3)	3.0 ± 0 (4), 3.0–3.0
<i>Hypocnemoides melanopogon</i>	1.0 ± 0.1 (12), 0.5–1.5	0.07 ± 0.01 (10), 0.01–0.12	–	4.0 ± 0.0 (10), 4.0–4.0	2.3 ± 0.3 (9), 1.0–4.0	1.0 (9)	3.5 (6)	2.9 ± 0.1 (7), 2.5–3.0
<i>Hylophylax punctulata</i>	1.4 ± 0.2 (5), 1.0–2.0	0.11 ± 0.04 (5), 0.02–0.20	–	4.0 ± 0.0 (5), 4.0–4.0	1.8 ± 0.4 (5), 1.0–3.0	1.0 (2)	3.5 (1)	2.5 ± 0 (1), 2.5–2.5
<i>Dendrocincla fuliginosa</i>	1.8 ± 0.2 (5), 1.0–2.0	0.23 ± 0.08 (5), 0.01–0.44	0.0 ± 0.0 (5), 0.0–0.0	3.6 ± 0.2 (5), 3.0–4.0	1.8 ± 0.2 (5), 1.0–2.0	1.0 (1)	2.0 (1)	2.7 ± 0.3 (3), 2.0–3.0
<i>Xiphorhynchus obsoletus</i>	2.2 ± 0.1 (13), 2.0–3.0	0.47 ± 0.07 (13), 0.10–0.96	0.3 ± 0.2 (11), 0.0–2.0	3.6 ± 0.4 (9), 0.0–4.0	1.6 ± 0.3 (10), 0.0–3.0	0.0 (3)	2.0 (2)	2.5 ± 0.2 (4), 2.0–3.0
<i>Xiphorhynchus guttatus</i>	2.0 ± 0.0 (17), 2.0–2.0	0.38 ± 0.05 (17), 0.10–0.82	0.4 ± 0.1 (15), 0.0–1.0	3.4 ± 0.3 (17), 0.0–4.0	2.0 ± 0.1 (17), 1.0–3.0	1.0 (5)	2.0 (3)	2.4 ± 0.2 (9), 2.0–3.0
<i>Formicarius colma</i>	0.1 ± 0.1 (7), 0.0–0.5	0.00 ± 0.00 (7), 0.0–0.03	–	3.9 ± 0.1 (7), 3.0–4.0	2.9 ± 0.1 (7), 2.5–3.0	3.0 (1)	3.5 (4)	2.9 ± 0.1 (4), 2.5–3.0
<i>Vireo olivaceus</i>	3.0 ± 0.0 (25), 3.0–3.0	0.91 ± 0.01 (21), 0.77–0.97	2.3 ± 0.1 (21), 1.5–3.0	3.9 ± 0.1 (22), 3.0–4.0	2.6 ± 0.1 (18), 1.0–3.0	1.5 (9)	1.5 (9)	1.8 ± 0.1 (13), 1.0–2.0
<i>Cyanocorax violaceus</i>	2.9 ± 0.1 (8), 2.5–3.0	0.78 ± 0.03 (6), 0.70–0.89	1.5 ± 0.3 (3), 1.0–2.0	3.0 ± 1.0 (4), 1.0–2.0	1.3 ± 0.7 (3), 0.0–2.0	1.0 (4)	1.0 (1)	1.0 ± 0 (1), 1.0–1.0
<i>Thryothorus leucotis</i>	1.3 ± 0.2 (13), 1.0–3.0	0.13 ± 0.05 (10), 0.01–0.52	1.5 ± 0.0 (1), 1.5–1.5	4.0 ± 0.0 (11), 4.0–4.0	3.0 ± 0.2 (9), 2.0–4.0	1.0 (10)	3.5 (5)	2.7 ± 0.2 (7), 2.0–3.0
<i>Dendroica striata</i>	3.0 ± 0.0 (16), 3.0–3.0	0.88 ± 0.02 (16), 0.75–0.96	2.2 ± 0.1 (16), 2.0–2.5	3.6 ± 0.2 (14), 1.0–4.0	2.8 ± 0.2 (13), 1.0–4.0	1.0 (8)	1.5 (7)	2.0 ± 0.1 (11), 1.5–2.5
<i>Hemithraupis flavicollis</i>	2.9 ± 0.0 (93), 2.0–3.0	0.87 ± 0.01 (93), 0.40–1.00	2.2 ± 0.1 (75), 1.5–3.0	3.6 ± 0.1 (88), 1.0–4.0	2.4 ± 0.1 (86), 1.0–3.0	1.0 (36)	1.5 (22)	1.9 ± 0.1 (45), 1.0–3.0
<i>Tachyphonus cristatus</i>	2.9 ± 0.0 (58), 2.0–3.0	0.84 ± 0.02 (57), 0.44–1.00	2.2 ± 0.1 (43), 1.0–3.0	3.7 ± 0.1 (56), 0.0–4.0	2.2 ± 0.1 (53), 0.0–3.0	1.5 (23)	1.5 (9)	2.0 ± 0.1 (24), 1.0–3.0
<i>Thraupis palmarum</i>	2.8 ± 0.1 (15), 2.0–3.0	0.83 ± 0.05 (14), 0.36–1.00	2.1 ± 0.2 (12), 1.5–3.0	3.0 ± 0.3 (15), 1.0–4.0	2.0 ± 0.2 (15), 0.0–3.0	1.0 (10)	1.5 (2)	2.1 ± 0.3 (6), 1.0–3.0
<i>Euphonia rufiventris</i>	3.0 ± 0.0 (13), 3.0–3.0	0.93 ± 0.02 (13), 0.80–1.00	2.4 ± 0.2 (11), 2.0–3.0	2.8 ± 0.3 (13), 0.0–4.0	1.9 ± 0.2 (13), 1.0–3.0	1.0 (4)	1.5 (3)	1.6 ± 0.2 (4), 1.0–2.0
<i>Tangara velia</i>	3.0 ± 0.0 (19), 3.0–3.0	0.93 ± 0.02 (19), 0.80–1.00	2.4 ± 0.1 (18), 1.5–3.0	3.4 ± 0.3 (18), 0.0–4.0	2.1 ± 0.2 (18), 0.0–3.0	1.0 (5)	1.5 (2)	2.2 ± 0.4 (3), 1.5–3.0
<i>Dacnis flaviventer</i>	3.0 ± 0.0 (18), 3.0–3.0	0.97 ± 0.01 (17), 0.90–1.00	2.7 ± 0.1 (17), 2.0–3.0	3.3 ± 0.2 (18), 2.0–4.0	1.9 ± 0.2 (16), 1.0–3.0	3.0 (6)	1.0 (5)	1.5 ± 0.2 (10), 1.0–2.0
<i>Dacnis cayana</i>	3.0 ± 0.0 (64), 2.0–3.0	0.90 ± 0.01 (64), 0.60–1.00	2.2 ± 0.1 (53), 1.0–3.0	3.3 ± 0.1 (61), 0.0–4.0	2.3 ± 0.1 (60), 0.0–4.0	1.0 (28)	1.5 (14)	1.9 ± 0.1 (29), 1.0–3.0
<i>Chlorophanes spiza</i>	3.0 ± 0.0 (18), 3.0–3.0	0.90 ± 0.02 (18), 0.72–1.00	2.0 ± 0.1 (15), 1.5–3.0	3.2 ± 0.3 (17), 0.0–4.0	2.1 ± 0.2 (17), 0.5–3.5	1.0 (10)	2.0 (5)	2.4 ± 0.2 (7), 2.0–3.0
<i>Cyanerpes nitidus</i>	3.0 ± 0.0 (57), 2.0–3.0	0.89 ± 0.01 (56), 0.54–1.00	2.2 ± 0.1 (50), 1.0–3.0	3.5 ± 0.1 (56), 1.0–4.0	2.2 ± 0.1 (54), 0.0–3.5	1.0 (23)	1.5 (12)	1.9 ± 0.1 (27), 1.0–3.0
<i>Cyanerpes caeruleus</i>	2.7 ± 0.1 (15), 2.0–3.0	0.68 ± 0.05 (15), 0.40–1.00	1.9 ± 0.2 (9), 1.0–3.0	3.9 ± 0.1 (15), 3.0–4.0	1.9 ± 0.2 (15), 1.0–3.0	1.0 (6)	1.5 (2)	2.6 ± 0.2 (7), 2.0–3.0
<i>Pitylus grossus</i>	1.5 ± 0.6 (5), 0.0–3.0	0.35 ± 0.20 (5), 0.0–0.93	2.0 ± 0.0 (1), 2.0–2.0	3.8 ± 0.2 (5), 3.0–4.0	2.0 ± 0.3 (5), 1.0–3.0	1.0 (3)	3.5 (2)	2.5 ± 0.3 (3), 2.0–3.0

Species	forest stratum	relative height	tree position	% leaf cover	% cover	leaf position	light habitat	illumination
<i>Psarocolius viridis</i>	3.0 ± 0.0 (13), 3.0–3.0	0.94 ± 0.01 (12), 0.85–1.00	2.3 ± 0.1 (12), 2.0–3.0	3.5 ± 0.3 (12), 1.0–4.0	2.3 ± 0.2 (12), 1.0–3.0	1.5 (4)	1.5 (3)	1.8 ± 0.4 (4), 1.0–3.0
<i>Gymnostinops bifasciatus</i>	3.0 ± 0.0 (31), 2.0–3.0	0.91 ± 0.03 (27), 0.32–1.00	2.2 ± 0.1 (26), 1.0–3.0	3.6 ± 0.1 (27), 1.0–4.0	2.4 ± 0.1 (24), 1.0–4.0	1.0 (11)	1.5 (4)	1.8 ± 0.2 (7), 1.0–3.0
<i>Cacicus cela</i>	2.9 ± 0.1 (35), 2.0–3.0	0.82 ± 0.03 (29), 0.32–1.00	2.1 ± 0.1 (19), 1.0–3.0	3.6 ± 0.1 (30), 2.0–4.0	2.1 ± 0.2 (25), 0.0–3.0	1.0 (15)	1.5 (5)	2.3 ± 0.1 (11), 2.0–3.0
<i>Icterus chryscephalus</i>	3.0 ± 0.0 (12), 3.0–3.0	0.95 ± 0.02 (9), 0.88–1.00	2.1 ± 0.3 (10), 1.0–3.0	3.3 ± 0.3 (10), 1.0–4.0	2.1 ± 0.2 (10), 1.0–3.0	1.0 (5)	1.0 (2)	1.6 ± 0.2 (4), 1.0–2.0