

Forest structure and territory size relationship in the neotropical understory insectivore *Henicorhina leucosticta*

Luis Esteban Vargas^{*,1}, Natalie Viviana Sánchez[†] and Gerardo Avalos^{*,‡}

* Escuela de Biología, Universidad de Costa Rica, 2060 San Pedro, San José, Costa Rica

† Instituto Internacional en Conservación y Manejo de Vida Silvestre, Universidad Nacional, 1350–3000 Heredia, Costa Rica

‡ The School for Field Studies, Center for Sustainable Development Studies, 10 Federal St., Salem, MA 01970, USA

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Abstract: The neotropical terrestrial insectivore *Henicorhina leucosticta* (Troglodytidae) maintains long-term territories through vocalizations and forages among leaf litter trapped in the understory vegetation and ground litter. The relationship between forest structure and *H. leucosticta* territory size was studied in La Selva Biological Station, Costa Rica, during the non-breeding season in 2009. Forest structure was measured by assessing canopy openness and leaf area index (LAI) using hemispherical photography, while territory size was estimated with the playback technique using local conspecific vocalizations. Mean territory area was 3.8 ± 2.8 ha (mean \pm SD, $n = 10$). Territory radius length was similar in old-growth forest and abandoned agro-forest plantations. We found that *H. leucosticta* territory size decreased as median LAI increased. We propose that LAI is related to territory size through the amount of leaf fall and subsequent leaf litter accumulation over the understory plants, which constitutes an important reservoir of arthropod prey and nest materials for *H. leucosticta*. The long-term supply of food resources is likely to affect territory size in this species, as well as other insectivorous birds with similar foraging behaviour. These results are congruent with the structural cues hypothesis.

Key Words: canopy openness, forest structure, LAI, playback, structural cues hypothesis, territoriality, wrens

INTRODUCTION

In temperate regions, it has been proposed that insectivorous birds indirectly monitor prey abundance by assessing habitat structure while adjusting territory size accordingly (Marshall & Cooper 2004, Pasinelli 2000, Renken & Wiggers 1989, Seastedt & MacLean 1979). This constitutes the basis of the structural cues hypothesis, which proposes that birds adjust territory size using habitat structure as predictor of prey abundance within a given site over time (Seastedt & MacLean 1979, Smith & Shugart 1987). Canopy cover is considered a structural cue for the ovenbird (*Seiurus aurocapillus*, Smith & Shugart 1987) and the pileated woodpecker (*Dryocopus pileatus*, Renken & Wiggers 1989) during the breeding season.

In contrast to the generally short breeding season of birds in temperate regions, insectivorous birds in tropical forests typically defend all-purpose territories year-round and form long-term pair bonds with often

low reproductive success (Stutchbury & Morton 2001). Thus, for many tropical insectivores the capacity of a given territory to supply enough food for the mated pair and subsequent progeny throughout the year is of great importance. Given that there is considerable variation in territory size of tropical insectivorous birds within populations (Morton *et al.* 2000, Terborgh *et al.* 1990), we asked if the structural cues hypothesis would apply to terrestrial insectivores that hold long-term territories in the tropical rain forest.

As a first step, here we examined the relationship between forest structure, as reflected in canopy openness and leaf area index (LAI), and non-breeding territory size in the neotropical insectivorous bird *Henicorhina leucosticta* (Cabanis). In addition to canopy openness, we also included LAI to describe the forest structure within the territories because arthropod abundance and biomass are positively associated with LAI in tropical lowland rain forests (Dial *et al.* 2006). Therefore, we expect to find relatively smaller territories in sites with low levels of canopy openness and high LAI values, because these forest structural characteristics represent potentially

¹ Corresponding author. Email: luis.vargascastro@ucr.ac.cr

higher prey abundance. We also explored possible differences between old-growth forest and abandoned agro-forest sites in terms of habitat structure and *H. leucosticta* territory size. Agro-forest systems modify the original forest structure, and structural parameters such as LAI change in relation to this disturbance (Dietz *et al.* 2007). Hence, an effect of previous land use on forest structure and consequently on *H. leucosticta* territory size is expected, if habitat structure is related to territory size. To our knowledge, this is the first study to investigate the relationship between forest structure and territory size in a tropical understorey insectivorous bird.

MATERIALS AND METHODS

Study area

The study was conducted from June to August of 2009 at La Selva Biological Station in the north-eastern Caribbean lowlands of Costa Rica (1600 ha, 10°25'N, 84°00'W, 30–150 m asl). Rainfall distribution is weakly seasonal with a wet season from May to December (Sanford *et al.* 1994). Mean annual precipitation is ~4000 mm y⁻¹ with at least 100 mm of rain mo⁻¹ (Sanford *et al.* 1994). We worked in two forest types classified according to their historical land use: old-growth forest, and abandoned agro-forest plantations (McDade & Hartsorn 1994). The agro-forest area was formerly planted with cocoa (*Theobroma cacao* L.), peach palm (*Bactris gasipaes* Kunth) and *Cordia alliodora* Oken, and was abandoned in the 1960s (Lieberman & Lieberman 1987, McDade & Hartshorn 1994). The old-growth forest has had no documented history of recent human disturbance (Lieberman & Lieberman 1987).

Study species

Henicorhina leucosticta is a common dweller of the lower understorey of mature tropical lowland rain forests and adjacent shady secondary growth (Stiles & Skutch 1989, Winker *et al.* 1996), from central Mexico to northern South America (Clements & Shany 2001). This species preys on arthropods, mostly insects, by searching mainly among the leaf litter trapped over palms, ferns and other understorey plants and also in the ground litter. *Henicorhina leucosticta* breeds from February to May and builds two types of nest (Skutch 1960, Stiles & Skutch 1989). Breeding nests are made during the breeding season, located well hidden and close to the ground (Skutch 1960). Dormitory nests are structures built year-round, used to sleep at night in slender saplings, palms or climber tangles, in higher positions (0.6–3 m) and each individual can have up to four dormitory nests

in its territory (Skutch 1960). Territories are defended year-round by single individuals or monogamous pairs (Stutchbury & Morton 2001). Both sexes sing and respond to playbacks of conspecific songs within their territory (Winker *et al.* 1996), and apparently react more aggressively towards local than unknown songs (Stutchbury & Morton 2001). Females have repertoires composed of five to six song types which are shared with neighbouring females as a local dialect, whereas males have larger song repertoires of up to 30 song types, in which most song types are different from those in the repertoires of other local males (Stutchbury & Morton 2001).

Song recording and editing

Songs of *Henicorhina leucosticta* were recorded in the field using an Olympus LS-10 digital recorder and a Sennheiser ME66/K6 microphone, at 48 kHz and 24-bit resolution. We made a sound file consisting of two parts of 1-min duration each, using Raven Pro 1.4 sound analysis software (Cornell Lab of Ornithology, Ithaca, New York). The first part was composed by a set of contact calls, and the second part by a local conspecific song recorded at La Selva, which was taken from the song repertoire of a randomly selected individual whose territory was not included in the present study. This sound file, hereafter referred to as 'stimulus', was made to elicit a territorial defence response.

Estimation of territory size through playbacks

Ten territories were studied and classified by forest type according to the land-use map of La Selva Biological Station for the year 2000 (Organization for Tropical Studies, http://www.ots.ac.cr/index.php?option=com_wrapper&Itemid=352). Five territories were located in the old-growth forest and five in abandoned agro-forest plantations. In each territory we observed the individuals for a 2-h period to mark the location of foraging and dormitory nest sites, the location of territorial disputes, and the position where calls or songs were emitted. The locations of each sighting were calculated using compass bearings, direct distances between these marks, and reference points of the geographic grid system of La Selva. We plotted the observations for each territory on a map and drew a polygon joining the external marks as the perimeter. We considered the polygon centroid as the centre of the territory. Interestingly enough, we found dormitory nests very close to the centre in eight territories.

Territory size was estimated using the playback technique following Falls (1981), with some modifications as indicated below. We started a set of playbacks of the stimulus in the central point of the territory to

estimate one radius length. We played back the stimulus successively in 20-m intervals, each time farther from the central point, and noted when the individual or pair stopped advancing towards the speakers. We marked the last point where the birds showed territorial defence movements as the territory boundaries. Considering habituation as a possibility, we played back the stimulus again inside the territory and the defensive behaviour was elicited again in all cases, thus habituation was discarded.

Playbacks were made using Radioshack 40–1441 speakers held at a height of 1 m, at a constant amplitude level comparable to natural song. The playback points were located on the territory maps, and the minimum linear distance between the central point and the territory boundary was used as a radius to calculate circular areas for each one. We used ArcView GIS 3.3 (ESRI, California) to calculate territory areas and make a map of the territories. Territories were considered to be circular for ease of measurement in the field, actual territory shapes were unknown. However, since a circular area is a function of its radius and territory radii were directly measured in the field, we report the results concerning forest structure variables using territory radius as the indicator of territory size. All the playback points of a given territory were tested on a continuous session in the same day, without losing visual or acoustic contact with the target bird or birds. Two birds from different territories were colour banded. Two pairs of territories were adjacent, one territory of one pair was held by a marked individual, in the other case a territorial dispute between neighbours provoked by the experimental playbacks was observed, thus facilitating the boundaries determination.

Assessment of forest structure using hemispherical photography

We took digital hemispherical photographs across sites separated by 20 m following linear transects from the central point of the territory to the boundary. We took from three to eight photos in each territory depending on the magnitude of its radius, and 50 photos in total. All photographs were taken at 1.5 m height using a Nikon Coolpix 5000 digital camera with an 8-mm Nikon fish-eye lens. We oriented the camera so the top of each photograph was aligned with the geographic North. Photographs were taken only under overcast conditions to avoid direct beams of sunlight from obscuring the contrast between forest cover and open sky (Rich 1990).

Photographs were analysed with Gap Light Analyzer version 2.0 software (Forest Ecology Lab, Simon Fraser University, Burnaby, BC, Canada) using the default threshold level to distinguish pixels between sky and non-sky classes. Canopy structure parameters, such as gap fraction or the complementary canopy cover, can be extracted from the photograph. We used the images to

calculate the percentage of canopy openness (PCO) and leaf area index (LAI), in order to characterize the overall structure of the canopy and lower vegetation within the territories. PCO measures the percentage of open sky seen from a point beneath the forest canopy (Frazer *et al.* 1999). LAI is a measure of canopy foliage content, defined as the total one-side leaf area per unit ground surface area (Asner *et al.* 2003, Bréda 2003). LAI estimation through hemispherical photography is widely used as a non-destructive method in which LAI is determined from gap fraction measurements by inverting a light interception model (Bréda 2003, Chason *et al.* 1991, Jonckheere *et al.* 2005, Stenberg *et al.* 1994). Gap Light Analyzer in addition divides the canopy and calculates partial LAI values extracted from two concentric rings within the image (Stenberg *et al.* 1994). The complete image represents a 180° field of view, the zenith is the vertical axis in the centre of the image at 0°, and the horizons at the edges are 90° from the zenith. We used the LAI 4 Ring estimate, which is the effective LAI integrated over zenith angles 0° to 60° because it gives a less biased LAI estimate than Ring 5 (Chason *et al.* 1991, Stenberg *et al.* 1994).

Statistical analyses

We tested for differences in territory radius between forest types using the Mann–Whitney U-test (Zar 1996), and Student's t-tests were used to analyse PCO and LAI differences between forest types. Since we found no difference in PCO or LAI between forest types, we pooled the data to examine further relationships between PCO, LAI and territory size. We decided to use median values of PCO and LAI to circumvent the effects of extreme values of some of the territories. Lastly, we examined the relationships between these two forest structural variables and territory size using linear regression models. We used the Akaike's Information criterion with a small sample size correction (AICc) for model selection, then we calculated Δ AICc and the Akaike's weights (Burnham & Anderson 2002). The model with the lowest AICc value was then used to examine territory size variation in relation to forest structure characteristics. All tests were done using R version 2.7.1 statistical software (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Territory size

Territory radius did not show differences between forest types ($U = 17$, $P > 0.05$) (Table 1). When all territories were pooled, *Henicorhina leucosticta* mean territory radius length was 103 ± 37.8 m (mean \pm SD)

Table 1. Territory size and forest structure of *Henicorhina leucosticta* territories by forest type (mean \pm SD) at La Selva, Costa Rica, July 2009.

	Forest type	
	Old-growth forest	Abandoned agro-forest
Territory size		
Radius (m)	117 \pm 48.0	89.4 \pm 28.4
Area (ha)	4.9 \pm 3.6	2.7 \pm 1.8
Number of territories	5	5
Forest structure		
Canopy openness (%)	7.78 \pm 1.41	7.67 \pm 2.17
Leaf Area Index (LAI)	2.92 \pm 0.33	3.05 \pm 0.53
Number of photographs	27	23

Table 2. Linear regression models set of *Henicorhina leucosticta* territory radius in relation to forest structural variables at La Selva, Costa Rica, July 2009. Models are ranked using Akaike's Information Criterion with a small sample size correction (AICc). Null = territory radius model without forest structure parameters. LAI = leaf area index, PCO = percentage of canopy openness. The Npar column gives the number of parameters used in each model.

Model	AICc	Δ AICc	AICw	Npar
Radius \sim LAI	103	0.00	0.54	2
Null	106	2.11	0.19	1
Radius \sim PCO + LAI	106	2.62	0.15	3
Radius \sim PCO	107	3.04	0.12	2

($n = 10$) and mean circular territory area was 3.8 ± 2.8 ha (mean \pm SD) ($n = 10$). Half of the territories were defended by pairs, and only one territory was defended by a single individual. The rest of the territories were occupied by three or four individuals (pairs with immatures).

Forest structural variables

We did not observe differences in PCO between the territories found in old-growth forest and abandoned agro-forest sites ($t = -0.29$, $P = 0.77$) (Table 1). In addition, territories located in old-growth forests did not differ in LAI relative to those within abandoned agro-forest sites ($t = 1.03$, $P = 0.31$) (Table 1).

Most territories showed considerable variation in both PCO and LAI evident along their radii. The linear regression model that only included LAI best explained *H. leucosticta* territory size variation (Table 2). We found that territory radius was negatively correlated with median LAI ($r = -0.64$, $P = 0.04$, $n = 10$), and median LAI explained 41% of the *H. leucosticta* territory size variation (Figure 1).

DISCUSSION

Playback technique and territory size

We observed that *Henicorhina leucosticta* kept reacting vigorously to the stimulus and did not seem to habituate.

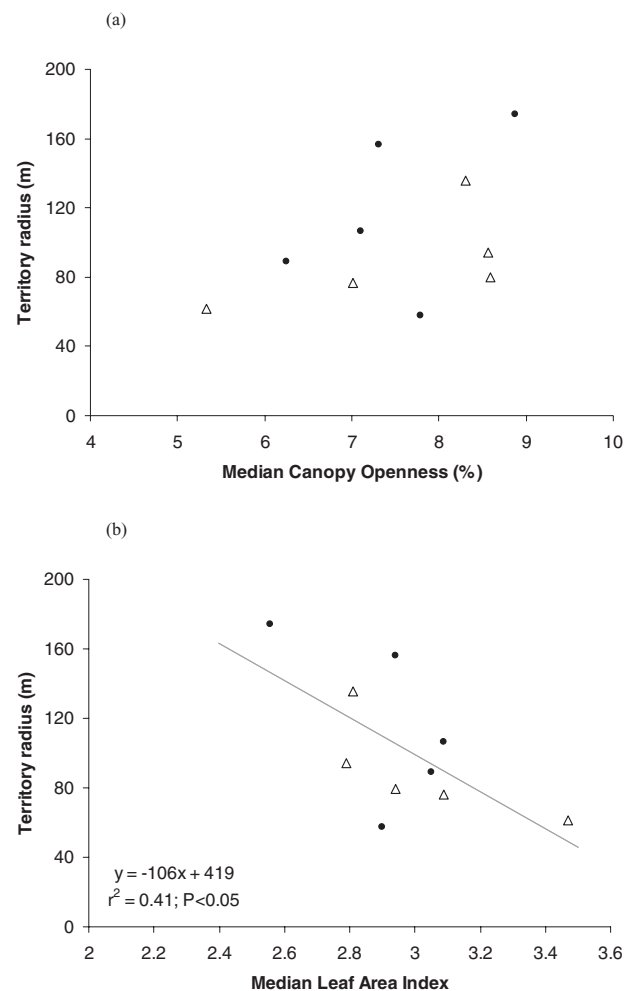


Figure 1. Relationship of *Henicorhina leucosticta* territory radius with median percentage of canopy openness (a) and median leaf area index (b) at La Selva, Costa Rica, July 2009. Closed circles and open triangles correspond to territories located in old-growth forest and abandoned agro-forest respectively.

When playbacks are used as an experimental tool, habituation can be an issue (Thompson *et al.* 1973). Simpson (1984) did not find evidence of habituation in the Carolina wren (*Thryothorus ludovicianus*). *Thryothorus ludovicianus* and *H. leucosticta* have a comparable singing style in the sense that each song is a succession of repeated short phrases (Mann *et al.* 2009, Stiles & Skutch 1989). A resistance to habituation of repeated conspecific songs could be associated with this singing style (Simpson 1984). Both a strong reaction to playbacks and low or lack of habituation to repeated songs, are characteristics that make *H. leucosticta* especially suitable for using the playback technique to estimate its territory size. The territory boundaries were very clear in all cases, nevertheless we recommend the measurement of a number of radii per each territory and then average these to improve the accuracy of this procedure for future use.

Robinson *et al.* (2000) reported a territory size range (0–2 ha) for *H. leucosticta* in Panama, which is somewhat lower than our mean territory size at La Selva. However, further comparisons are not easy since they used the spot-mapping technique, while we used field playbacks instead. Even estimations of territory size using the same technique could give different results for the same species, such as the musician wren (*Cyphorhinus arada*) whose territory was 22.7 ha in Brazil (Stouffer 2007), but only 11 ha in Peru (Terborgh *et al.* 1990) using in both cases the spot-mapping method. Use of a different technique to measure territory size may account for the difference observed between the study of Robinson *et al.* (2000) and ours. However, many ecological factors, such as habitat structure, may affect territory size differentially in two distinct locations.

Habitat structure in old-growth forest and abandoned agro-forest

Abandoned agro-forest had canopy openness and LAI values comparable to those of the old-growth forest. The agro-forest we studied has been abandoned for more than 40 y (Lieberman & Lieberman 1987). Secondary forests in humid lowlands of Costa Rica recovered a similar structure to the original forest in 30–50 y after abandoning farming plots (Ewel 1980). Forest structure should recover faster in abandoned agro-forest sites than in comparison with a more extremely disturbed site (i.e. after farming), because some of the original forest trees remain in the agro-forest (Holl *et al.* 2000). In addition, LAI increases at a faster rate relative to other forest structural characteristics in the wet tropical lowlands after a given disturbance (Dietz *et al.* 2007, Ewel 1980). Therefore, it is expected to have similar levels of LAI and canopy openness in the old-growth forest and the abandoned agro-forest after that period of recovery. In congruence with this lack of structural differences between old-growth forest and abandoned agro-forest, forest type did not have a detectable effect on *H. leucosticta* territory size, an expected result if territory size is related to forest structure and the two forest types had similar structure.

The LAI values we obtained in both forest types were about half the landscape LAI of 6.00 found in a previous study at La Selva (Clark *et al.* 2008), in which LAI was measured directly by harvesting foliage. A key assumption in the estimation of LAI with hemispherical photography is that the leaves are randomly distributed through the canopy (Chason *et al.* 1991, Stenberg *et al.* 1994). In contrast, the leaves in the forest canopies are grouped in branches and trees. The deviation of the canopy foliage from a random distribution has been accepted as the main reason for constantly obtaining LAI

underestimations when using indirect methods such as hemispherical photography (Bréda 2003, Chason *et al.* 1991). However, the spatial variability of effective LAI, as estimated by indirect methods, is reliable and a correction factor can be used to obtain accurate LAI values (Chason *et al.* 1991). For our purpose, we were more interested in the relative spatial variation of forest structural variables among territories than on exact LAI values, therefore our LAI estimations are functional to analyse *H. leucosticta* territory size in relation to forest structural characteristics.

Habitat structure and territory size

Canopy openness and LAI were found to be highly variable within territories. High variability of these canopy structural variables across a territory reflects the small-scale spatial heterogeneity at the plant community-level characteristic of tropical rain forests (Wirth *et al.* 2001), exposing a wide overlap of microhabitat conditions inside *H. leucosticta* territories.

Studies concerning the structural cues hypothesis have found a negative relationship between canopy cover and territory size (Renken & Wiggers 1989, Smith & Shugart 1987). Conversely to our expectation, median canopy openness was not included in the best model describing the relationship between *H. leucosticta* territory size and forest structure. Median LAI alone best explained territory size variation, showing a negative relationship in which territory size decreased as median LAI increased. Even though these two forest structure variables are negatively related (Kabakoff & Chazdon 1996), they are not redundant and describe different biological aspects of the forest structure.

LAI is positively associated with total arthropod biomass and abundance, as well as with the abundance of 13 out of 14 arthropod groups in tropical lowland rain forests (Dial *et al.* 2006). Dial *et al.* (2006) also demonstrated that total leaf area explained 85% of the variability in arthropod abundance and arthropod density did not vary with height from the ground level to the canopy's highest trees. In addition, plant and arthropod biomass are positively associated in tropical rain forests (Sayer *et al.* 2010). The fact that arthropod abundance correlates well with tropical rain forest structure, and the existence of a negative relationship between LAI and territory size, is compatible with the idea that LAI could be used by *H. leucosticta* as a forest structural cue to indirectly assess prey abundance.

Greater foliage content in the canopy represents an advantage to *H. leucosticta* in terms of its foraging and nest building behaviour. Since LAI measures foliage area per unit of ground area (Asner *et al.* 2003, Cournac *et al.* 2002), *H. leucosticta* territories with higher LAI are

more likely to have greater leaf fall and subsequently greater leaf litter accumulation over the understorey plants. In fact, leaf litter collections are used as a method to estimate LAI (Chason *et al.* 1991, Dufrière & Bréda 1995, Veneklaas 1991). Fallen leaves are intercepted by branches, climber tangles, ferns and small palms in the understorey and constitute a very important reservoir of arthropods for *H. leucosticta* and many other understorey insectivorous birds. These leaves trapped over the understorey plants are known as the aerial leaf litter (Gradwohl & Greenberg 1982). Comparably, highest arthropod abundance corresponded with the greatest leaf litter depth at La Selva (Lieberman & Dock 1982). Additionally, *H. leucosticta* builds dormitory nests year-round, each individual having a number of these dormitory nests within its territory (Skutch 1960), and frequently searches for skeletons of partially decayed leaves and small brown leaves within the aerial leaf litter. Therefore, high LAI within a forest area could be associated with more potential prey microhabitats to forage in as well as more nest material sources for *H. leucosticta*, resulting in smaller territories that guarantee the food and nest building requirements in the long term for this species.

Our results showed that LAI explained a considerable part of *H. leucosticta* territory size variation. However, territory size of tropical understorey insectivores is probably the result of the interaction between habitat structure and other factors, such as interspecific competition (Robinson & Terborgh 1995, Wilson 1975), population density (Robinson *et al.* 2000) and predation risk (Lima 1998). Here we emphasize the role of forest structure on territory size and its possible function as a predictor of arthropod abundance for these species. Habitat structural cues could be useful for species that defend long-term territories especially after territory switching or first-time territory acquisition by juveniles, because food supply within the new territory is unknown. Variable rates of territory switching have been reported in the bay wren *Thryothorus nigricapillus* (Levin 1996), buff-breasted wren *Thryothorus leucotis* (Stutchbury & Morton 2001) and dusky antbird *Cercomacra tyrannina* (Morton *et al.* 2000). However, more research is needed to understand the territory dynamics of tropical understorey insectivores.

In conclusion, we found that territory size is related to forest structure in a neotropical understorey insectivorous bird. These results are congruent with the structural cues hypothesis, given that median LAI is negatively related to territory size and LAI is positively associated with arthropod abundance in tropical rain forests. The mechanism we propose by which forest structure and territory size are connected gives rise to new research questions based on an integrative ecological approach. We urge the next step to be the measurement of aerial

leaf litter mass and its respective arthropod abundance within the territories of *H. leucosticta*, and other tropical insectivores with similar foraging behaviour, in order to investigate the interactions between these understorey micro-habitat characteristics and forest canopy structure variables, such as LAI, in relation to territory size over the long term.

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LITERATURE CITED

- ASNER, G. P., SCURLOCK, J. M. & HICKE, J. A. 2003. Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecology and Biogeography Letters* 12: 191–205.
- BRÉDA, N. J. J. 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *Journal of Experimental Botany* 54:2403–2417.
- BURNHAM, K. P. & ANDERSON, D. R. 2002. *Model selection and inference: a practical information-theoretic approach*. (Second edition). Springer-Verlag, New York. 488 pp.
- CHASON, J. W., BALDOCCHI, D. D. & HUSTON, M. A. 1991. A comparison of direct and indirect methods for estimating forest canopy leaf area. *Agricultural and Forest Meteorology* 57: 107–128.
- CLARK, D. B., OLIVAS, P. C., OBERBAUER, S. F., CLARK, D. A. & RYAN, M. G. 2008. First direct landscape-scale measurement of tropical rain forest leaf area index, a key driver of global primary productivity. *Ecology Letters* 11:163–172.
- CLEMENTS, J. F. & SHANY, N. 2001. *A field guide to the birds of Peru*. Ibis Publishing Company, Temecula. 283 pp.
- COURNAC, L., DUBOIS, M. A., CHAVE, J. & RIÉRA, B. 2002. Fast determination of light availability and leaf area index in tropical forests. *Journal of Tropical Ecology* 18:295–302.
- DIAL, R. J., ELLWOOD, M. D. F., TURNER, E. C. & FOSTER, W. A. 2006. Arthropod abundance, canopy structure, and microclimate in a Bornean lowland tropical rain forest. *Biotropica* 38: 643–652.
- DIETZ, J., HÖLSCHER, D., LEUSCHNER, C., MALIK, A. & AMIR, M. 2007. Forest structure as influenced by different types of community forestry in a lower montane rainforest of Central Sulawesi, Indonesia. Pp. 133–148 in Tschardtke, T., Leuschner, C. Guhardja, E., Zeller, M. & Bidin, A. (eds.). *The stability of tropical rainforest margins, linking*

- ecological, economic and social constraints of land use and conservation. Springer, Berlin.
- DUFRENE, E. & BRÉDA, N. 1995. Estimation of deciduous forest leaf area index using direct and indirect methods. *Oecologia* 104: 156–162.
- EWEL, J. 1980. Tropical succession: manifold routes to maturity. *Biotropica* 12:2–7.
- FALLS, J. B. 1981. Mapping territories with playback: an accurate census method for songbirds. *Studies in Avian Biology* 6:86–91.
- FRAZER, G. W., CANHAM, C. D. & LERTZMAN, K. P. 1999. *Gap Light Analyzer (GLA). Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Users manual and program documentation.* Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York. 36 pp.
- GRADWOHL, J. & GREENBERG, R. 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. *Ecology* 63:581–583.
- HOLL, K. D., LOIK, M. E., LIN, E. H. V. & SAMUELS, I. A. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* 8: 339–349.
- JONCKHEERE, I., NACKAERTS, K., MUYS, B. & COPPIN, P. 2005. Assessment of automatic gap fraction estimation of forests from digital hemispherical photography. *Agricultural and Forest Meteorology* 132:96–114.
- KABAKOFF, R. P. & CHAZDON, R. L. 1996. Effects of canopy species dominance on understorey light availability in low-elevation secondary forest stands in Costa Rica. *Journal of Tropical Ecology* 12:779–788.
- LEVIN, R. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiments. *Animal Behaviour* 52:1093–1106.
- LIEBERMAN, D. & LIEBERMAN, M. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969–1982). *Journal of Tropical Ecology* 3:347–358.
- LIEBERMAN, S. & DOCK, C. F. 1982. Analysis of the leaf litter arthropod fauna of lowland tropical evergreen forest site (La Selva, Costa Rica). *Revista de Biología Tropical* 30:27–34.
- LIMA, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive and ecological perspectives. *Advances in the Study of Behavior* 27: 215–290.
- MANN, N. I., DINGESS, K. A., BARKER, F. K., GRAVES, J. A. & SLATER, P. J. B. 2009. A comparative study of song form and duetting in neotropical *Thryothorus* wrens. *Behaviour* 146:1–43.
- MARSHALL, M. R. & COOPER, R. J. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology* 85:432–445.
- MCDADE, L. A. & HARTSHORN, G. S. 1994. La Selva Biological Station. Pp. 6–18 in McDade, L., Bawa, K. S., Hespeneide, H. & Hartshorn, G. S. (eds.). *La Selva: ecology and natural history of a neotropical rain forest.* The University of Chicago Press, Chicago. 486 pp.
- MORTON, E. S., DERRICKSON, K. C. & STUTCHBURY, B. J. 2000. Territory switching behavior in a sedentary tropical passerine, the Dusky Antbird (*Cercomacra tyrannina*). *Behavioral Ecology* 11:648–653.
- PASINELLI, G. 2000. Oaks (*Quercus* sp.) and only oaks? Relations between habitat structure and home range size of the middle spotted woodpecker (*Dendrocopos medius*). *Biological Conservation* 93:227–235.
- RENKEN, R. B. & WIGGERS, E. P. 1989. Forest characteristic related to Pileated Woodpecker territory size in Missouri. *The Condor* 91:642–652.
- RICH, P. M. 1990. Characterizing plant canopies with hemispherical photographs. *Remote Sensing Reviews* 5:13–29.
- ROBINSON, S. K. & TERBORGH, J. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* 64:1–11.
- ROBINSON, W. D., BRAWN, J. D. & ROBINSON, S. K. 2000. Forest bird community structure in Central Panama: influence of spatial scale and biogeography. *Ecological Monographs* 70:209–235.
- SANFORD, R. L., PAABY, P., LUVALL, J. C. & PHILLIPS, E. 1994. Climate, geomorphology, and aquatic systems. Pp. 19–33 in McDade, L., Bawa, K. S., Hespeneide, H. & Hartshorn, G. S. (eds.). *La Selva: ecology and natural history of a neotropical rain forest.* The University of Chicago Press, Chicago.
- SAYER, E. J., SUTCLIFFE, L. M. E., ROSS, R. I. C. & TANNER, E. V. J. 2010. Arthropod abundance and diversity in a lowland tropical forest floor in Panama: role of habitat space vs. nutrient concentrations. *Biotropica* 42:194–200.
- SEASTEDT, T. R. & MACLEAN, S. F. 1979. Territory size and composition in relation to resource abundance in Lapland Longspurs breeding in Arctic Alaska. *The Auk* 96:131–142.
- SIMPSON, B. 1984. Test of habituation to song repertoires by Carolina Wrens. *The Auk* 101:244–254.
- SKUTCH, A. F. 1960. *Life histories of Central American birds II.* Cooper Ornithology Society, California. 593 pp.
- SMITH, M. & SHUGART, H. H. 1987. Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* 68: 695–704.
- STENBERG, P., LINDER, S., SMOLANDER, H. & FLOWER-ELLIS, J. 1994. Performance of the LAI-2000 plant canopy analyzer in estimating leaf area index of some Scots pine stands. *Tree Physiology* 14:981–995.
- STILES, G. & SKUTCH, A. 1989. *A guide to the birds of Costa Rica.* Cornell University Press, Ithaca. 580 pp.
- STOUFFER, P. C. 2007. Density, territory size, and long-term spatial dynamics of a guild of terrestrial insectivorous birds near Manaus, Brazil. *The Auk* 124:291–307.
- STUTCHBURY, B. J. M. & MORTON, E. S. 2001. *Behavioral ecology of tropical songbirds.* Academic Press, London. 110 pp.
- TERBORGH, J., ROBINSON, S. K., PARKER, T. A., MUNN, C. A. & PIERPONT, N. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60: 213–238.
- THOMPSON, R. F., GROVES, P. M., TEYLER, T. J. & ROEMER, R. A. 1973. A dual-process theory of habituation: theory and behavior. Pp. 239–271 in Peeke, H. V. S. & Herz, M. J. (eds.). *Habituation I: Behavioral studies.* Academic Press, New York.

- VENEKLAAS, E. J. 1991. Litterfall and nutrient fluxes in two montane tropical rain forests, Colombia. *Journal of Tropical Ecology* 7: 319–336.
- WILSON, E. O. 1975. *Sociobiology: the new synthesis*. The Belknap Press of Harvard University Press, Cambridge. 697 pp.
- WINKER, K., KLICKA, J. T. & VOELKER, G. 1996. Sexual size dimorphism in birds from southern Veracruz, Mexico. II. *Thryothorus maculipectus* and *Henicorhina [leucosticta] prosthelauca*. *Journal of Field Ornithology* 67:236–251.
- WIRTH, R., WEBER, B. & RYEL, R. J. 2001. Spatial and temporal variability of canopy structure in a tropical moist forest. *Acta Oecologica* 22:1–10.
- ZAR, J. H. 1996. *Biostatistical analysis*. (Third edition). Prentice Hall, New Jersey. 662 pp.