AN EXPERIMENTAL CENSUS METHOD AND ESTIMATES OF POPULATION DENSITY OF A BLACK HOWLER MONKEY (*ALOUATTA PIGRA*) HIGHLAND POPULATION IN THE SIERRA YALIJUX, GUATEMALA

Swen C. Renner¹, Regula Rieser² and Robert H. Horwich³

Abstract

Groups of the Guatemalan black howler monkey (*Alouatta pigra*) in a fragmented northern Guatemalan cloud forest in the Sierra Yalijux were analyzed for group composition and size using an ornithological census technique. Audio and visual records were combined to estimate each group's home range size. The 361 observations in 2002 estimated 50 individuals in seven groups. Two home range classes were observed with ≤ 1.87 ha and ≥ 2.87 ha. Compared to other recent studies, the density of *A. pigra* in the Sierra Yalijux is considerably higher than in other areas $(83.3/\text{km}^2 \text{ vs. } 15.1/\text{km}^2 \text{ in Quintana Roo}$ and $23.0/\text{km}^2$ in Palenque) but about half the density found in Belize $(178/\text{km}^2)$. We discuss the relevance of the ornithology assessment method for howler monkeys.

Key words: Alouatta pigra, Neotropics, Guatemala, cloud forest, Sierra Yalijux, ecology, GIS, home range, minimal convex polygon, saraguate

Resumen

Utilizando una técnica ornitológica de censos se analizaron la composición y tamaño de grupos del mono aullador negro Guatemalteco (*Alouatta pigra*) en un bosque nublado fragmentado al norte de Guatemala en la Sierra Yalijux. A partir de 361 observaciones hechas en 2002 se estimaron 50 individuos en siete grupos. Se encontraron dos clases de tamaño de área de uso vital ≤ 1.87 ha $y \geq 2.87$ ha. Comparada con aquellas de otros estudios recientes, la densidad de *A. pigra* en la Sierra Yalijux es considerablemente más alta que en otras áreas $(83.3/\text{km}^2 \text{ vs. } 15.1/\text{km}^2 \text{ en Quintana Roo y } 23.0/\text{km}^2 \text{ en Palenque})$ pero cerca de la mitad de la densidad encontrada en Belice $(178/\text{km}^2)$. Discutimos la relevancia del método de evaluación ornitológico utilizado para los monos aulladores.

Palabras Clave: Alouatta pigra, Neotrópicos, Guatemala, bosque nublado, Sierra Yalijux, ecología, GIS, área de dominio vital, mínimo polígono convexo, saraguate

Introduction

The black howler monkey, *Alouatta pigra*, endemic to Mesoamerica, is threatened due to widespread habitat destruction causing severe population declines. The *IUCN 2004 Red List of Threatened Species* classifies *A. pigra* as Endangered (A4c) (see Rodríguez-Luna *et al.*, 1996a, 1996b; Crockett, 1998; Cuarón *et al.*, 2003), and it is listed on Appendix I of CITES – the Convention on International Trade in Endangered Species of Wild Flora and Fauna. *A. pigra* occurs in the tropical and semi-deciduous forests of Yucatán (Mexico), Belize, western Honduras and northern parts of Guatemala (Emmons and Feer, 1997; Reid, 1997). *A. pigra* is highly territorial, with each group (generally of about five to ten individuals) occupying relatively exclusive ranges (Reid, 1997).

Currently, there are considerable regional differences in the conservation status of the black howler, with populations in areas with high deforestation being more threatened than others. Populations of *A. pigra* in Belize are comparatively well-studied (e.g., Horwich and Johnson, 1984; Horwich *et al.*, 2001a, 2001b; Estrada *et al.*, 2002a, 2002b, 2004). Although *A. pigra* is thought to occur at lower elevations (Horwich and Johnson, 1986), the status of *A. pigra* in the central mountains of Guatemala remains relatively unknown. We here add data on a highland population of *A. pigra* and discuss the use of an ornithological census method applied to assess howler monkeys. We discuss density and territoriality of the *A. pigra* highland population.

¹ Conservation & Research Center, National Zoological Park, Smithsonian Institution, 1500 Remount Road, Front Royal, VA 22630, USA, e-mail: <renners@si.edu>

² Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

³ Community Conservation, 50542 One Quiet Lane, Gays Mills, WI 54631, USA

Methods

Study site

We studied a population of *A. pigra* in a tropical cloud forest on the northern slopes of the central mountain ridge of northern Guatemala (Fig. 1), in the southernmost part of the species' distribution (Emmons and Feer, 1997). The study site is near the community of Chelemhá, 10.8 km north of Tucurú, Alta Verapaz (central co-ordinates: 90°04′W, 15°23′N; 1,980–2,550 m a.s.l.). The site is part of the Sierra Yalijux which merges in the west with the Sierra Caquipec (90°11′W, 15°23′N, 2,000–2,200 m a.s.l.) 12 km west of Chelemhá. To the north are the lowlands of El Petén.

Human disturbance in the primary forest of the study area is limited to subsistence hunting and occasional logging. The forests of the highlands of the Sierra Yalijux, while isolated from other forests, are relatively intact, with only 3.08% being lost between 1986 and 2000. This is a relatively low mean annual deforestation rate of 0.2% (Voigt, 2004; Markussen and Renner, 2005; Renner et al., 2006). Neighboring the forests of the Sierra Yalijux are two further large forest fragments, totaling 5,500 ha (Sierra Yalijux: 2,200 ha; Sierra Caquipec: 3,200 ha; unnamed fragment in between: - 100 ha) of mature pine-oak cloud forests (Markussen, 2004; Renner et al., 2006). All three forest fragments are separated from each other (Markussen and Renner, 2005; Renner et al., in press), and are 52 km east and 15 km north, respectively, from the nearest mature highland cloud forests of Sierra de Chamaa and Sierra de las Minas. The nearest lowland rainforest of El Petén is 25 km north of the forest fragments. A. pigra is not reported there and is most unlikely to migrate such a distance, even though they may cross open areas on the ground. The three fragments are not fragmented themselves and each consists of closed forest cover. Further forest patches of small size (< 20ha) are found in the surrounding areas of these three major fragments. All forest is surrounded by different land use, including secondary vegetation and taller secondary forest. This tall secondary forest is approximately 15 years old and 20 m tall and has already established two vegetation strata (Renner et al., 2006b).

The deforestation rate in the Sierra Yalijux was around 0.2% for 1986 to 2000 (Markussen, 2004; Voigt, 2004; Markussen and Renner, 2005; Renner *et al.*, in press) and low for Guatemala (country mean 1.7%). For further details on the region refer to Markussen and Renner (2005), Renner (2003, 2005) and Renner *et al.* (2006a, 2006b).

Census protocol

We applied a survey method in Chelemhá that is commonly used in bird surveys. Triangulation and assessment of vocalizing male individuals has been established in ornithology for a long time. The method is commonly used to assess individual bird territories or relative abundance for birds in temperate forests and in the tropics either applying

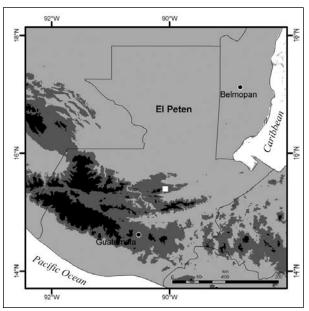


Figure 1. The study site (*white circle*) in Guatemala and altitudes >1,000 m (*gray shaded area*) and >2,000 m (*black shaded area*).

point counts or transect-assessments. An observer records all songs and sights along a transect or point count grid and notes species, time, date and estimated or measured distance from the census grid. Here we used the established ornithological transect grid (Renner, 2003; Renner *et al.*, 2006) to assess the howler monkey population. The observers (SCR, RR) noted time, direction and estimated distance of howling individuals. One observer (RR) then located the howling groups and visually observed the groups in greater detail.

We carried out a survey of A. pigra along a 2,000 m transect line near the community of Chelemhá between March and October in 2001 and 2002. We surveyed all transects on a monthly basis for five days per month, from 08:00 to 14:30. From July 22 to September 26, 2002, surveys were carried out daily. Each survey day we proceeded slowly along transects. We recorded all instances of howling, determining the direction by compass bearing and estimating the distance in three categories (close: < 100 m, medium: 100-300 m, and far: > 300 m). To determine the exact observer's location we established fixed points every 25m along transects using global positioning systems (GPS). When two observers were carrying out the survey the troops were located by triangulation. Once we heard or saw a howler group we followed it as long as possible to determine their troop composition as to age and sex as described by Reid (1997) and Emmons and Feer (1997).

Groups were considered to be discrete units when audio observations indicated spatial distances of more than 100 m. Groups A to D and G (exceptions: E and F; Table 1) were recorded by simultaneous vocalizations four

times during the study period with an indicated in-between difference of more than 100 m. Often adjacent groups will roar at each other in close proximity at territorial borders. Sometimes it is impossible to tell whether they are different troops until they move away from each other and the territory border (Horwich, pers. obs.). Thus, in addition to the audible locating procedures, all groups (A to G; Table 1) were observed visually several times. Groups that could not be seen were not included.

Analysis

We mapped all locations of *A. pigra* troops in the study region with ArcGIS 9.1 and classified the land cover by analyzing a Landsat ETM+ scene (path 020, row 049 of January 23, 2000) with ground-truthing data (Renner and Markussen, in press). For analyses of the home range we used the ArcView 3.3 Animal Movement extension to calculate the minimal convex polygon (MCP) and the kernel home range (KHR). For the KHR we used the 25, 50, 75 and 95% confidence intervals and plotted the results. For the total population estimate we added the maximum observed troop sizes and assumed this cumulative number represents the total number of individuals in the study plot.

We also established a transect of 2,000 m in the Sierra Caquipec close to the small village of Chicacnab, and for 14 days surveyed the *A. pigra* population. The Sierra Caquipec is the western extension of the Sierra Yalijux but the forests, with similar pine-oak cloud forest vegetation, are isolated by a 500 m gap. This second site was included so that we could have some idea as to whether the population density in Chelemhá is high or low compared to other forest fragments in the region.

Results

We observed seven groups of *A. pigra* with 50 individuals in the 60.05 ha study site near Chelemhá (Fig. 2, Table 1). All groups were separable by territorial vocalizations and visual observations. Home range size varied from 1.01 to 5.53 ha (mean 3.03 ha \pm 1.69 sd.) as measured with the minimal convex polygons (Table 1). The seven groups ranged in size from six to ten individuals with 50 individuals in total. The mean number of males per group was 1.50 ± 0.55 , and the

number of females was 1.33 ± 0.55 (Table 1). The population density of the forest fragment was 83.3 individuals per km².

Further groups were registered by their vocalizations outside our study plot (Fig. 2). One group occupied a primary forest patch (isolated from the Sierra Yalijux; 17.80 ha) approximately 700 m to the south of group D. Two other groups were located 500 m north and 900 m west of group A, and another two troops approximately 1.1 km and 2.2 km, east-north-east of group G; the latter four all within the Sierra Yalijux. However, the home range size estimate for the distant groups is very rough, because they were far away and never seen. The distance increased the error for area-estimation. We also observed howlers in the vicinity of the study area along a path of 4,500 m; that path was used on a monthly basis during the study period.

A. pigra in Chelemhá exhibited more frequent territorial howling than in Chicacnab (12 km west of Chelemhá). In Chicacnab we only heard one group howling 500 m away but never could observe them. The surveys close to Chicacnab (Sierra Caquipec) revealed only one howling individual in the far distance of the settlement in primary forests. Density estimates could not be determined here. In the Sierra Yalijux, A. pigra used mainly primary forest or old secondary growth at least 15 m in height with at least two strata (see Renner et al., 2006, for further description of the vegetation). Thus, 90% (= 1,800 m) of the survey transects were in primary cloud forest and 10% in old secondary forest.

Discussion

Remote assessment using vocalization and triangulation

We applied a survey method in Chelemhá howlers that is commonly used in bird surveys. While we could determine the howling units of *A. pigra* by triangulation and remote assessment, visual contact for group census and composition is essential since usually only one or two adult monkeys participate in howling while the remainder of the group stays silent. Thus a combination of both methods is needed for a detailed census of howlers. However, the method could be useful to estimate gross

Table 1. Groups of *Alouatta pigra* observed in the Sierra Yalijux near Chelemhá in 2002.

Group	Total	Adult Male	Adult Female	Sub-Adult Male	Sub-Adult Female	Sub-Adult	Infant	Area (ha)
A	9	1	1	-	-	-	1	1.05
В	8	2	2	-	-	-	3	4.87
С	9	2	1	-	1	-	1	4.01
D	-	-	-	-	-	-	-	5.53
Е	8	1	2	1	-	-	-	1.02
F	6	1	-	-	-	-	1	1.87
G	10	2	2	-	-	3	1	2.87

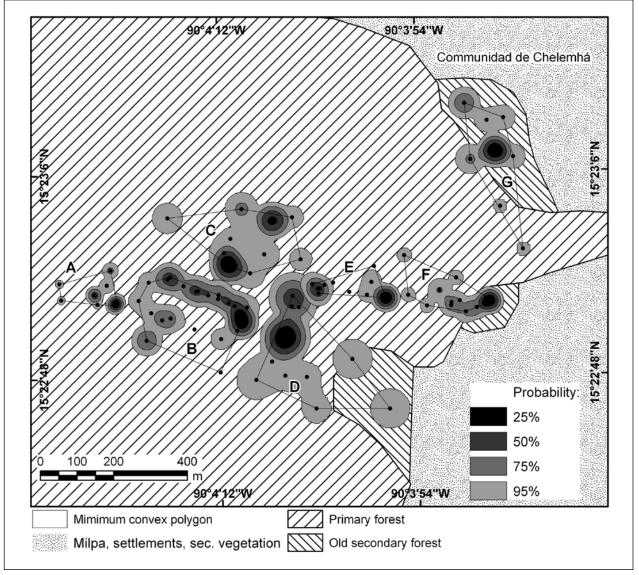


Figure 2. Records of the black howler monkey (*Alouatta pigra*) in the Sierra Yalijux, near the settlement of Chelemhá in 2002. For observations on the groups (A to G) see Table 1. Probabilities are derived from the Kernel Home Range; Minimum Convex Polygons are derived from the outermost border of observations per group. Groups were separated according to simultaneously observed howling of groups.

densities of howlers in unstudied areas in shorter time periods by vocalization records alone. The distinction between *A. pigra* groups in the Sierra Yalijux was generally reliable and clearly separable due to the observations and territorial howling of the group members, however we cannot exclude the possibility that in some instances solitary males were howling.

Howler density and territorial overlap

Howling has been observed to have a territorial function in *A. seniculus* and *A. pigra* (Sekulic, 1982; Estrada *et al.*, 2004) although this may not always be the case (Estrada *et al.*, 2002b, 2004). Some authors have argued that howling is more correctly a mechanism only for "intergroup spacing" (Kitchen *et al.*, 2004), and Sekulic (1982b), studying *Alouatta seniculus*, reported on "floating territories".

There is evidence that A. pigra troops occupy their own exclusive range (Reid, 1997) and that they defend this range (Horwich 1983a). However, for A. pigra (Ostro et al., 2001; Pavelka et al., 2003), A. seniculus (Crockett and Janson, 2000), and other mammals (Pen and Weissing, 2000), home range overlap has been reported. If this were true in Chelemhá by this survey method, territory size might decrease and the separation of groups might not be apparent. A. pigra populations in Belize always showed some range overlap (Horwich 1983a, b) especially as densities increased (Horwich, pers. obs.). Horwich (1983a) reported a female crossing into another territory to breed with the male away from her troop, who later threatened the same male in an inter-troop territorial dispute. Thus, there appear to be clear boundaries where adjacent troops howl at each other across the territory line and distinctions are possible only by a combination of audio and visual observations. Audible and remote detection as well as distinguishing the troops by howling alone, as suggested here as an alternative, might be more difficult, since in some cases two troops are howling at one location and are not recognizable as two distinguished troops without a visual double check. Our data for groups E and F (Fig. 2) illustrate this since no simultaneous or interactive howling was observed. Thus, they could be merged into one group. However, since troops over 10 individuals are rare in *A. pigra*, these are probably distinct troops.

Home ranges in this study are larger than from other study sites (see Estrada et al., 2004), and the population density in this study is intermediate compared to other sites. For example, lower densities are reported for A. pigra in various sites in Mexico (Gonzales-Kirchner, 1998; Estrada et al., 2002a; Estrada et al., 2004), including Yaxchilán (12.8/ km²), Quintana Roo (15.1/km²), Calakmul (15.2/km²), and Palenque (23.0/km²). Black howlers in Tikal (El Petén, Guatemala) also show low population density (17.8/km²). However, higher density estimates as in Chelemhá have been reported in Belize, with up to 178 individuals per km² (Horwich et al. 2001). The population was considered to be crowded due to fragmentation (Silver et al., 1998; Ostro et al. 1999, 2000; Horwich et al., 2001). The Sierra Yalijux has a clearly higher population density than the Mexican and northern Guatemalan sides but is still below numbers from more fragmented landscapes of Belize.

Crowding populations?

As observed by Ostro et al. (2001), low density populations consist of one male with two females and high density populations of multi-males with > 2 females. The groups we observed in Chelemhá consist of more than one male and several females (with some exceptions, Table 1), and therefore are most likely high-density groups. The comparatively high population density of A. pigra in Chelemhá implies crowding in the remaining cloud forest. However, distribution in Chelemhá is patchy. Several groups in addition to the seven groups as shown in Figure 2 are present in the area. While the seven groups in Chelemhá seem to clump together, there is no indication of other individuals between the widely spaced groups. Therefore we conclude that the populations have a patchy distribution, probably due to patchy distribution of nutrition in the Chelemhá mature forests. However it remains open whether or not *A*. pigra crowds in response to the decreased habitat (Markussen and Renner, 2005). Other research teams report crowded populations from fragmented forest patches in Belize (Silver et al., 1998; Chapman and Balcom, 1998; Ostro et al. 1999, 2000; Horwich et al., 2001) with approximately twice as high population densities than we found in the Sierra Yalijux (compare above).

Fragmentation and deforestation in the Sierra Yalijux
Fragmentation and deforestation influences behavior and distribution of *A. pigra* (e.g., Silver *et al.*, 1998; Estrada *et al.*, 2002b). Forests are the major habitat for *A. pigra* as for

most of the other howler species (Estrada et al., 2002b), even when disturbed (Lyon and Horwich, 1996). No individual of any group in the Sierra Yalijux has been observed in any vegetation used by humans, except for tall secondary forest (Fig. 2). Only once during our study an individual of A. pigra was reported in a corn field and shot by a local farmer (A. Schumacher, pers. comm.). This individual was likely to have been hunted in mature forest, where the hunter feigned a case of food competition, as only rarely are the howlers consumed by locals following poor harvesting seasons (D. Unger, pers. comm.). Normally, consumption of howler meat is despised by the local community. Secretive behavior in Chicacnab might be one howler response to hunting (K. Eisermann, pers. comm.). However, A. pigra can utilize almost any kind of habitat and will come to the ground to cross narrow forest gaps and will feed in scrub areas or in areas low to the ground (Horwich, pers. obs.).

Acknowledgments

The study was performed in accordance with the current laws of Guatemala and CONAP (Comisión Nacional de Áreas Protegidas) authorized the study (No. 139-2001). We would like to thank Danielle Shanahan, Pia Terranova, and Anthony Rylands for help on English and valuable comments on earlier versions of the manuscript. In addition, our special thanks are going to Vera and Markus Reinhard, Armin Schumacher, and all local people of the Comunidad de Chelemhá for their great support during the study period in the field and accommodation, as well as to David Unger, Knut Eisermann, and Claudia Avendaño.

References

Chapman, C. A. and Balcomb, S. R. 1998. Population characteristics of howlers: Ecological conditions or group history. *Int. J. Primatol.* 19: 385–403.

Crockett, C. M. 1998. Conservation biology of the genus *Alouatta. Int. J. Primatol.* 19: 549–578.

Crockett, C. M. and Janson, C. H. 2000. Infanticide in red howlers: female group size, male composition, and a possible link to folivory. In: *Infanticide by Males and Its Implications*, C. P. van Schaik and C. H. Janson (eds.), pp. 75–98. Cambridge University Press, Cambridge.

Cuarón, A. D., de Grammont, P. C., Cortés-Ortiz, L., Wong, G. and Silva, J. C. S. 2003. *Alouatta pigra*. In: IUCN 2004. *2004 IUCN Red List of Threatened Species*. . Accessed 6 February 2005.

Emmons, L. H. and Feer, F. 1997. *Neotropical Rainforest Mammals: A Field Guide*. Second edition. The Chicago University Press, Chicago.

Estrada, A., Luecke, L., van Belle, S., Barrueta, E. and Rosales Meda, M. 2004. Survey of black howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilán, Mexico and Tikal, Guatemala. *Primates* 45: 33–39.

Estrada, A., Castellanos, L., Garcia, Y., Franco, B., Muñoz, D., Ibarra, A., Rivera, A., Fuentes, E. and Jimenez, C.

- 2002a. Survey of the black howler monkey, *Alouatta pigra*, population at the Mayan site of Palenque, Chiapas, Mexico. *Primates* 43: 51–58.
- Estrada, A., Mendoza, A., Castellanos, L., Pacheco, R., van Belle, S., García, Y. and Muñoz, D. 2002b. Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. *Am. J. Primatol.* 58: 45–55.
- González-Kirchner, J. P. 1998. Group size and population density of black howler monkey (*Alouatta pigra*) in Muchukux forest, Quintana Roo, Mexico. *Folia Primatol.* 69: 260–265.
- Horwich, R. H. 1983a. Breeding behaviors in the black howler monkey (*Alouatta pigra*) of Belize. *Primates* 24: 222–230.
- Horwich, R. H., Brockett, R. C., James, R. A. and Jones, C. B. 2001a. Population growth in the Belizean black howling monkey (*Alouatta pigra*). *Neotrop. Primates* 9: 1–7.
- Horwich, R. H., Brockett, R. C., James, R. A. and Jones, C. B. 2001b. Population structure and group productivity of the Belizean black howling monkey (*Alouatta pigra*): Implications for female socioecology. *Primate Report* 61: 47–65.
- Horwich, R. H. 1983b. Species status of the black howler monkey, *Alouatta pigra*, of Belize. *Primates* 24: 288–289.
- Horwich, R. H. and Johnson, E. D. 1984. Geographic distribution and status of the black howler monkey. *IUCN/SSC Primate Specialist Group Newsletter* (4): 25–27.
- Horwich, R. H. and Johnson, E. D. 1986. Geographical distribution of the black howler (*Alouatta pigra*) in Central *America. Primates* 27: 53–62.
- Lyon, J. and Horwich, R. H. 1996. Modification of tropical forest patches for wildlife protection and community conservation in Belize. In: *Forest Patches in Tropical Landscapes*, J. Shelhas and R. Greenberg (eds.), pp. 205–230. Island Press, Washington, DC.
- Markussen, M. 2004. Forest Conversion and Soil Degradation of Tropical Montane Cloud Forests in Guatemala (Alta Verapaz). Investigation in the Framework of Biodiversity Research in Sensitive Tropical Ecosystems. Shaker Verlag, Berlin. In German.
- Markussen, M. and Renner, S. C. 2005. Biotic and abiotic aspects as a base for the conservation of biodiversity in a tropical montane cloud forest (Guatemala). In: *Valuation and Conservation of Biodiversity Interdisciplinary Perspectives on the Convention on Biological Diversity*, M. Markussen, R. Marggraf, R. Buse, H. Garrelts, M. A. Máñez-Costa and S. Menzel (eds.), pp.357–372. Springer, Berlin.
- Ostro, L. E. T., Silver, S. C., Koontz, F. W., Young, T. P. and Horwich, R. H. 1999. Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belice, Central America. *Biol. Conserv.* 87: 181–190.
- Ostro, L. E. T., Silver, S. C., Koontz, F. W. and Young, T. P. 2000. Habitat selection by translocated black howler monkeys in Belize. *Animal Conservation* 3: 175–181.

- Ostro, L. E. T., Silver, S. C., Koontz, F. W., Horwich, R. H. and Brockett, R. 2001. Shifts in social structure of black howler (*Alouatta pigra*) groups associated with natural and experimental variation in population density. *Int. J. Primatol.* 22: 733–748.
- Pavelka, M. S. M., Brusselers, O. T., Nowak, D. and Behie, A. M. 2003. Population reduction and social disorganization in *Alouatta pigra* following a hurricane. *Int. J. Primatol.* 24: 1037–1055.
- Pen, I. and Weissing, F. J. 2000. Optimal floating and queuing strategies: The logic of territory choice. *Am. Nat.* 155: 512–526.
- Reid, F. A. 1997. A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York.
- Renner, S. C. 2003. Structure and diversity of cloud forest bird communities in Alta Verapaz, Guatemala, and implications for conservation. Niedersächsische Staats- und Landesbibliothek, Göttingen. http://webdoc.sub.gwdg.de/diss/2003/renner/». Accessed 27 January 2004.
- Renner, S. C. 2005. The Resplendent Quetzal (*Pharoma-chrus mocinno*) in the Sierra Yalijux, Alta Verapaz, Guatemala. *J. Ornithol.* 146: 79–84.
- Renner, S. C., Waltert, M. and Mühlenberg, M. 2006a. Comparison of bird communities in primary versus young secondary tropical montane cloud forest in Guatemala. *Biodiv. Conserv.* 15: 1545–1575.
- Renner, S. C., Voigt, M. and Markussen, M. 2006b. Regional deforestation in a tropical montane cloud forest in Alta Verapaz, Guatemala. *Ecotropica* 12: 43–49.
- Rodríguez-Luna, E., Cortés-Ortiz, L., Mittermeier, R. A. and Rylands, A. B. 1996a. *Plan de Acción para los Primates Mesoamericanos*. IUCN/SSC Primate Specialist Group, Xalapa, Veracruz, Mexico.
- Rodríguez-Luna, E., Cortés-Ortiz, L., Mittermeier, R. A., Rylands, A. B., Wong Reyes, G., Carrillo, E., Matamoros, Y., Nuñez, F. and Motta Gill, J. 1996b. Hacia un plan de acción para los primates Mesoamericanos. *Neotrop. Primates* 4(Suppl.): 9–23.
- Sekulic, R. 1982a. The function of howling in red howler monkeys (*Alouatta seniculus*). *Behavior* 81: 38–54.
- Sekulic, R. 1982b. Daily and seasonal patterns of roaring and spacing in four red howler *Alouatta seniculus* troops. *Folia Primatol.* 39: 22–48.
- Silver, S. C., Ostro, L. E. T., Yeager, C. P. and Horwich, R. H. 1998. Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. *Am. J. Primatol.* 45: 263–279.
- Voigt, M. 2004. Fernerkundungs- und GIS-gestützte Landnutzungsklassifikationen und Change Detection im Bergnebelwaldgebiet der Montaña Yalijux (Guatemala). Universität Göttingen, Göttingen.