

Density, Distribution, and Attributes of Tree Cavities in an Old-Growth Tropical Rain Forest

W. Alice Boyle¹

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, U.S.A.

Carissa N. Ganong²

Department of Biology, Mansfield University, Mansfield, PA 16933, U.S.A.

David B. Clark

Department of Biology, University of Missouri-St. Louis, St. Louis, MO 61321, U.S.A.

and

Marisa A. Hast³

Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, U.S.A.

ABSTRACT

Tree cavities are a critical resource for many animals, especially as nesting sites for birds. Patterns of cavity distribution in temperate forests are well studied, yet little is known of cavities in tropical forests, despite a hypothesized decrease in cavity availability with decreasing latitude. We studied cavity density and distribution in a wet lowland tropical forest in Costa Rica and compared our results with estimates from forests around the world. Cavities at our site were common, occurred frequently in living trees, and were often formed by damage or decay rather than by woodpeckers. Most cavities had small openings, and woodpecker-created cavities were nonrandomly oriented. Contrary to prediction, cavity density appears to increase from the poles to the tropics. We suggest potential mechanisms to explain these patterns.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: cavity density; cavity-nesting birds; Costa Rica; La Selva Biological Station; latitudinal gradient; nest-site limitation; snags; tropical rain forest.

ELUCIDATING THE GEOGRAPHIC PATTERNS OF SPECIES' DISTRIBUTION AND ABUNDANCE requires information on the distribution of critical resources. Microhabitats such as tree cavities can limit animal populations (von Haartman 1957) when that microhabitat is required for survival or reproduction. Cavities provide safe nesting sites for mammals, invertebrates, snakes, and especially birds (Hansell 2000). Most data on cavity distribution, abundance, characteristics, and the extent to which cavities limit populations of secondary cavity-nesting birds (species utilizing existing cavities) come from temperate regions (*e.g.*, Brawn 1988, Aitken & Martin 2004). Yet the relative safety of cavities compared to open nests appears to hold among latitudes, and may possibly be of even more value in tropical than temperate forests (Skutch 1985). Determining the role cavities play in tropical bird communities requires quantifying the abundance and use of cavities. Here we report results of the first step in this process: a descriptive study of cavity abundance and cavity characteristics from an old-growth tropical wet forest.

Forest dynamics differ between tropical and temperate regions in ways that could either decrease or increase cavity densities (Gibbs *et al.* 1993). Many temperate forest cavities are located in snags (*e.g.*, Raphael & White 1984, Land *et al.* 1989). Yet most tropical tree deaths are caused by weather events (*i.e.*, strong winds) that do not result in snags, and snag-forming disturbances such as fire or winter storms are rare (Putz *et al.* 1983, Gale & Barford 1999). Additionally, trees (Losos & Leigh 2004) and possibly snags (D. B. Clark, unpubl. data) persist on average for fewer years in tropical forest relative to temperate forests. Thus, cavity densities may be lower in tropical forests simply because cavities have less opportunity to accrue. Conversely, tropical forests may have more cavities due to: (1) availability of alternative cavity substrates (*e.g.*, arboreal termittaries; Brightsmith 2005b); (2) high decomposition rates potentially resulting in more decay-caused cavities; and (3) the abundance of arborescent palms. Palms have a unique trunk structure (tough fibrous exteriors, soft pithy cores) which may speed cavity formation processes.

In addition to cavity density, attributes influencing cavity suitability such as size (Carlson *et al.* 1998) and orientation (Butcher *et al.* 2002) likely vary with latitude. Large cavities with large openings may be disproportionately valuable in tropical forests due to the large size of many tropical cavity-nesting species (*e.g.*, *Ramphastos* toucans, *Buceros* hornbills, and *Ara* macaws). Non random cavity orientation in temperate forests is usually attributed to the thermal

Received 29 September 2006; revision accepted 22 May 2007.

¹ Corresponding author; current address: Department of Biology, University of Western Ontario, London, ON N6A 5B7, Canada; e-mail: alboyle@email.arizona.edu

² Current address: Department of Biology, University of Central Arkansas, Conway, AR 72035, U.S.A.

³ Current address: 3840 Cloverleaf Dr., Boulder, CO 80304, U.S.A.

consequences of sun angle and prevailing wind (Hardy & Morrison 2001, Wiebe & Swift 2001). Because ambient temperatures in the lowland tropics are typically within the thermal-neutral zone for most bird species (Calder & King 1974) and canopies shade and shelter most cavities from wind, cavities constructed for nesting would be expected to be oriented randomly in lowland tropical forests.

To our knowledge, the only data on cavity abundance, distribution, and characteristics from tropical forests is limited to five studies from scattered locations around the tropics, and only three (Pattanavibool & Edge 1996, Stoneman *et al.* 1997, Brightsmith 2005a) describe characteristics of all cavities rather than just the cavities suitable for particular species. Improved understanding of cavity resource availability in the tropics will provide baseline data for comparisons with ever-increasing secondary and selectively logged forests, and inform conservation efforts directed at tropical secondary cavity-nesting species such as parrots (Stotz *et al.* 1996). Our goals were to quantify patterns of cavity abundance in an old-growth tropical wet forest, describe characteristics of these cavities relevant to their use by cavity-nesting birds, and examine the relationship between latitude and cavity density by comparing our results with published data.

We worked at La Selva Biological Station in NE Costa Rica (10°25'53" N, 84°00'13" W; mean annual temperature: 26°C; annual rainfall: ~4000 mm; Sanford *et al.* 1994). Forests at La Selva are comprised of *ca* 100 woody spp \geq 10 cm diameter/ha, and are dominated by *Pentaclethra macroloba* (Mimosoideae) in the canopy and palms (Aracaceae) in the understory (Lieberman *et al.* 1996, Clark & Clark 2000). We studied cavities in 12 of 18 0.5 ha (100 \times 50 m) plots established for an ongoing study of forest dynamics (Clark & Clark 2000). Plots were located in upland old-growth forest using a random design stratified by slope and soil (flat alluvial and ultisol soils, ultisol slopes). During June–July 2005, we counted cavities in all snags in 12 plots (four in each of the three edaphic conditions, 6 ha total) and in all live trees \geq 10 cm dbh in two of the 10 \times 10 m subplots within each plot. We searched for cavities using 10 \times 40 power binoculars, circling the tree at distances of 1–15 m. We defined cavities as openings in the tree above ground level, extending into the trunk, not visibly open to the ground or sky, and at least 2.5 cm estimated diameter. Our methods are comparable to those used in other studies (*e.g.*, Brightsmith 2005a).

We classified trees containing cavities as either palms or 'hardwoods' (all dicots). We further classified cavities as either: (1) presumed to have been excavated by woodpeckers ($>$ 25% of circumference regularly circular and not located at broken branch point); or (2) presumed to have been created by mechanical damage, invertebrate or microbial decay, or excavation by other vertebrates. When cavities appeared to have been first excavated by woodpeckers then subsequently decayed we assigned the cavity to the 'damage/decay' category. Some damage/decay cavities may have been misclassified if by chance they had highly regular openings. We estimated cavity entrance size using an aluminum pole marked at 5 cm intervals held adjacent to the cavity, and we determined cavity orientation using a compass.

To estimate cavity density, we summed all cavities found in the 12 plots (snags) or 24 subplots (trees), divided these numbers by the area surveyed (6 ha for snags; 0.24 ha for trees), then summed those values to obtain landscape-level estimates. To explore the relationship between substrate and cavity density, we constructed an ANOVA model (including soil and slope as fixed effects) using N cavities/plot (N snag cavities + $[N$ live tree cavities in both subplots/0.04]) as the response variable. To compare the proportion of stems containing \geq 1 cavity in palms versus hardwoods, we used Fisher's exact tests (Sokal & Rohlf 1995). Because tree types differed in the frequency with which they contained cavities, we compared the proportion of stems with cavities in snags versus live trees separately for palms and hardwoods. We used stem rather than cavity as the unit of replication in these analyses because multiple cavities in a single tree may not represent independent cavity-forming events.

We compared the proportion of cavities presumed to have been created by woodpeckers versus damage/decay and determined whether the frequency of these cavity types differed between snags and live trees using Fisher's exact tests. We explored whether cavity characteristics (cavity origin, tree type, and snag vs. live tree) were associated with variation in cavity size using an ANOVA model (with all three factors treated as fixed effects). We modeled cavity opening sizes as ellipses and described the distribution of cavity opening sizes by fitting log-normal, Poisson and exponential distributions to the data. We used Rayleigh's Uniformity test (Zar 1999) to detect deviations from random cavity orientation for woodpecker holes using Oriana statistical software (ver. 2.0, Kovach Computing Services 2006).

To compare cavity densities at our site with densities from forests at other latitudes, we searched the Web of Science (accessed September 2006) using the term 'cavity' in combination with 'density,' 'abundance,' 'snag,' 'tree,' 'nest and bird,' as well as 'hollow' in combination with 'bird' and 'nest.' We supplemented these sources with literature cited by authors of articles in our original search. To evaluate the relationship between cavity density and latitude (median value if more than one noted), we used multiple linear regression, controlling for forest type (old-growth or managed/logged forest), and minimum cavity opening area (if authors defined criteria) by including these as model covariates.

We counted 195 cavities in 66 of the 153 snags found in the 12 0.5-ha plots, and 19 cavities in 14 of the 130 live trees in the 24 0.01-ha subplots. Thus, cavities occur at La Selva at densities of 32.5/ha in snags and 79.2/ha in live trees, or 111.7 cavities/ha, of which 29 percent are in snags. Cavity densities ranged from 9–131/ha in the 12 plots, and mean (\pm SE) cavs/ha did not differ between alluvial (64.0 ± 29.2) and residual soils (63.8 ± 29.0 ; $F_{1,9} = 0.05$, $P = 0.834$), nor between flat (60.3 ± 16.6) and steep slopes (71.0 ± 24.1 ; $F_{1,9} = 0.17$, $df = 10$, $P = 0.72$).

Snags were more likely to contain cavities than were live trees (Fisher's exact test, $P < 0.0001$); 43.1 percent of snags versus 10.8 percent of live trees contained \geq 1 cavity. Overall, hardwoods were twice as likely to contain cavities as palms (33.0% vs. 15.3%; $P = 0.004$), but this difference was due to an absence of cavities in live palms. Dead palms and hardwood snags differed little

in their likelihood of containing cavities (31.4% vs. 47.4%; $P = 0.12$).

Woodpeckers apparently created 79 (36.9%) of the 214 cavities of which 76 (96%) were in snags and three in live trees. Thus, woodpecker cavities at La Selva occurred in densities of 25.2 cavs/ha ($[76/6 \text{ ha}] + [3/0.24 \text{ ha}]$). Most (88.2%) of the damage/decay cavities occurred in snags. However, woodpecker cavities were even more likely to be found in snags (96.2%) than were damage/decay cavities ($P = 0.049$). Most cavities had small openings; 55 of 214 had openings $\leq 10 \text{ cm}^2$. Woodpecker cavities reached a maximum opening size of 240 cm^2 , whereas damage/decay cavities reached a maximum of 471 cm^2 , and median opening size of woodpecker cavities was 19.7 cm^2 smaller than damage/decay cavities. However, cavity opening size did not depend on cavity origin (woodpecker vs. damage/decay, mean difference $2.8 \pm 4.9 \text{ cm}^2$, $F_{1,210} = 0.99$, $P = 0.32$), tree type (palm vs. hardwood, mean difference $6.6 \text{ cm}^2 \pm 6.4 \text{ cm}^2$, $F_{1,210} = 2.20$, $P = 0.14$), or whether the cavity was in a snag or live tree (mean difference $10.9 \pm 8.2 \text{ cm}^2$, $F_{1,210} = 0.50$, $P = 0.48$; whole model, \ln -transformed areas, $F_{3,210} = 1.4$, $P = 0.25$). The size distribution of cavity openings was not well described by any standard parametric distributions (in all cases, P -values for goodness of fit tests were < 0.01). The orientation of woodpecker cavity openings was nonrandomly distributed ($Z = 5.1$, $N = 79$, $P = 0.006$). Mean azimuth of woodpecker cavities was 39.6° with a circular variance of 0.746. Nearly half (49.4%) of all cavities were oriented roughly N–NE (340° – 80°).

We found 62 cavity density estimates from forests at latitudes ranging from 35° S to $67^\circ 44' \text{ N}$ (Table S1). Forty-one estimates came from old-growth forests, with the remaining 21 from managed, disturbed, or selectively logged forests. We found too few southern hemisphere studies to separately analyze latitudinal gradients in each hemisphere. Therefore, we used absolute latitude in our analyses. Latitude was neither linearly ($F_{1,60} = 2.9$, $P = 0.10$) nor curvilinearly ($F_{2,59} = 1.40$, $P = 0.25$) related to cavity density in the complete data set. However, these results were confounded by differences among studies in criteria used to identify cavities. Only 13 studies (17 estimates; Table S1) provided sufficient methodological detail to determine the minimum size criteria used to define ‘cavity.’ After restricting analyses to those 17 estimates and including minimum opening area as a covariate, latitude was negatively associated with cavity density ($R^2 = 0.54$, $F_{2,14} = 8.2$, $P = 0.004$; Fig. 1). With each 10° increase in latitude, mean cavity density decreased by $44.7 (\pm 11.4) \text{ cavs/ha}$ ($t = -3.9$, $df = 14$, $P = 0.002$). Even after excluding a tropical outlier with extremely high cavity density estimates (Pattanavibool & Edge 1996; 407 cavs/ha in old-growth forest; Table S1), a 10° increase in latitude was associated with $24.9 (\pm 6.0)$ fewer cavs/ha ($F_{1,13} = 17.1$, $P = 0.001$; Fig. 1). The relationship between latitude and cavity density was not related to forest age or disturbance ($F_{1,13} = 0.1$, $P = 0.71$).

Cavity density at La Selva was high relative to estimates from temperate forests. However, comparison of densities at our site with other tropical sites (Table S1; Fig. 1) suggests that La Selva may not be typical in the humid tropics. It is unlikely that our high estimates reflect methodological differences; many authors of the

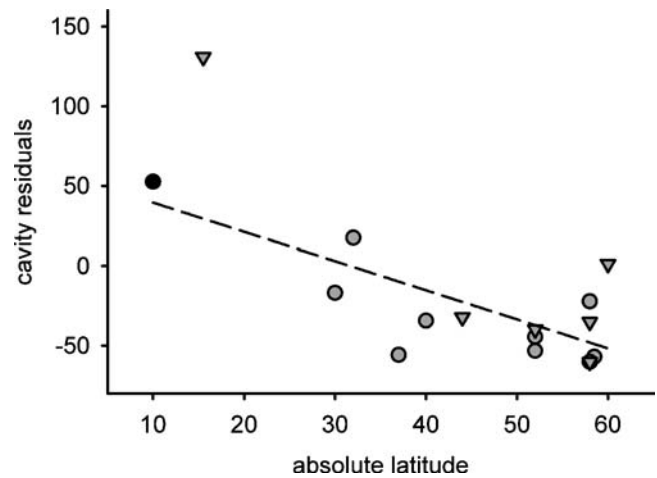


FIGURE 1. Relationship between absolute latitude (northern and southern hemispheres combined) and cavity density/ha after controlling for minimum cavity opening size criteria used in different studies ($y = 266.5 - 4.466 \text{ latitude} - 0.888 \text{ min. cavity entrance}$, $R^2 = 0.54$, $F_{2,14} = 8.2$, $P = 0.004$). Circles represent estimates of cavity density from old-growth forests and triangles represent estimates of cavity density from managed, selectively logged, or otherwise disturbed forests. The solid black circle represents the cavity density estimate from La Selva.

studies in Table S1 used cavity-searching methods similar to ours, and nine of the 13 other studies that specified their size criteria used cavity opening size minima similar to ours ($\leq 50 \text{ mm diam.}$). High cavity density at La Selva does not necessarily contradict Gibbs *et al.* (1993) who hypothesized that cavities are more likely to be limiting in the tropics due to tropical avifaunas containing proportionately more secondary cavity-nesting species and fewer primary cavity-nesting species than temperate avifaunas. More work on cavity occupancy rates, nest site selection, and reproductive success in relation to cavity characteristics will be necessary to reject this hypothesis. Nevertheless, our study suggests that even with relatively few primary cavity nesting species, tropical cavity density—a key factor affecting cavity availability—can be high due to high densities of cavities created by other processes.

As in other forests from other sites, snags at La Selva contained a disproportionate number of cavities, especially woodpecker cavities, implying that forest managers should consider snags in tropical forest as critical wildlife resources. Interestingly, virtually all cavities in live trees occurred in dead branches or in places where branches had broken from the tree (C. N. Ganong & M. A. Hast, pers. obs.). An unexplored hypothesis potentially explaining high tropical cavity densities is that tropical trees might contain more branches of suitable diameter in which cavities can form, or a higher incidence of dead branches in live trees. Alternatively, tropical trees may be subject to higher rates of pathogen attack which could lead to broken branch points being transformed into a decay-caused cavity more often than in temperate trees. These hypotheses could be tested by comparing branch diameters, the incidence of dead branches, and

the incidence of cavities in broken branch points between forests of high and low cavity abundance. Palms comprise ~25 percent of trees at our site (Clark & Clark 2000). Once palms die, they do not seem to function differently than hardwoods with respect to cavity formation. However, palms were unique in never containing cavities when alive. This observation may reflect the fact that palms do not branch, and the majority of our live-tree cavities occurred in dead branches.

We did not expect to find nonrandom cavity orientation at our site. While we cannot explain why tropical woodpeckers would orient their holes preferentially to the N–NE, our finding suggests that alternative hypotheses explaining nonrandom cavity orientation should be tested, and the thermoregulatory consequences of different cavity directions in tropical forests ought to be explored.

Cavities suitable for large birds may be of disproportionate importance to birds of conservation concern. Only 55 (25.7%) of the cavities in this study had cavity openings ≥ 60 cm², which is similar to the lower size cut-offs in studies of large secondary cavity-nesting species (e.g., Saunders *et al.* 1982, Soulliere 1988). Even though large cavities were relatively uncommon at La Selva, our data set yields estimates of 28.7 large cavs/ha which is still substantially higher than comparable large-cavity estimates in the above studies (0.7 and 16.0 cavs/ha, respectively). We found much higher cavity densities than in any of the temperate forests in our data set, and propose that availability of appropriate nesting substrate may not structure tropical bird communities in the ways observed in temperate forests. Tests of this hypothesis will require collecting data on cavity use and suitability from multiple tropical sites. Obtaining data on cavity use is not a trivial task; during approximately 300 person-hours of field work for this study, we never saw birds entering or leaving any cavity on our plots. Given the importance of cavities to tropical avifaunas, the lack of basic information on cavity distribution is daunting. However, a relatively modest investment in further research should quickly lead to a much deeper understanding of how cavities function in structuring populations of tropical forest birds.

ACKNOWLEDGMENTS

We thank OTS and NSF for funding through the 2005 La Selva REU Program, and gratefully thank OTS/La Selva staff, especially P. Arroyo, for support. L. Campos and W. Miranda assisted in the field. J. Hurtado improved the wording in the Spanish abstract. Plot data were developed with support from NSF, the Andrew W. Mellon Foundation, and Conservation International (TEAM), which is made possible by a grant from the Gordon & Betty Moore Foundation.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Table S1. *Studies reporting tree cavity density estimates per unit area from forests of different latitudes and ages.*

LITERATURE CITED

- AITKEN, K. E. H., AND K. MARTIN. 2004. Nest cavity availability and selection in aspen-conifer groves in a grassland landscape. *Can. J. For. Res.* 34: 2099–2109.
- BRAWN, J. D. 1988. Selectivity and ecological consequences of cavity nesters using natural vs. artificial nest sites. *Auk* 105: 789–791.
- BRIGHTSMITH, D. J. 2005a. Competition, predation and nest niche shifts among tropical cavity nesters: Ecological evidence. *J. Avian Biol.* 36: 74–83.
- BRIGHTSMITH, D. J. 2005b. Competition, predation and nest niche shifts among tropical cavity nesters: Phylogeny and natural history evolution of parrots (Psittaciformes) and trogons (Trogoniformes). *J. Avian Biol.* 36: 64–73.
- BUTCHER, L. R., S. A. FLEURY, AND J. M. REED. 2002. Orientation and vertical distribution of Red-naped Sapsucker (*Sphyrapicus nuchalis*) nest cavities. *Western North American Naturalist* 62: 365–369.
- CALDER, W. A., AND J. R. KING. 1974. Thermal and caloric relations of birds. *In* D. S. Farner and J. R. King (Eds.). *Avian biology*, pp. 259–413. Academic Press, New York, New York.
- CARLSON, A., U. SANDSTRÖM, AND K. OLSSON. 1998. Availability and use of natural tree holes by cavity nesting birds in a Swedish deciduous forest. *Ardea* 86: 109–119.
- CLARK, D. B., AND D. A. CLARK. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *For. Ecol. Manage.* 137: 185–198.
- GALE, N., AND A. S. BARFOD. 1999. Canopy tree mode of death in a western Ecuadorian rain forest. *J. Trop. Ecol.* 15: 415–436.
- GIBBS, J. P., M. L. HUNTER, AND S. M. MELVIN. 1993. Snag availability and communities of cavity-nesting birds in tropical versus temperate forests. *Biotropica* 25: 236–241.
- HANSELL, M. 2000. *Bird nests and construction behaviour*. Cambridge University Press, Cambridge, UK.
- HARDY, P. C., AND M. L. MORRISON. 2001. Nest site selection by Elf Owls in the Sonoran Desert. *Wilson Bull.* 113: 23–32.
- KOVACH COMPUTING SERVICES. 2006. Oriana. Anglesey, UK.
- LAND, D., W. R. MARION, AND T. E. OMEARA. 1989. Snag availability and cavity nesting birds in Slash Pine plantations. *J. Wildl. Manage.* 53: 1165–1171.
- LIEBERMAN, D., M. LIEBERMAN, R. PERALTA, AND G. S. HARTSHORN. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol.* 84: 137–152.
- LOSOS, E. C., AND E. G. LEIGH JR. 2004. *Tropical forest diversity and dynamism*. University of Chicago Press, Chicago, Illinois.
- PATTANAVIBOOL, A., AND W. D. EDGE. 1996. Single-tree selection silviculture affects cavity resources in mixed deciduous forests in Thailand. *J. Wildl. Manage.* 60: 67–73.
- PUTZ, F. E., P. D. COLEY, K. LU, A. MONTALVO, AND A. AIELLO. 1983. Up-rooting and snapping of trees: Structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011–1020.
- RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildl. Monographs* 86: 1–66.
- SANFORD, R. L., JR., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. *In* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois.
- SAUNDERS, D. A., G. T. SMITH, AND I. ROWLEY. 1982. The availability and dimensions of tree hollows that provide nest sites for Cockatoos (Psittaciformes) in Western Australia. *Aust. Wildl. Res.* 9: 541–556.

- SKUTCH, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. *In* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley (Eds.). *Neotropical ornithology*, pp. 575–594. The American Ornithologists' Union, Washington, DC.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. Freeman & Hall, New York, NY.
- SOULLIERE, G. J. 1988. Density of suitable Wood Duck nest cavities in a northern hardwood forest. *J. Wildl. Manage.* 52: 86–89.
- STONEMAN, G. L., M. E. RAYNER, AND F. J. BRADSHAW. 1997. Size and age parameters of nest trees used by four species of parrot and one species of cockatoo in south-west Australia: Critique. *Emu* 97: 94–96.
- STOTZ, D. E., J. W. FITZPATRICK, T. A. PARKER III, AND D. K. MOSKOVITS. 1996. *Neotropical birds: Ecology and conservation*. The University of Chicago Press, Chicago, Illinois.
- VON HAARTMAN, L. 1957. Adaptation in hole-nesting birds. *Evolution* 11: 339–347.
- WIEBE, K. L., AND T. L. SWIFT. 2001. Clutch size relative to tree cavity size in Northern Flickers. *J. Avian Biol.* 32: 167–173.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, London, UK.