

## BREEDING BIOLOGY OF PALE-EYED THRUSHES (*TURDUS LEUCOPS*) IN THE CLOUD FOREST OF NORTHEASTERN ECUADOR

Konrad Halupka<sup>1</sup> & Harold F. Greeney<sup>2</sup>

<sup>1</sup>Department of Avian Ecology, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland. *E-mail*: halupka@biol.uni.wroc.pl

<sup>2</sup>Yanayacu Biological Station & Center for Creative Studies, c/o 721 Foch y Amazonas, Quito, Ecuador.

**Resumen.** – **Biología reproductiva del Mirlo Ojipálido (*Turdus leucops*) en bosques nublados del noreste de Ecuador.** – La biología reproductiva del Mirlo Ojipálido ha sido documentado con observaciones sobre unos pocos nidos, aunque es un pájaro con distribución amplio. Presentamos los resultados de estudios realizados de 2003-05 en bosque nublado primario (elevación 1950–2100 m) en las laderas de Los Andes en el este de Ecuador. La temporada reproductiva dura desde diciembre hasta Junio, pero parece que la reproducción esta muy bajo durante ciertos años. Colectamos datos sobre 35 anidaciones. Nidos fueron construidos pegados en los troncos de árboles y también por los filos de carreteras, con un rango de altura sobre el suelo de 0.8 a 3.2 m. Los nidos eran construidos de musgos, con una copa de fibras negras. Algunos de los nidos eran reutilizados para varias anidaciones. Solo las hembras incubaron dos, o en ocasión un huevo. Huevos eran de color verde-olivo hasta azul claro, con manchas cafés. El periodo de incubación era 14 días. Los pichones crecieron lentamente en comparación con otros mirlos, saliendo del nido después de 18 días. En promedio, 41% de los nidos fueron exitosos. Documentamos, varias veces, el perdido de solo una porción de la anidada. Dos hembras fueron atacadas durante incubación y estimamos que hasta 15% de las hembras mueren o están heridos durante la animación. Concluimos que la biología reproductiva del Mirlo Ojipálido muestra una mezcla de características de especies tropicales (anidada reducida y crecimiento lento de pichones) y especies templadas (alto nivel de reproducción y de costo a los adultos). La reproducción errática que se documenta en nuestro trabajo podría representar un problema potencial para la conservación ya que es un factor que aumenta la varianza en el número de individuos de la población.

**Abstract.** – Breeding biology of the Pale-eyed Thrush (*Turdus leucops*) has previously been documented through observations at only a few nests, despite its wide distribution within humid montane forests—a globally important habitat of conservation concern. We present the results of studies carried out from 2003–05 in a primary cloud forest (elevation 1950–2100 m) on the eastern slopes of the Ecuadorian Andes. The breeding season lasts from December to June, but it appears that reproduction is greatly reduced during some years. We collected data on 35 breeding attempts. Nests were built in trees and, occasionally, on road embankments. Nest height ranged from 0.8 to 3.2 m. Nests were mossy cups lined with fine rootlets. Some nests were reused for more than one breeding attempt. Females incubated two or, rarely, one egg. Eggs were olive green to light blue with red-brown markings. Incubation lasted 14 days. Nestlings grew rather slowly when compared to other thrushes, and fledged after 18 days. On average, 41% of nests in which incubation began fledged young. We recorded several instances of partial brood-loss. Two incubating females were attacked by a predator and we estimate that as many as 15% of females might be killed or injured during incubation. We conclude that the reproductive biology of the Pale-eyed Thrush shows a mixture of traits characteristic of both tropical (small clutch size and slow nestling growth rate) and north-temperate species (high breeding success and parental costs of repro-

duction). The erratic breeding documented in our study might be a potential problem for conservation as a factor increasing variance in the population number.

**Key words:** Pale-eyed Thrush, *Turdus leucops*, *Platycichla*, Turdidae, Ecuador, natural history, reproduction biology.

## INTRODUCTION

The Pale-eyed Thrush has been only recently moved to the genus *Turdus*. Previously it was, together with the Yellow-legged Thrush (*T. flavipes*), included in genus *Platycichla*; however, DNA analyses changed taxonomic position of both species (Klicka *et al.* 2005, Voelker *et al.* 2007).

Pale-eyed Thrushes are distributed from the Guyana Shield (Guyana, Venezuela and Brazil; Milensky *et al.* 2005) throughout most of the Andes, on both slopes, from Venezuela (Verea *et al.* 1999) and Colombia (Hilty 1977, Donegan & Dávalos 1999, Renijfo 1999, Londoño 2005), south through Ecuador (Marin & Carrion 1991), Peru (Davis 1986), and Bolivia (Brumfield & Maillard 2007). Despite their wide geographic distribution, Pale-eyed Thrushes are restricted to a rather narrow altitudinal band of tropical cloud forests that are currently the focus of much attention as endangered, biologically diverse habitats (Hamilton 1995, Bruijnzeel & Hamilton 2000). Thus, research on the breeding biology of all cloud forest species is important from a conservation perspective. In addition, more data are needed to link empirical knowledge and theoretical explanations of latitudinal variation in avian life histories (Stutchbury & Morton 1999).

To date, the breeding biology of Pale-eyed Thrushes is known from descriptions of four nests in Ecuador and Colombia (Marin & Carrion 1991, Londoño 2005). Here we present the results of observations of 35 breeding attempts in northeastern Ecuador. We describe breeding phenology, habitat and nest-site selection, parental behaviour, nest success, clutch sizes, duration of incubation

and nestling periods, and nestling growth and development.

## METHODS

Data were collected from 2003 to 2005 in the northeastern Ecuadorian Andes, on the private birding reserve of Cabañas San Isidro, next to the Yanayacu Biological Station and Center for Creative Studies (00°35'S, 77°53'W), at elevations of 1950–2200 m a.s.l. The reserve encompasses about 1500 ha of primary cloud forest adjoining the 188,000 ha Antisana Reserve.

Nests were found by systematically searching the understory vegetation, especially epiphytes on tree trunks, in the vicinity of places where some activity of thrushes (singing, nest building, alarm calling, feeding, etc.) were observed or by accidentally flushing adults from nests. In 2004 and 2005, between mid-February and mid-May, the study site was explored in the morning and afternoon (4–10 hours daily) and effort was directed toward finding nests of thrushes. During the remaining months of 2004 and 2005, as well as in 2003, nests were found opportunistically in the vicinity of Yanayacu Biological Station.

The amount of data collected at each nest varied. We are convinced, however, that the subsample of nests described in more detail is representative for the general population. A few remote nests were only visited once. Other nests were checked every 1–5 days until they failed or fledged. Nests were visited more frequently (every 1–2 days) near the expected hatching or fledging dates and when collecting data on nestling growth. Nest visits were as brief as possible and, when nestling mass exceeded 40 g, we observed nests from

a distance to avoid causing premature fledging. After the nest fledged or was depredated, we measured nest and nest-site characteristics (cf. Clement & Hathaway 2000) to the nearest 1 cm using a measuring tape. Density of canopy at the nest was measured with a forest spherical densitometer (manufactured by RE Lemon, Bartelsville, OK, USA). Canopy density was scored as a percentage of sky visible using the average of four measurements taken 6 m from the nest, at 90° intervals around the substrate tree.

We measured eggs to the nearest 0.1 mm using standard vernier calipers and egg mass to the nearest 0.001 g using a digital microgram balance that was calibrated before each weighing using a standard 50 g weight. Nestlings were weighed ( $\pm 0.25$  g) every 1–3 days with a Pesola spring balance. The growth curve relating body mass to age was fitted to the logistic function:

$$\text{Mass}(\text{age}) = A / (1 + b \exp(-K \text{ age}))$$

where  $A$  is the asymptotic body mass and  $K$  is the growth rate coefficient (Ricklefs 1976). The age (in days) at which the curve inflected was calculated as  $\ln(b)/K$  and the inverse measure of growth rate was calculated using the formula  $4.4/K$ . We followed Ricklefs' (1976) convention of making the day of hatching day one.

To minimize disturbance, we last weighed nestlings when 14–16 days old and body masses were about 40 g. Because nestling body mass could still increase after this, the asymptotic body mass might be slightly underestimated and the growth rate coefficient overestimated (cf. Remeš & Martin 2002).

Logistic curve coefficients were calculated with a resampling method (Crowley 1992), allowing us to avoid problems with pseudoreplication (data from siblings should not be treated as independent). To do this, we randomly selected only one recorded body mass from each of the 19 nests included in the anal-

ysis. If the resulting 19-point data subset did not cover at least 12 days, the resampling procedure was repeated until this minimal time span criterion (i.e., the time when the s-shaped growth pattern becomes apparent) was met. Thereafter, using the least squared method, the logistic curve was fitted to the data and the resulting equation recorded. This re-sampling procedure was iterated 2000 times. Following the Central Limit Theorem (cf. Crowley 1992), mean values and standard deviations of the resampling distributions of the growth curve coefficients approximate the general population's growth parameters and estimates of standard errors.

At each approach to the nest, we recorded the distance at which the incubating/brooding adult flushed from the nest, and any associated behaviours. If the nest was predated, and the date of predation could not be exactly determined, failure was assigned as the day in the mid-point between the last two visits. If nestlings on the penultimate nest check appeared ready to fledge, but were gone with no signs of predation (e.g., blood, feathers, or disturbed nest site) at the next visit, the nest was considered successful.

Descriptive statistics are presented as means  $\pm$  SD, unless otherwise stated. Survival rates of nests and incubating adult birds were estimated using the Mayfield (1975) method and standard errors for Mayfield statistics were calculated with the algorithm described by Johnson (1979).

## RESULTS

*Breeding phenology.* Pale-eyed Thrushes appeared to breed in our study area rather erratically. Only 4 nests were found from January to May 2003. No nests were found from February to May 2004, even though adult birds were frequently observed and heard and other sympatric thrushes did breed (Greeney & Halupka 2008). However, from December

2004 to June 2005, with the same effort invested in nest searching, we collected data on 31 breeding attempts.

During the 2004–2005 breeding season, the earliest nest, with incubation already underway, was found on 2 December. Nestlings from the latest nests fledged from 1 to 15 June. During seven years of nest searching in the area (HFG unpubl.), no active Pale-eyed Thrush nests have been found from June to November, and most clutches were initiated in December and January. Thus, breeding attempts are initiated during about six months of the year in our area.

*Nests, nest sites, and nest patches.* Of 32 nests, 27 (84.4%) were in trees and five on the ground on roadside embankments. Nest height ranged from 1.15 to 3.20 m for nests in trees (mean =  $1.96 \pm 0.50$  m,  $n = 27$ ) and from 0.8 to 2.3 m for nests on banks (mean =  $1.58 \pm 0.55$  m,  $n = 5$ ). Cups were generally circular, but the side of the cup was often thinner, or even lacking, where the rim adjoined the supporting substrate. Mean outer cup diameter was  $13.2 \pm 1.02$  cm, mean inner cup diameter was  $8.1 \pm 0.86$  cm, and mean cup depth was  $5.2 \pm 1.2$  cm ( $n = 19$  nests). The outer layer of 5 nests collected from trees and dissected, consisted of green moss and there was a variable amount of soil at the bottom of the cup or, in one nest, a large amount of wood dust. The cup lining consisted of thin, dark rootlets. The green moss in outer walls blended well with the naturally growing moss and other epiphytes on tree trunks, therefore nests were well camouflaged when observed from below or the side. However, nests were generally poorly concealed from above and only a few were partially sheltered by the stems of ferns or other epiphytes. For most nests, incubating or brooding adults were easily seen by observers approaching the nest, indicating that adults also had a clear and unobstructed view from the nest.

Nest trees had a mean diameter at breast height of  $41 \pm 19.2$  cm ( $n = 14$ ). Eleven nests were on the side of the trunk, and supported by epiphytes, protruding bark, or both. One nest was in a large tree fork, and two were in shallow hollows on the side of a trunk. Within a 6-m-radius around nest trees, an average of  $6.5 \pm 2.8$  trees reached the canopy layer of the forest and the mean number of smaller trees and tree ferns in the sub-canopy was  $10.6 \pm 7.3$ . The mean percentage of sky visible (measured with a spherical densitometer) was  $35.5 \pm 6.8\%$ . These figures were very close to statistics calculated for randomly selected patches within the forest, where nests were not detected (KH unpubl.).

For two nests, two consecutive clutches were initiated in 2005. Unfortunately, even though we knew the date of fledging of young from the first broods (7 March and 7 April), nests were not checked again until 25 March and 18 April, respectively, and incubation was already underway at both nests. Therefore, we do not know how many days elapsed between fledging and re-nesting. Also, individuals were not marked so we do not know if the same pair initiated both clutches.

*Eggs and incubation period.* At 27 nests where incubation had begun, two had one-egg clutches and 25 had two-egg clutches. Eggs were olive green to light blue, with brown to red-brown blotches. Spots were irregular, heavier, and overlapping near the blunt end of the egg.

Eggs ( $n = 36$  from 21 nests) ranged from 25.8 to 32.6 mm in length (mean =  $28.99 \pm 1.50$  mm) and from 18.6 to 21.5 mm in width (mean =  $20.12 \pm 0.69$  mm). Two recently laid eggs in one nest weighed 6.07 g and 5.98 g, respectively. In two other nests with two-egg clutches where incubation had just begun, mean egg mass was 7.2 and 6.4 g, respectively. At five nests, eggs ( $n = 9$ ) were weighed at 3 to 6-day intervals during incubation to docu-

ment loss of mass (= water loss; Rahn & Ar 1974), and the mean mass loss was  $71.4 \pm 34.9$  mg (range = 21–124 mg) per day, or, using the mean fresh egg mass as the initial mass,  $1.09 \pm 0.63\%$  per day. The length of the incubation period (measured from clutch completion to hatching of entire clutch) at the only nest where we had detailed laying data was 14 days. In two other nests found after incubation had begun, we recorded 13 and 14 days until hatching.

*Development of nestlings.* At nine nests with 2-egg clutches, both eggs hatched within 24 hours of laying. Primary feather pins broke skin around day 5–6 and emerged from sheaths when nestlings were 10–12 days old. Eyes opened on days 9–10, and nestlings fledged when  $18.6 \pm 1.2$  days old ( $n = 5$  nests). In three other nests fledging was apparently provoked by the approach of an observer and nestlings left the nest at ages of 16, 18, and 19 days.

During the period of fastest growth (day 5 to day 9), the increase in body mass was approximately linear and nestlings ( $n = 32$  from 19 nests) on average gained 2.7 g/day (SE = 0.35). The asymptotic body mass attained by nestlings close to fledging was 43.1 g (SE = 5.5), or 69% of the mean body mass (62.5 g; range = 59.5–65.0 g) of three adult males captured near our study area (C. Dingle pers. com.). Growth rate expressed by the K parameter of the logistic equation equaled 0.36 (SE = 0.05). The growth curve inflected at day 7 post-hatching, and nestlings took 12.2 days to grow from 10% to 90% of the asymptote.

*Breeding success.* The survival rate of nests during egg laying was not estimated because we had too few data. During incubation, two of 24 nests were abandoned and five were depredated, including two where the incubating female was apparently killed (with many

feathers found on the empty nests). Thus, the daily survival rate of nests during the incubation stage was 0.958 (SE = 0.016; 160 successful days and seven days with a failure). Using an incubation period of 14 days (including the hatching day), we calculated that 55% of nests survive until hatching. The daily risk of death to the incubating bird at the nest was 1.2% (SE = 0.8; 165 nest-days without predation, two fatal days). Over the entire incubation stage, the adults' risk of being killed or injured was 15.5%.

During the nestling period, out of 22 nests, three were depredated and two failed when the nestlings died of unknown causes. In the latter nests, nestlings were underfed and cold and we observed partial losses (of an egg in one nest and a newly hatched chick in the second) several days before the nests were deserted. Partial losses also were observed in two other nests that both eventually fledged one nestling. In these nests the difference in body mass between nestlings gradually increased and the smaller chick eventually died (15 and 11 days after hatching). The smaller chicks' body masses at the last check where they remained alive were, respectively, 75.2% and 74.2% of their nest-mate's mass.

Daily survival rate of nests during the nestling stage was 0.983 (SE = 0.008, 22 nests observed, 286 successful days, 5 days with failure). Using a 17-day nestling period (without the hatching day), this yields an estimated 75% nest survival from hatching to fledging. Combining these data with estimates from incubation, 41% of nests where incubation begins are predicted to fledge at least one young. The mean number of fledglings per successful nest ( $n = 15$ ) was  $1.7 \pm 0.5$ .

*Adult behaviour at nests.* Only females were observed incubating eggs ( $n = 11$  nests at which sex of the incubating parent was determined at least once) and brooding young ( $n = 6$  nests). At three nests, diurnal brooding con-

tinued until 9–12 days after hatching, when the contour feathers of nestlings were emerging from their sheaths. Sporadic, non-quantified video recordings at several nests (HFG unpubl.) revealed that both adults provisioned nestlings.

During incubation, modal flush distance at 14 newly discovered nests was 0.5 m (range = 0.5–2 m). This sudden and conspicuous flushing from the nest, in conjunction with alarm calling and, in several cases, distraction displays (flying in a slow and fluttery manner), however, was not the rule. Some females left nests when observers were at much greater distances and, even though nest checks during incubation were frequent, such females were rarely seen on the nest. During nest checks, adults gave alarm calls while well hidden in vegetation close to the nest. Alarm calls were given even during the early stages of incubation.

## DISCUSSION

Most nests of Pale-eyed Thrushes in our study were located in trees. Similarly, two nests found by Londoño (2005) were also in trees. We found five Pale-eyed Thrush nests on the ground on road embankments, and Marin & Carrion (1991) also reported nests on embankments. While the reason for such variability in nest site selection is unclear (there were many potential nesting trees in the forest adjoining the road), it appears that ground nests are unusual in the forest interior, as we found no nests on the numerous vertical banks along streams in our study area.

Four of the five Pale-eyed Thrush nests we examined contained soil (not simply decaying nest material) and the remaining nest had a layer of wood dust. In contrast, two nests from Colombia examined by Londoño (2005) and a single nest from the western slope of Ecuadorian Andes described by

Marin & Carrion (1991) consisted only of moss and rootlets. These observations suggest there is variation within and between populations of Pale-eyed Thrushes in choice of nest materials.

Growth rates of nestling Pale-eyed Thrushes in our study ( $K = 0.36$ ) were similar to those of nestlings of a sympatric thrush, the Andean Solitaire ( $K = 0.33$ ; Greeney & Halupka 2008). Coefficients reported for nine North American thrush species (genera *Catharus*, *Sialia*, *Hylocichla*, and *Turdus*) are higher (range: 0.44–0.69; Remeš & Martin 2002). Growth rates of Pale-eyed Thrushes also appear to be rather slow compared to other tropical species. For passerines with an adult body mass less than 100 g, Ricklefs (1976) reported a range of  $K$  values between 0.278 and 0.604. Even compared to other tropical thrushes, including species from montane forests in Venezuela (Ricklefs 1976), Pale-eyed Thrushes in our study grew relatively slowly. Greeney & Halupka (2008) suggested that similarly slow growth of Andean Solitaires might be due to their rich in fruits, low-protein diet, and the relatively low temperatures at about 2000 m a.s.l., where they breed. The same factors may contribute to the slow growth of nestling Pale-eyed Thrushes because they breed during the same period of the year as Andean Solitaires and also feed nestlings a high percentage of fruits (Londoño 2005, HFG pers. observ.). The brood reduction observed at some nests also suggests that food resources may have been limiting for Pale-eyed Thrushes in our study.

Estimated nest success for Pale-eyed Thrushes in our study was relatively high (41% of nests in which incubation begins were predicted to fledge at least one young), comparable to values from North America (41% average for shrub or low-foliage nesting species; Martin 1995) and higher than that for three thrush species that breed in montane

forests in Argentina (23–29%, calculated from Tables 2 and 5 in Auer *et al.* 2007) and for understory open-cup nesting birds in a lowland humid forest of Panama (32–38%; Table 2 in Robinson *et al.* 2000). The survival rates of Pale-eyed Thrush nests were also comparable to those of Andean Solitaires in the same study area (39%; Greeney & Halupka 2008). In both species, parent birds choose similar nesting sites and behave in similar ways when approached during incubation or brooding, thus such a high similarity of the breeding success statistics is not surprising.

We also found high predation rates on incubating females of both species, with daily risks of 1.2% in the Pale-eyed Thrush and 2.5% in the Andean Solitaire. Extrapolated over the entire incubation period, this suggests that 15.5% and 32% of females, respectively, would be attacked. Our statistics might be overestimated because the presence of adult feathers at the nest does not necessarily indicate a fatal attack. On the other hand, we only used the incubation period in our calculations and the true exposure period would also include time when nestlings are brooded, thus producing even higher estimates. It is often argued that tropical birds typically have relatively low annual mortality, at least when compared to closely-related species from the temperate zone (Ricklefs 1997, Stutchbury & Morton 1999). Thus a high incidence rate of predation attempts in our population might support alternative models of life histories in tropics (Karr *et al.* 1990, McGregor *et al.* 2007, Blake & Loiselle 2008).

The current conservation status of Pale-eyed Thrushes is that of "least concern" because they are widely distributed and, where they occur, common (BirdLife International 2008). Pale-eyed Thrush nests have been found in areas outside of mature cloud forest, including secondary growth (Marin & Carrion 1991) and a Chinese Ash (*Fraxinus chinensis*)

plantation (Londoño 2005). Additionally, research carried out in Colombia (Renijfo 1999) suggests that Pale-eyed Thrushes are tolerant of forest fragmentation. Conversely, however, the erratic inter-annual breeding documented in our study is a noteworthy consideration for future evaluations of the conservation status of this species, as it is a potential factor increasing demographic stochasticity (Simberloff 1988).

Most characteristics of the breeding biology of the Pale-eyed Thrush agree with generalizations made for other tropical birds (Stutchbury & Morton 1999). Namely, the Pale-eyed Thrush has a long breeding season, small clutch size, and slow-growing nestlings. Two traits, however, seem to be unique. First, Pale-eyed Thrushes in our area show breeding success comparable to temperate species. Second, our data demonstrate that the cost of reproduction in this species, intensified by the vulnerability of incubating females, may be relatively high. Although these differences suggest that the nesting strategy of the Pale-eyed Thrush shows characteristics of both high-latitude and tropical species, further studies are needed to confirm these patterns in other parts of its range.

#### ACKNOWLEDGMENTS

We thank C. Dingle, R. Gelis, R. Lynch, and J. Simbaña for help with field work. C. Bustamante and M. Lysinger kindly allowed us to collect data in the birding reserve of Cabañas San Isidro. We also thank anonymous reviewers for suggestions on how to improve the manuscript and M. Torralva for helping with the translation of abstract to Spanish. KH was supported by the State Committee for Scientific Research, Republic of Poland (2PO4F 03226). HFG is supported by Matt Kaplan and John V. Moore through the Population Biology Foundation, as well as by Field Guides Inc. and the Maryland Audubon Soci-

ety. This is publication number 165 of the Yanayacu Natural History Research Group.

## REFERENCES

- Auer, S. K., R. D. Bassar, J. J. Fontaine, & T. E. Martin. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *Condor* 109: 321–333.
- Birdlife International. 2008. Species factsheet: *Turdus leucops*. Downloaded from <www.birdlife.org> on 20 January 2009.
- Blake, J. G., & B. A. Loiselle. 2008. Estimates of apparent survival rates for forest birds in eastern Ecuador. *Biotropica* 40: 485–493.
- Bruijnzeel, L. A., & L. S. Hamilton. 2000. Decision time for cloud forests. IHP Humid Tropics Programme, Series No. 13, UNESCO, Paris, France.
- Brumfield, R. T., & Z. Maillard. 2007. Birds of the central Rio Paracti Valley, a humid montane forest in Departamento Cochabamba, Bolivia. *Ornitol. Neotrop.* 18: 321–337.
- Clement, P., & R. Hathaway. 2000. Thrushes. C. Helm, London, UK.
- Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. *Ann. Rev. Ecol. Syst.* 23: 405–447.
- Davis, T. J. 1986. Distribution and natural history of some birds from the departments of San Martín and Amazonas, northern Peru. *Condor* 88: 50–56.
- Donegan, T. M., & L. M. Dávalos. 1999. Ornithological observations from Reserva Natural Tambito, Cauca, south-west Colombia. *Cotinga* 12: 48–55.
- Greeney, H. F., & K. Halupka. 2008. Nesting biology of the Andean Solitaire (*Myadestes ralloides*) in northeastern Ecuador. *Ornitol. Neotrop.* 19: 213–219.
- Hamilton, L. S. 1995. Montane cloud forest conservation and research: a synopsis. *Mount. Res. Develop.* 15: 259–266.
- Hilty, S. L. 1977. *Chlorospingus flavovirens* rediscovered, with notes on other Pacific Colombian and Cauca Valley birds. *Auk* 94: 44–49.
- Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96: 651–661.
- Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, & J. D. Brawn. 1990. Survival rates of birds of tropical and temperate forests - will the dogma survive? *Am. Nat.* 136: 277–291.
- Klicka, J., G. Voelker, & G. M. Spellman. 2005. A molecular systematic revision of the "true thrushes" (Turdinae). *Mol. Phyl. Evol.* 34: 486–500.
- Londoño, G. A. 2005. A description of the nest and eggs of the Pale-eyed Thrush (*Platycichla leucops*), with notes on incubation behavior. *Wilson Bull.* 117: 394–399.
- McGregor, R., M. J. Whittingham, & W. Creswell. 2007. Survival rates of tropical birds in Nigeria, West Africa. *Ibis* 149: 615–618.
- Marin A., M., & J. M. Carrion B. 1991. Nests and eggs of some Ecuadorian birds. *Ornitol. Neotrop.* 2: 44–46.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65: 101–127.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- Milensky, Ch. M., W. Hinds, A. Aleixo, & M. de Fátima C. Lima. 2005. Birds. Pp. 43–74 in Hollowell, T., & R. P. Reynolds (eds.). Checklists of the terrestrial vertebrates of the Guiana Shield. *Bull. Biol. Soc. Washington* 13.
- Rahn, H., & A. Ar. 1974. The avian egg: incubation time and water loss. *Condor* 76: 147–152.
- Remeš, V., & T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. *Evolution* 56: 2502–2518.
- Renjifo, L. M. 1999. Composition changes in a subandean avifauna after long-term forest fragmentation. *Conserv. Biol.* 13: 1124–1139.
- Ricklefs, R. E. 1976. Growth rates of birds in the humid new world tropics. *Ibis* 118: 179–207.
- Ricklefs, R. E. 1997. Comparative demography of new world populations of thrushes (*Turdus* spp.). *Ecol. Monogr.* 67: 23–43.
- Robinson, W. D., T. R. Robinson, S. K. Robinson, & J. D. Brawn. 2000. Nesting success of understory forest birds in central Panama. *J. Avian Biol.* 31: 151–164.
- Roff, D. A., V. Remeš, & T. E. Martin. 2005. The evolution of fledging age in songbirds. *J. Evol.*

- Biol. 18: 1425–1433.
- Simberloff, D. 1998. Small and declining populations. Pp. 116–134 *in* Sutherland, W. D. (ed.). Conservation science and action. Blackwell Science Ltd., Oxford, UK.
- Stutchbury, B. J. M., & E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, San Diego, CA.
- Verea, C., A. Solorzano, & A. F. Badillo. 1999. Pesos y distribución de aves del sotobosque del Parque Nacional Henri Pittier al norte de Venezuela. *Ornitol. Neotrop.* 10: 217–231.
- Voelker, G., S. Rohwer, R. C. K. Bowie, & D. C. Outlaw. 2007. Molecular systematic of a speciose, cosmopolitan songbird genus: defining the limit of, and relationships among, the *Turdus* thrushes. *Mol. Phyl. Evol.* 42: 422–434.

