ORNITOLOGIA NEOTROPICAL 21: 225–239, 2010

THE RUDDY-CAPPED NIGHTINGALE-THRUSH (*CATHARUS FRANTZII*) IN EL SALVADOR: NOTES ON THE LIFE HISTORY AND ECOLOGY OF TWO ISOLATED POPULATIONS

Joseph Taylor[1] & Oliver Komar

SalvaNATURA, Colonia Flor Blanca, 33 Avenida Sur #640, San Salvador, El Salvador.
E-mail: joe.taylor@birdlife.org

Resumen. – *Catharus frantzii* en El Salvador: Notas sobre la historia de vida y ecología de dos poblaciones aisladas. – Presentamos datos sobre poblaciones de *Catharus frantzii* en Parque Nacional (PN) Los Volcanes y PN Montecristo, El Salvador, colectados entre Noviembre 2003 y Junio 2008. La especie, considerada en peligro de extinción a nivel nacional, se reproduce durante toda la temporada lluviosa en El Salvador, mayormente desde Mayo hasta Agosto, con aves en condición reproductiva capturadas hasta Octubre. La especie muda durante un período prolongado, principalmente después de la reproducción. Las capturas de adultos en redes de niebla aumentan durante la temporada lluviosa (Mayo–Octubre) y bajan en frecuencia durante la temporada seca (Noviembre–Abril), posiblemente reflejando un cambio en comportamiento de forrajeo o una migración altitudinal parcial. No hay diferencias significativas en la supervivencia, productividad y proporción de aves no-reproductivas entre las dos poblaciones. Las capturas máximas de la especie fueron 2,9 veces más altas en PN Los Volcanes, una diferencia que correlaciona a vegetación más densa y también a la presencia de menos competidores potenciales. La alta densidad y número de especies en la vegetación de PN Los Volcanes podría resultar de la topografía más escarpada o actividad reciente del volcán. Sin embargo, detectamos una declinación significativa en las capturas de adultos en PN Los Volcanes; actividad volcánica, cambio de clima, competencia y las actividades de humanos son posibles causas.

Abstract. – We present data on populations of the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*) at Los Volcanes National Park (NP) and Montecristo NP, El Salvador, collected between November 2003 and June 2008. This species, considered endangered at the national level, breeds throughout the rainy season in El Salvador, mostly from May to August, with birds in breeding condition captured into October. The species exhibits a protracted period of mainly post-breeding molt. The adult capture rates for both sites across the year show a peak during the rainy season (May–October), falling to lower capture rates in the dry season (November–April), perhaps due to changing feeding habits or partial altitudinal migration. Apparent survival and productivity and the proportion of probable floaters did not differ significantly between the sites. The peak capture rate for the species was 2.9 times higher at Los Volcanes NP, a difference which correlates with denser vegetation, as well as the presence of fewer potential competitors. The apparently higher vegetation density and species richness at Los Volcanes NP could be due to the effect of steeper topography or recent volcanic activity. However, we detected a significant decline in the capture rate of adults at Los Volcanes NP; volcanic activity, climate change, competition, and human activities are suggested as possible causes.

Key words: Ruddy-capped Nightingale-Thrush, *Catharus frantzii*, apparent survival, breeding biology, capture probability, Central America, cloud forest, molt, population trend.

---

[1] *Current address*: BirdLife International, Wellbrook Court, Girton Road, Cambridge, CB3 0NA, UK.

INTRODUCTION

Conservation efforts and taxonomic research for birds in the Neotropics are hampered by a shortage of data on the life history and ecology of many species. Particular concern has been expressed in the past over the low ratio of published studies to national bird species richness and human population density in Guatemala, Honduras, Nicaragua, and El Salvador (Winker 1998). Komar (1998) also noted the slow development of biological research in El Salvador. However, since November 2003 there has been a monthly bird monitoring program operating in this country, involving the mist-netting and banding of birds, which is producing valuable data (Komar *et al.* 2009a). This provides an opportunity to improve on our existing knowledge of species in the region. There are already adequate data available from the monitoring program for the initial study of some species, one of which is the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*, Turdidae). This species is considered endangered at the national level in El Salvador, based on IUCN Red List methodology, with a range restricted mostly to just four small patches of cloud forest (Komar *et al.* 2009b). Early research on the species focused on its separation from the closely related Russet Nightingale-Thrush (*C. occidentalis*) (Rowley & Orr 1964, Phillips 1969), and further research is required into its taxonomy, as it possibly comprises multiple evolutionary species (Navarro-Sigüenza & Peterson 2004). Two subspecies are thought to occur in El Salvador, with *C. f. alticola* found from south-western El Salvador to south-eastern Chiapas, and *C. f. juancitonis* occurring in north-western El Salvador and Honduras (Dickey & van Rossem 1938, Phillips 1991). Both of these possible subspecies are threatened by habitat fragmentation, volcanism, and climate change, in a region that has already suffered extensive habitat clearance (Komar 1998). Thus, further research could prove useful for conservation planning and taxonomic evaluation.

The Ruddy-capped Nightingale-Thrush is a monomorphic resident of cloud forests from central Mexico to western Panama, and as such occupies a disjunct range throughout this region (Howell & Webb 1995), and is known to be highly sedentary (Rangel-Salazar *et al.* 2008b). Females construct cup-nests, with an outer lining of moss and an inner lining of roots and plant fibers, in bushes or small understory trees, and lay a clutch of two eggs (Skutch 1960, Rowley & Orr 1964, Raitt & Hardy 1970). Only the female incubates and this occurs over a period of 15–16 days, followed by a fledging period of 14–16 days (Skutch 1960). In the Sierra de Tecpán in Guatemala and Cordillera Central of Costa Rica, Skutch (1960) noted that the species sang mostly from March to August, with the exact timing of singing and nesting activity varying geographically, and found nests from April to July. Raitt & Hardy (1970) noted that birds in Mexico were singing and territorial in April and May, and found one nest in May. Komar (2002) trapped adults in reproductive condition at Montecristo National Park (NP), El Salvador, in June and July 1999, and a recently fledged juvenile on 18 June. Surveys have also suggested that, for this species, the cloud forest at Montecristo NP harbored a density of 1.40 ± 0.05 pairs ha^{-1} in 1999 (Komar 2002); and the cloud forest at Los Volcanes NP harbored a density of 2.12 pairs ha^{-1} in 1995 (O. Komar unpubl. data).

The species was more recently studied at Cerro Huitepec Biological Reserve, Chiapas, Mexico, where it was found that pairs nesting in primary forest exhibited higher breeding success and occurred at higher densities than those nesting in secondary forest (Rangel-Salazar *et al.* 2008a). During the same study, parents were observed feeding fledglings up to four weeks after they had left the nest, and juveniles remained on the natal territory for up to four months (Rangel-Salazar 2006). Renesting after failure of first clutches was also noted (Rangel-Salazar *et al.* 2008a). In addition, the species' survival was found not to differ between primary and secondary forest (Rangel-Salazar 2006, Rangel-Salazar *et al.* 2008b).

So far, only the recent study at Cerro Huitepec has benefited from hundreds of captures and recaptures over multiple years (Rangel-Salazar 2006, Rangel-Salazar *et al.* 2008b). We now have an opportunity to gain new insights from another large data set. The present study, utilizing banding data gathered at two sites in El Salvador, serves to provide further insights into the breeding seasonality, as well as molt regime, population trend and apparent survivorship, for two isolated but neighboring populations of the Ruddy-capped Nightingale-Thrush currently assigned to different subspecies.

METHODS

Banding data for the Ruddy-capped Nightingale-Thrush were gathered from two cloud forest sites in El Salvador (Fig. 1): Los Volcanes NP - Los Andes Sector (Santa Ana Volcano) (13°52'N, 89°37'W), hereafter 'Los Volcanes', and at Montecristo NP - Cloud Forest Station (14°24'N, 89°23'W), hereafter 'Montecristo'. These sites are separated by about 75 km of lowlands that are inhospitable for the Ruddy-capped Nightingale-Thrush. Los Volcanes contains a total of 1724 ha of cloud forest, compared with c. 2500 ha of contiguous cloud forest, protected and unprotected, at Montecristo and adjoining areas in El Salvador, Guatemala, and Honduras (Komar 2002). Phillips (1991), corroborating earlier authors, stated that two different subspecies occur at the two sites, with *C. f. alticola* at Los Volcanes and *C. f. juancitonis* at Montecristo.

Data were collected from November 2003 to June 2008, as part of SalvaNATURA's bird monitoring program. Sampling began at Los Volcanes in November 2003, and at Montecristo in November 2005. At Los Volcanes, 16 standard (12 × 2.5 m) mist nets were deployed within an area of 8.1 ha, at 1990–2080 m a.s.l., and at Montecristo, 16 standard mist nets were set up within an area of 7.6 ha, at 2100–2200 m a.s.l. (Andino *et al.* 2008). The nets were positioned in exactly the same places throughout the study period. Mist nets were generally opened at first-light and closed at dusk in the absence of rainfall or high winds, in order to gather a target of 400 net-hours over three days of field work for each monthly pulse. However, weather conditions resulted in the sampling of less than 400 net-hours in some months over the study period. The number of net-hours sampled averaged 356 net-hours month^{-1} for Los Volcanes and 367 net-hours month^{-1} for Montecristo. Every effort was made to visit these sites each month, but this was not possible for Los Volcanes during 12 months over the study period, owing in part to the threat of volcanic eruption in 2005. This study involves the analysis of data collected during more than 27,400 net-hours, which produced 595 captures of at least 264 individuals of the Ruddy-capped Nightingale-Thrush.

Biometrics were collected following methods given by Pyle (1997). The length of the right unflattened wing chord was measured to the nearest 0.5 mm with a stopped wing-rule and mass measured to the nearest gram using either a digital or spring balance. Birds were aged by plumage and skull ossification, and sexed by signs of breeding condition. As in the majority of passeriform bird species (Pyle 1997, Froelich 2003), juvenile individuals were distinguished from adults by a combination of juvenile plumage, molt limits, tail (rectrix) shape, and skull ossification scored as 1–4 (R. Juárez pers. com.). During processing, birds

FIG. 1. Map showing the fragmented distribution of the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*) at four sites in El Salvador (shaded areas), and the location of study sites at Los Volcanes and Montecristo National Parks.

were scored for the condition of a brood patch (0–4), shape and size of the cloacal protuberance (0–3), body molt (0–4), and flight-feather molt (None, Adventitious, or Symmetric). Breeding activity was judged to be taking place by the occurrence of birds with cloacal protuberances scored as 2 or 3 (males in breeding condition), or with brood patches scored as 2, 3, or 4 (females in breeding condition). Hatch-year birds were assumed to have fledged locally. Molt timing was studied by looking at the capture rate of adults with body molt scored as 2, 3, or 4, or with symmetric flight-feather molt. Score thresholds were used to ensure that birds showing ambiguous or 'borderline' characteristics were removed from the analysis. It should be noted that there are inherent biases in the measurement of the biometrics used here, resulting from the use of multiple fieldworkers, wing-rules, and balances. Such biases are reduced as much as is practical through the careful training of fieldworkers and calibration of equipment.

We studied seasonal variation in the breeding condition and molt of adult birds, and the abundance of hatch-year birds, by summing the total numbers of relevant captures in all years at each study site for that month and converting this to the capture rate in birds 100 net-hours^{-1}. Birds were not counted more than once during one month, but for some of our analyses, recaptures in subsequent months and years were included when these were judged to be independent of the original banding event and any other recapture events in different months (Marini & Durães 2001). For the comparison of the capture rate of adults throughout the year at the two sites, only data from 2006 and 2007 were combined because the two sites received a similar level of sampling effort during those periods, with data only missing for January 2006 and March 2007 at Los Volcanes. Throughout this study, the calculation of monthly capture frequencies involved a relatively small proportion of birds that were not banded for various reasons; the importance of including their data in the analysis outweighed the small risk counting them more than once in a given pulse.

The body mass and wing-chord length of birds banded as adults at the two sites and for males and females banded as adults were compared using the Student's t-test (two-tailed), to detect any significant differences between the two sites, and between males and females at both sites. Only data from banded birds were used, as the use of data from birds that could not be banded for various reasons would carry a risk of pseudoreplication. All mean values are displayed with ± 1 standard deviation. Apparent breeding productivity at the two sites, measured as the ratio of females with brood patches to hatch-year birds caught, was compared for 2006 and 2007 separately using Fisher's Exact test. Once again these years were selected because similar levels of year-round sampling effort were achieved at the two sites. This analysis included birds that were caught but could not be banded, as the importance of including their data in the interests of achieving a more complete picture outweighed the risk of them being counted more than once in the same year. Fisher's Exact tests were also carried out to compare the ratio of recaptured to once-captured birds throughout all years, as those that are captured only once are potentially floaters or transients (Rangel-Salazar 2006, Rangel-Salazar *et al.* 2008b).

Apparent adult monthly survival probability and monthly capture probability were estimated with the Jolly-Cormack-Seber Method, using program MARK Version 5.1 (White & Burnham 1999). The analysis included 107 birds banded after their hatch year and recaptured at least once. Birds that were not recaptured were not included as these birds probably represent floaters and distort the estimation of survival for locally resident birds. Models included constant ($\Phi.$, $P.$), and time- and site-effects, and site and time interactions ($\Phi s{*}t$, $P s{*}t$). Models were selected based on Akaike's Information Criterion (AIC_c), and Akaike Weights (AIC_c Weights) were used to evaluate the relative support for each model. Monthly survival estimates were raised to the 12th power to estimate annual survival probabilities.

Population trend analysis was carried out separately for the two sites through time series decomposition analysis, using an additive model, of the monthly capture rate (birds 100 net-hours^{-1}) of adult birds. Time series decomposition analysis was carried out in order to remove the influence of seasonal trends from the data. Linear regression analysis was then performed on the seasonally adjusted data, plotted against monthly pulse number.

A basic assessment of vegetation density was carried out at the two sites, through the visual estimation of the percentage cover of the ground layer in an estimated circle plot of 6 m radius from the centre of each mist net, and of the middle and canopy layers along the line of each net. The Student's t-test (two-tailed) was used to test the significance of differences between the two sites.

Minitab 15 was used for all statistical and time series analyses. For all statistical analyses, the results were considered to be significant when $P \leq 0.05$.

RESULTS

The monthly capture rate of adult birds in breeding condition suggests that the species generally breeds from April through October, with the peak in breeding activity occurring from May to August (Fig. 2). The monthly capture rate of females in breeding condition peaked in May at Los Volcanes and August at Montecristo. Females in breeding condition occurred mainly from April through September, with some captured as late as December at Los Volcanes. The data for males in breeding condition indicate peaks in May at both sites, with males in breeding condition occurring almost year-round at Los Volcanes, but occurring from April to July only at Montecristo. The comparison of the graphs for the two sites suggests that adults in breeding condition occur over a shorter time period at Montecristo. Mist-net capture data on the first appearance of hatch-year birds demonstrate that young birds are starting to fledge in June at Los Volcanes and August at Montecristo.

Data on the occurrence of body molt and flight-feather molt in adult birds suggests a predominantly post-breeding molt regime, which starts earlier and is more protracted at Los Volcanes. Breeding activity and molt appear to overlap slightly, with peaks in the capture rate of females in breeding condition and adults in molt coinciding in August at Montecristo. However, only 2% of all adults captured exhibited both breeding condition and molt scored above the defined thresholds.

For both sites combined, 52% of birds banded after their hatch year were not recaptured. At Los Volcanes, 54% of birds banded as adults were not recaptured, and at Montecristo 44% of adults were not recaptured, but the difference between the two sites was not significant (Fisher's Exact, $P = 0.301$). In contrast, 83% of birds banded at both sites during their hatch year were not recaptured, indicating that adults were recaptured more frequently than were young birds (Fisher's Exact, $P = 0.0005$).

Following survival and capture probability analysis, the favored model ($\Phi.$, Pt, $\mathrm{AIC_c} = 1478.214$, $\mathrm{AIC_c}$ Weight = 0.754) and second favored model (Φs, Pt, $\mathrm{AIC_c} = 1480.457$, $\mathrm{AIC_c}$ Weight = 0.246) suggest that there is only a slight effect of site on survival probability, while capture probability is influenced by time (for the remaining models, $\mathrm{AIC_c} \geq 1499.044$, $\mathrm{AIC_c}$ Weights ≤ 0.00002). Overall annual adult survival for both sites combined was 0.68, and was slightly higher at Montecristo (0.71) compared to Los Volcanes (0.68).

The monthly capture rates of adult birds at the two sites, during 2006 and 2007 combined (Fig. 3), show peaks in May at Los Volcanes and July at Montecristo. The rate of capture during the peak months is 2.9 times higher at Los Volcanes (May, 6.25 birds 100 net-hours^{-1}), compared to Montecristo (July, 2.17 birds 100 net-hours^{-1}).

Time series decomposition analysis suggests that there are negative trends in the monthly capture rate of adult birds at both sites (Figs. 4 and 5); although the trend is more marked at Los Volcanes ($Yt = 4.187 - 0.049 \times t$) compared to Montecristo ($Yt = 1.371 - 0.024 \times t$). Linear regression analyses of the seasonally adjusted data indicate a significant decline over 5 years at Los Volcanes ($r = 0.6146$, $df = 43$, $P = 0.0001$), whilst the negative trend at Montecristo is not significant ($r = 0.3105$, $df = 31$, $P = 0.084$).

Apparent breeding productivity, as measured by the ratio of hatch-year birds to adult females in breeding condition caught at each site in 2006 and 2007, was approximately

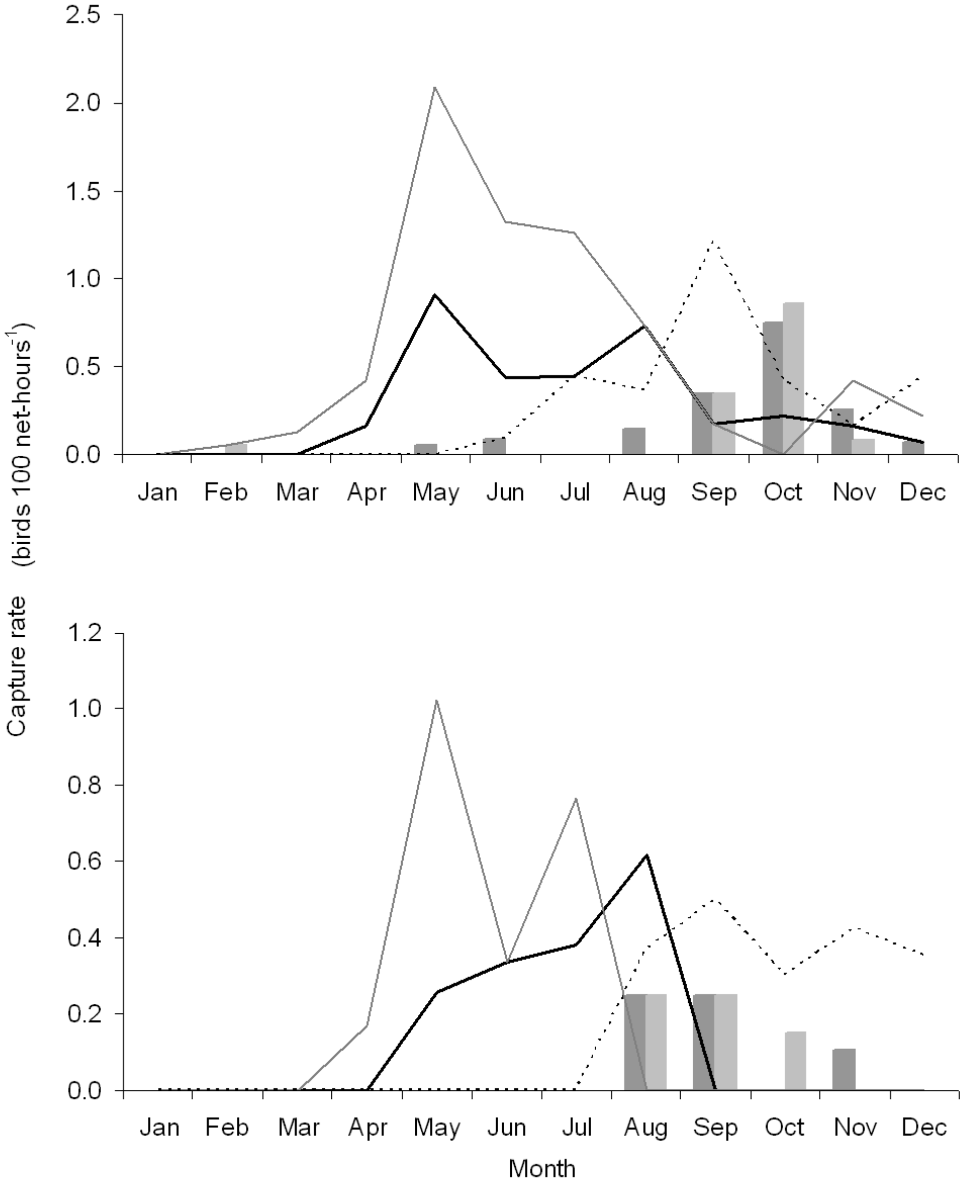

FIG. 2. Monthly mist-net capture rates (birds 100 net-hours^{-1}) for all years combined from November 2003 to June 2008, for Los Volcanes National Park (upper graph) and Montecristo National Park (lower graph), El Salvador, of the Ruddy-capped Nightingale-Thrush (*Catharus frantzii*): Black line = adult females with brood patch; gray line = adult males with cloacal protuberance; dashed line = hatch-year birds; dark gray bars = adults with body molt; light gray bars = adults with symmetric flight-feather molt.

equal at both sites. Although ratios appear higher at Montecristo (1.38, 1.00) compared to Los Volcanes (0.92, 0.88) in both years, these differences were not significant in either

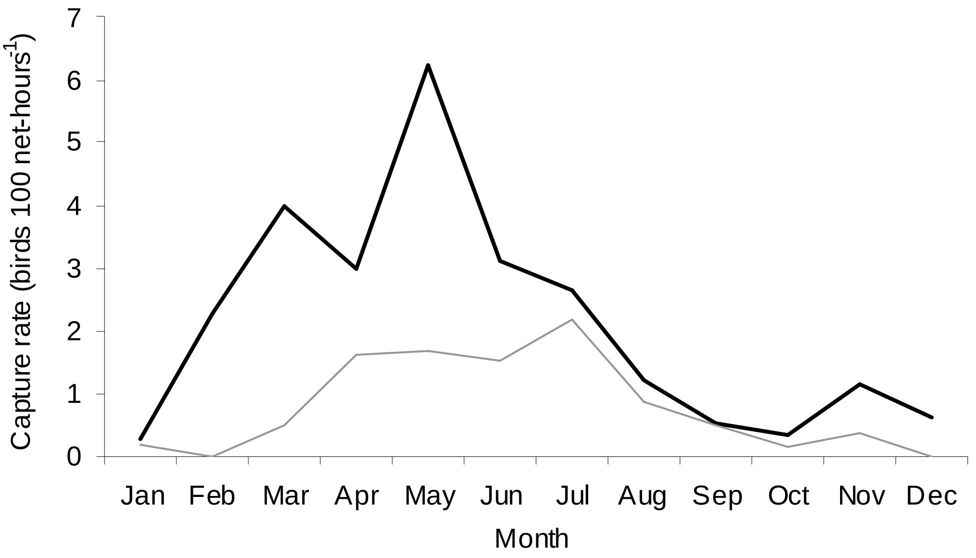

FIG. 3. Monthly mist-net capture rates (birds 100 net-hours^{-1}) for 2006 and 2007 combined, of adult Ruddy-capped Nightingale-Thrushes (*Catharus frantzii*) at two sites in El Salvador: Black line = Los Volcanes; gray line = Montecristo.

2006 (Fisher's Exact, P = 0.551) or 2007 (Fisher's Exact, P = 1.000).

There was no significant difference (t = 0.12, df = 47, P = 0.906) between the mean wing-chord lengths of adult birds at Los Volcanes (84.32 ± 4.08mm, n = 183) and Montecristo (84.20 ± 5.91 mm, n = 40). Despite no significant difference between the mean mass (t = -0.38, df = 66, P = 0.706) of females (29.7 ± 3.0 g, n = 40) and males (29.5 ± 2.4 g, n = 72), the mean wing chord was significantly longer (t = 3.79, df = 76, P = 0.0001) in males (85.8 ± 3.8 mm, range 78–100 mm, n = 71) compared to females (82.8 ± 4.2 mm, range 68–91 mm, n = 41).

Basic habitat surveys (Fig. 6) revealed that ground vegetation density was significantly higher (t = 4.84, df = 28, P = 0.0001) at Los Volcanes (57.5 ± 18.8%, n = 16) compared to Montecristo (28.8 ± 14.5%, n = 16). However, the middle layer cover was very similar (t = 0.20, df = 29, P = 0.845) at Los Volcanes (37.5 ± 18.1%, n = 16) and Montecristo (36.3 ± 17.8%, n = 16). The difference in the ground vegetation density is perhaps due to the lower canopy cover at Los Volcanes (59.1 ± 18.1%, n = 16) compared with Montecristo (68.8 ± 13.1%, n = 16), although this difference is not significant (t = -1.73, df = 27, P = 0.094). It should be noted that the basic and rapid assessment of vegetation density used here is likely to suffer from observer estimation error; however, the same observer surveyed both sites, and the substantial difference in habitat structure suggests that the results confirm a real difference.

DISCUSSION

Data on the breeding condition of adult birds and occurrence of hatch-year birds suggest that the main nesting period is from May to August; beginning at the start of the rainy season. This conforms to the information given by Skutch (1960), who noted breeding activity from March to August. However, at Los Vol-

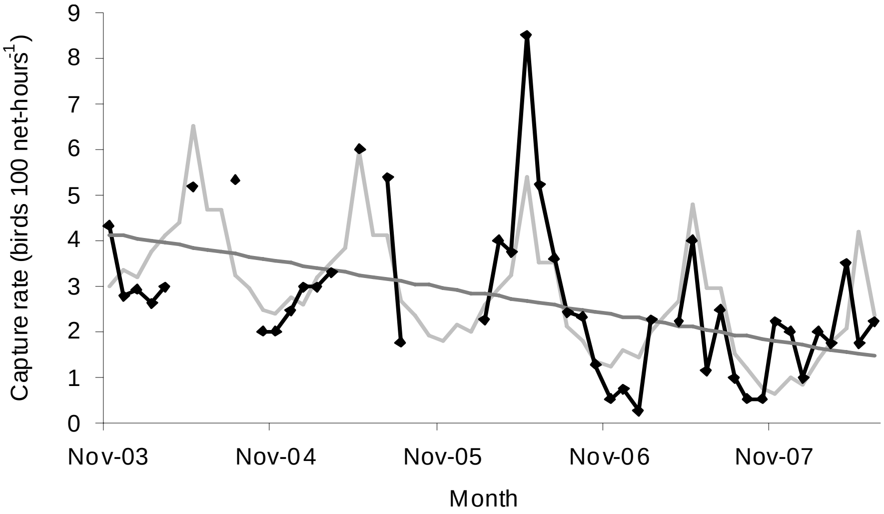

FIG. 4. Time series decomposition plot, utilizing an additive model, of the monthly capture rate of adult Ruddy-capped Nightingale-Thrushes (*Catharus frantzii*) at Los Volcanes National Park, El Salvador, from November 2003 to June 2008. Black line and data points = actual values; light gray line = fitted values; dark gray line = trend.

canes, breeding activity appears to continue until December, coinciding with the local rainy season, which may span from May to December. Males and females in breeding condition were trapped in November and December only during 2003, perhaps indicating that late breeding only occurs during some years. However, those two months were the first two months of data collection, and a plausible explanation may be that inexperienced field staff recorded false positive data on breeding condition during the first few months of the study.

At Cerro Huitepec Biological Reserve, the species breeds from February to September, with an apparent peak in May–June (J. L. Rangel unpubl., in Hiron *et al.* 2006), suggesting some consistency in the timing of peak breeding across the central portion of the species' range, with variation in the limits of the breeding season. The species forages for invertebrates and berries at and near ground level (Skutch 1960, Raitt & Hardy 1970, C. Chavez-Zichinelli unpubl., in Hiron *et al.* 2006), thus breeding during the rainy season would be expected in this species, as this is generally when the abundance of appropriate food is at its highest in tropical forests (e.g., Wolda 1978, Poulin *et al.* 1992). The development of breeding condition in males ahead of females and before the start of the rainy season may indicate that cues such as photoperiod, and not just rainfall, are influencing the onset of breeding condition (Hau *et al.* 1998, Wikelski *et al.* 2000, Hau 2001) and that males are competing for territories and females early in the season. The shape of the capture frequency curves for adults in breeding condition suggest that there may be a first nesting period with a peak in May and a renesting or second nesting period with a peak in July-August. However, there is no direct evidence from these study sites that a single female will produce two clutches in one breeding season.

The monthly capture rate of adults at each site during 2006 and 2007 combined shows an increase during January–May, followed later

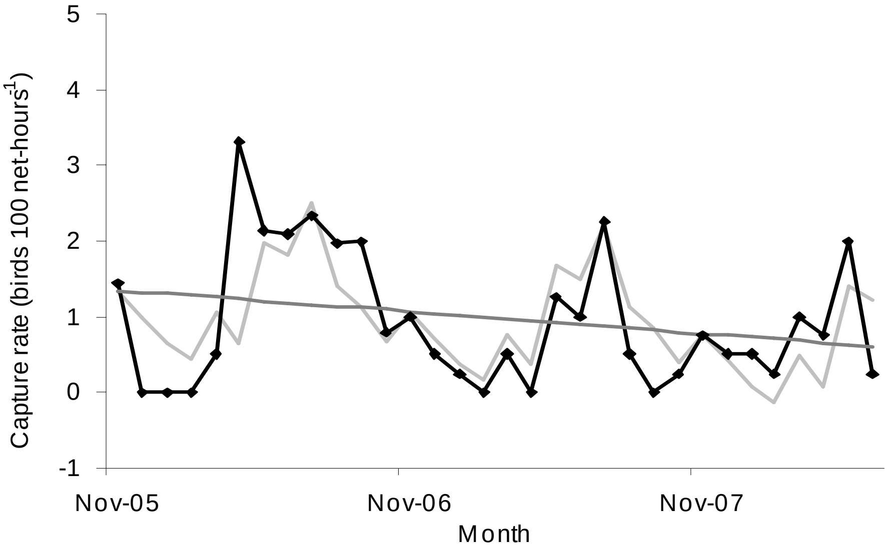

FIG. 5. Time series decomposition plot, utilizing an additive model, of the monthly capture rate of adult Ruddy-capped Nightingale-Thrushes (*Catharus frantzii*) at Montecristo National Park, El Salvador, from November 2005 to June 2008. Black line and data points = actual values; light gray line = fitted values; dark gray line = trend.

by a drop in numbers after the main breeding period, possibly owing to altitudinal migration or perhaps due to a change in behavioubehaviourr that reduces the chance of capture (Remsen & Good 1996). Further research could address this question.

The statistically significant difference in mean wing-chord length between the sexes conforms to the pattern shown by other *Catharus* species, in which males have longer wings on average (Pyle 1997), and thus is likely an ancestral trait not indicative of a current difference in dispersal or altitudinal movements undertaken by the sexes.

The overlap of breeding condition and molt throughout the population as a whole indicates considerable variation in the timing of these activities. Some overlap between breeding activity and molt is not unknown for bird species at tropical latitudes (e.g., Foster 1975, Marini & Durães 2001, Echeverry-Galvis & Córdoba-Córdoba 2008). However, only 2% of all adults trapped showed signs of both breeding condition and molt.

While delayed plumage maturation is known in some tropical members of the Turdidae family, especially in the genus *Turdus* (Escalona-Segura & Peterson 1997), there was no evidence in this study of the juvenal plumage extending beyond the hatch year, and no breeding condition individuals retained juvenal plumage.

There was no significant difference detected in the apparent productivity at the two sites; however, this analysis must be treated with caution because the ratio of juveniles to breeding females is unlikely to provide a reliable estimate of actual productivity, as it assumes that females and juveniles have equal capture probabilities, and that these do not differ in proportion between the sites. Generally lower productivity estimates of 0.44–0.90 offspring female^{-1} (assuming 1:1 sex ratio in broods) were found for this spe-

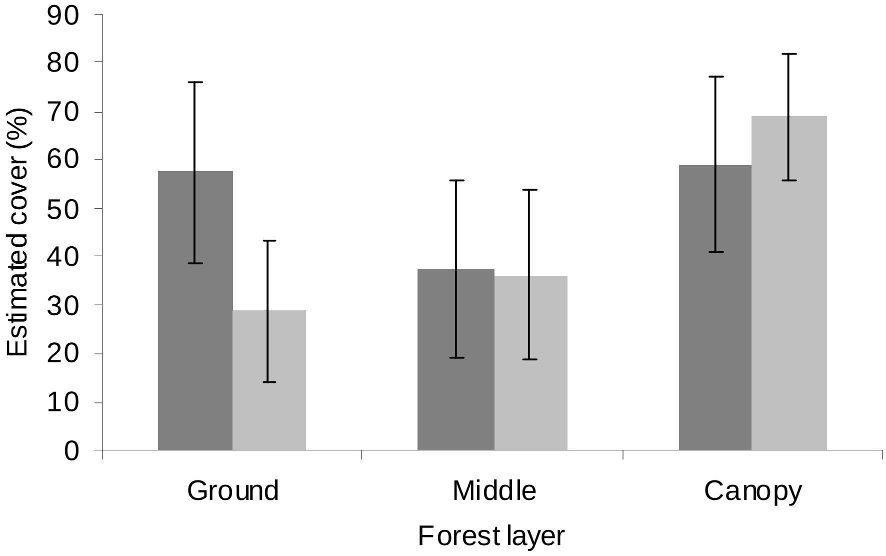

FIG. 6. Estimated percentage vegetation cover of the ground layer in estimated circle plots of 6 m radius from the centre of each net, and at the middle and canopy forest levels along the line of each net, at Los Volcanes National Park (dark gray bars) and Montecristo National Park (light gray bars), El Salvador, during August 2008. Error bars show ± 1 SD.

cies in primary forest at Cerro Huitepec Biological Reserve through a process of nest observations and modeling (Rangel-Salazar 2006, Rangel-Salazar *et al.* 2008b), but these estimates may not be comparable to estimates generated from mist net captures.

Survival analysis suggests that there is no difference in the survival probability between the two sites; however, capture probability was found to vary across months. For 2006 and 2007 combined, adult capture rates varied consistently across months, suggesting that seasonal changes in behaviour are affecting capture probability.

Time series decomposition analysis of the monthly capture rate suggests that there are negative trends at both sites, although this is significant only at Los Volcanes, a difference that could be due to the lower numbers captured or shorter sampling period at Montecristo. Caution is necessary because of the short time span over which the data have been collected; however, the sig-nificant decline at Los Volcanes could be due to several factors. First, the Santa Ana Volcano suffered an explosive eruption in October 2005 which destroyed part of the habitat patch (although not at the monitoring parcel) and may have caused ecosystem damage at the study area. Second, the volcano population may generally be more volatile due to fragmentation effects, since it occupies a smaller habitat patch. As such, it may be more susceptible to climate change or competition caused by species turnover (Komar *et al.* 2009b). Third, we suspect there may be greater disturbance by humans and livestock at Los Volcanes (pers. observ.). The resultant damage to vegetation could be disrupting breeding attempts and reducing nesting success.

When data on the capture of adults in breeding condition and hatch-year birds (Fig. 2) are compared between the sites, there appears to be a longer breeding season at Los Volcanes compared to Montecristo. This difference potentially reflects differences in the selection pressures (local adaptation) experienced by these two populations, which have probably been isolated from one another for close to 10,000 years, as they are not linked by suitable habitat and there is no evidence of movements between them. Present day montane humid forests were originally widespread in the lowlands but became restricted to higher elevations by c. 10,000 years ago, owing to Pleistocene warming (Watson and Peterson 1999), suggesting that the two study populations have been isolated over such a timescale. However, the appearance of a longer breeding season and protracted molt at Los Volcanes may also be explained by the much larger sample size compared to Montecristo; with more than four times as many adults captured at Los Volcanes, it is logical that various measures have shown a greater range of variation there.

The peak capture rate at Los Volcanes during May 2006 and 2007 combined is comparable to capture rates found for the same species during April–May in cloud forest, riparian forest, dry oak forest, and managed forest in Cerro Huitepec Biological Reserve by Hiron *et al.* (2006). However, the much lower peak capture rate at Montecristo, in July 2006 and 2007 combined, is lower than any capture rates found by Hiron *et al.* (2006), including that in managed forest, which might suggest that the population at Montecristo is profoundly limited. The lower capture rate at Montecristo could be indicative of high competition from other bird species that occupy similar niches, specifically species that forage for invertebrates and berries at or near ground level, such as Spotted Nightingale-Thrush (*Catharus dryas*) and Chestnut-capped Brush-Finch (*Arremon brunneinucha*), both of which are common at Montecristo and absent at Los Volcanes. Differences in interspecific competition between the sites could be due to differences in the local assemblages of resident species and their breeding seasons, and the local assemblages of migrants. However, a lower capture rate of Ruddy-capped Nightingale-Thrushes could also be due to increased predation, or to habitat effects, either on the population density itself or the chances of capture.

Habitat surveys indicate that the monitoring area at Los Volcanes possesses more luxuriant growth in the ground layer vegetation compared to Montecristo. Anecdotal observations also suggest that there is higher species richness in the ground flora at Los Volcanes. In contrast to the ground vegetation at Los Volcanes, the comparatively sparse cover at Montecristo comprises mainly waxy-leaved plants. This is likely to further influence the abundance and composition of invertebrate species. The lower canopy cover at Los Volcanes could be a product of the steeper topography at this site. In addition, intermittent volcanic eruptions of the Santa Ana Volcano at Los Volcanes may have prevented the establishment of dense canopy cover in patches of forest through habitat destruction caused by outgassing, ash falls, pyroclastic flows, and forest fires caused by ballistic projectiles; thus parts of the forest may in fact be relatively young. The intermittent addition of nutrients to the soil from ash fall may also have promoted the dense growth of ground vegetation. The idea that volcanic activity is affecting the species at Los Volcanes is supported by the pattern observed in the monthly capture rate of adults (Fig. 4). Despite the overall decline, the capture rate of adult birds peaked in May 2006, the first breeding season following the eruption in 2005, perhaps due to the displacement of surviving birds into the monitoring area following extensive damage to other parts of the forest, or an increase in resource availability within the study area.

Considerable care must be taken over the comparison of mist-net capture rates between sites, as differences may not reflect differences in breeding population densities, but rather could be due to variation in vertical distribution, flight behaviour, and spacing of territories, as well as the number of floaters present (Remsen & Good 1996). Variation in vertical distribution, flight behaviour and territory spacing was not studied as part of the bird monitoring program, and can not be controlled for in this study, but a slightly higher proportion of apparent floaters was detected at Los Volcanes.

The limitations of mist-netting set out by Remsen & Good (1996) require that only tentative conclusions be formed based on intraspecific differences in capture rates between sites and months such as those reported in this study. In addition to the behavioural differences that may affect capture rates, seemingly minor variation in methodology can have a strong influence on the outcome of mist-netting (Remsen & Good 1996). However, the Ruddy-capped Nightingale-Thrush is a relatively shy species that forages low in the understory and is difficult to observe (Dicky & van Rossem 1938, Skutch 1960). Mist-netting, as opposed to visual-auditory surveys, represents the most reliable method for surveying this species, especially females and juveniles, as well as males in the non-breeding season when they vocalize rarely.

The data presented in this study raise questions about the local population dynamics, movements, and ecology of the species. In light of these it would be appropriate to conduct detailed botanical surveys at the two sites in this study. Further research could establish the competitive relationships between the Ruddy-capped Nightingale-Thrush and other bird species, thus a detailed study into the feeding ecology of this species and others at Los Volcanes and Montecristo is required. Such a study may also shed light on why capture frequencies decline sharply in the non-breeding season. Further research is also required to assess the severity of threats, including nest predation, volcanism, climate change, and anthropogenic activities such as livestock grazing, and how they interact and impact bird species. Strategies for reducing the local impact of human activities will become increasingly important for species such as the Ruddy-capped Nightingale-Thrush, if their isolated populations continue to be threatened by potentially catastrophic natural events and the projected effects of climate change.

ACKNOWLEDGMENTS

We are grateful to the SalvaNATURA bird monitoring staff that collected the data used in this study: L. Andino, V. Galán, R. Juárez, I. Vega, C. Zaldaña, and J. Smith, as well as volunteers who assisted with data collection. El Salvador's Ministry of Environment and Natural Resources, Natural Heritage office, provided research permits for the monitoring study. We thank J. Fagan and L. Andino for comments on earlier drafts of this paper. In addition, we are grateful for comments received from K. Eisermann, S. McGehee, and an anonymous reviewer. J. L. Rangel-Salazar kindly provided copies of material ahead of publication. V. Henríquez kindly prepared the map.

This research would not have been possible without the financial support to the SalvaNATURA bird monitoring program by the following organizations: United States Agency for International Development, through its Improved Management and Conservation of Critical Hydrographic Watersheds project, the Institute for Bird Populations (including funds from the United States Fish & Wildlife Service), BirdLife International, the government of the Netherlands, donors to the SalvaNATURA annual birdathon, and sponsors of the 2007 and 2008 bird calendars, including Banco Cuscatlán, Grupo Roble, Consejo Salvadoreño del Café, Dizucar, Humane Society International, Mapfre (La Centroamericana), Plan Trifinio, and Telecom.

REFERENCES

Andino, L., V. Galán, & O. Komar. 2008. Cuarto Informe Anual, Proyecto de Monitoreo Permanente de Aves, Noviembre 2003 a Diciembre 2007. SalvaNATURA, San Salvador, El Salvador.

Dickey, D. R., & A. J. van Rossem. 1938. The birds of El Salvador. Chicago: Field. Mus. Nat. Hist. Zool. Ser. 23: 1–609.

Echeverry-Galvis, M. Á & S. Córdoba-Córdoba. 2008. Una visión general de la reproducción y muda de aves en el Neotrópico. Ornitol. Neotrop. 19 (Suppl.):197–205.

Escalona-Segura, G., & A. T. Peterson. 1997. Variable plumage ontogeny in the Black (*Turdus infuscatus*) and Glossy-Black Robins (*T. serranus*). Wilson Bull. 109: 182–184.

Foster, M. S. 1975. The overlap of molting and breeding in some tropical birds. Condor 77: 304–314.

Froehlich, D. 2003. Ageing North American landbirds by molt limits and plumage criteria. A photographic companion to the identification guide to North American birds, part 1. Slate Creek Press, Bolinas, California.

Hau, M. 2001. Timing of breeding in variable environments: Tropical birds as model systems. Horm. Behav. 40: 281–290.

Hau, M., M. Wikelski, & J. C. Wingfield. 1998. A neotropical forest bird can measure the slight changes in tropical photoperiod. Proc. Roy. Soc. Lond. B Biol. Sci. 265: 89–95.

Hiron, M., J. L. Rangel-Salazar, & B. Christensen. 2006. Coexistence of resident and migratory *Catharus* thrushes in a montane forest reserve of the northern Neotropics: On habitat use and morphology. Ornitol. Neotrop. 17: 383–394.

Howell, S. N. G., & S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford Univ. Press, Oxford, UK.

Komar, O. 1998. Avian diversity in El Salvador. Wilson Bull. 110: 511–533.

Komar, O. 2002. Birds of Montecristo National Park, El Salvador. Ornitol. Neotrop. 13: 167–193.

Komar, O., L. Andino, A. V. Galán, R. Juárez, & K. Wolfe. 2009a. Monitoring key biodiversity indicator species in southwestern El Salvador: Changes in bird populations during five years in El Salvador's Apaneca Biological Corridor. USAID & SalvaNATURA, San Salvador.

Komar, O., N. Herrera, L. E. Girón, & R. Ibarra Portillo. 2009b. The El Salvador Red List of birds. SalvaNATURA Biodiversity Series No. 3, San Salvador.

Marini, M. Â., & R. Durães. 2001. Annual patterns of molt and reproductive activity of passerines in south-central Brazil. Condor 103: 767–775.

Navarro-Sigüenza, A. G., & A. T. Peterson. 2004. An alternative species taxonomy of the birds of Mexico. Biota Neotrop. 4: http://www.biotaneotropica.org.br/v4n2/pt/abstract?taxonomic-review+BN03504022004.

Phillips, A. R. 1969. An ornithological comedy of errors: *Catharus occidentalis* and *C. frantzii*. Auk 86: 605–623.

Phillips, A. R. 1991. The known birds of North and Middle America: Part II. Allan R. Phillips, Denver, Colorado.

Poulin, B., G. Lefebvre, & R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73: 2295–2309.

Pyle, P. 1997. Identification guide to North American birds. Part 1. Institute for Bird Populations and Point Reyes Bird Observatory, Bolinas, California.

Raitt, R. J., & J. W. Hardy. 1970. Relationships between two partly sympatric species of thrushes (*Catharus*) in Mexico. Auk 87: 20–57.

Rangel-Salazar, J. L. 2006. Population dynamics of the Ruddy-capped Nightingale Thrush (*Catharus frantzii*) in the central highlands of Chiapas, Mexico. Ph.D. diss., Univ. of British Columbia, Canada.

Rangel-Salazar, J. L., K. Martin, P. Marshall, & R. W. Elner. 2008a. Influence of habitat variation, nest-site selection, and parental behavior on breeding success of Ruddy-capped Nightingale Thrushes (*Catharus frantzii*) in Chiapas, Mexico. Auk 125: 358–367.

Rangel-Salazar, J. L., K. Martin, P. Marshall, & R. W. Elner. 2008b. Population dynamics of the ruddy-capped nightingale thrush (*Catharus frantzii*) in Chiapas, Mexico: influences of density, productivity and survival. J. Trop. Ecol. 24: 583–593.

Remsen, J. V., & D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk 113: 381–398.

Rowley, J. S., & R. T. Orr. 1964. The status of Frantzius' Nightingale Thrush. Auk 81: 308–314.

Skutch, A. F. 1960. Life histories of Central American birds II. Pacific Coast Avifauna, no. 34. Cooper Ornithological Society, Berkeley, California.

Watson, D. M., & A. T. Peterson. 1999. Determinants of diversity in a naturally fragmented landscape: humid montane forest avifaunas of Mesoamerica. Ecography 22: 582–589.

White, G. C., & K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl.): S120–S139.

Wikelski, M., M. Hau, & J. C. Wingfield. 2000. Seasonality of reproduction in a Neotropical rain forest bird. Ecology 81: 2458–2472.

Winker, K. 1998. Recent geographical trends in Neotropical avian research. Condor 100: 764–768.

Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. J. Anim. Ecol. 47: 369–381.